Habitat and Diet Selection by the African Elephant at the Landscape Level:

a functional integration of multi-scale foraging processes

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“If you seek knowledge of the creatures of the earth, come close to Him who created all things, and He will give you enlightenment” anon.

This thesis is dedicated to those who overcome, for they know who He is.

Abstract

Understanding the role of elephant in the structure and functioning of African savanna ecosystems requires a mechanistic understanding of their habitat and diet selection at the landscape scale. To this end a functional approach based on optimal foraging theory was devised. Given a short foraging time per unit nutrient, a low level of cell wall digestion, and a limited ability to recycle microbial protein, it was hypothesised that elephants take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time to meet their nutritional demands. Accordingly, elephants were predicted to select habitats and diets that maximize their rate of intake of digestible energy and nutrients relative to what is available in the landscape. However, because safety, distance from surface water and shade also potentially influence foraging decisions by elephants, habitat and diet selection were predicted to be the result of a trade-off between the rate of intake of energy and nutrients and these non-dietary factors.

To test this prediction, a mechanistic ingestion model that was developed specifically for elephants was used to estimate the spatio-temporal pattern of the rate of protein intake achieved by elephants inhabiting a medium-sized reserve in a semi-arid savanna environment. The rate of protein intake was assumed to be a proxy measure of the rate of intake of digestible energy and nutrients. The response of elephants to the estimated pattern of intake was as per prediction, with both habitats and food types being selected in accordance with the rate maximizing premise.

The mechanistic approach to foraging used in the study provided possible functional explanations for several well known characteristics of the feeding behaviour of elephants. Differences in diet selection between bulls and cows were potentially explained in terms of sex related differences in the rate of protein intake across food types that were largely due to adult bulls harvesting heavier trunkloads than members of family units. Sexual segregation in habitat selection was potentially explained in terms of (1) sex related differences in the rate of protein intake across food types, and (2) the tendency of the short-term rate of protein intake to be a more important explanatory variable than cost distance from water for the spatial distribution of family units, with the converse being true for the spatial distribution of bulls. Seasonal change in the diet of elephants was well explained by temporal variation in the rate of protein intake across food types.

Distance from water was shown to have a strong influence on the distribution of elephants even in a medium-sized reserve that was relatively well supplied with surface water. The influence of surface water differed between the sexes and was strongly dependent on the spatio-temporal pattern of the rate of protein intake.

The study showed elephants to be primarily grazers, only switching to browse from woody plants when herbaceous forage of adequate quantity and quality is unavailable. This finding was used to construct an alternative hypothesis for the “elephant problem” that explains elephant-induced woodland loss in terms of (1) a man-induced shift in the diet of elephants from a historic diet of grass to a modern diet primarily composed of browse, and (2) a break down of the natural controls of elephant populations.

Implications for the management of elephant-vegetation systems are discussed, with proposed foci for management being the restoration of the historic diet and distribution of elephants by altering the boundaries of protected areas to incorporate key grass resources and restricting surface water to historic sites.

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Declaration

This thesis is the result of the author's original work
except where acknowledged or specifically stated in the text.
It has not been submitted for any other degree or examination
at any other university or academic institution.

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Table of contents

List of tables

List of figures

Chapter 1. A functional hypothesis of the foraging strategy of elephants

1.1. Introduction

For the past 50 years conversion of forest and woodland to shrubland or grassland has been a characteristic feature of reserves with high densities of elephants in east, central and southern Africa (Buechner & Dawkins, 1961; Buss, 1961; Buss & Savidge, 1966; Lamprey et al., 1967; Laws, 1970a; Laws, 1970b; Field, 1971; Thomson, 1973; Anderson & Walker, 1974; Croze, 1974; Leuthold, 1977; Guy, 1981; Barnes, 1982; Parker, 1983; Barnes, 1983; Barnes, 1985; Dublin et al., 1990; Ruess & Halter, 1990; Tafangenyasha, 1997; Trollope et al., 1998; Robinson et al., 2001; Mapaure & Campbell, 2002). Excessive damage to woodland was first noticed in 1930 in Murchison Falls National Park, Uganda (Laws, 1970a) and, by the 1960's, was also reported from protected areas in Tanzania, Kenya, Zambia, Zimbabwe and South Africa (Kalemera, 1987; Martin et al., 1992).

The destruction of forests and woodlands has been brought about by elephants felling or ring barking mature trees and suppressing recruitment from the shrub layer (Western & Maitumo, 2004), although factors such as fire, drought and other herbivores have also played a role (Barnes, 1983; Pellew, 1983; Dublin et al., 1990; Birkett, 2002).

In the 1970's and 1980's populations of elephants in east Africa were dramatically reduced by poaching (Eltringham & Malpas, 1980; Douglas-Hamilton, 1987; Barnes & Kapela, 1991), curtailing woodland loss in this region (Prins & Van der Jeugd, 1993). In southern Africa, however, the level of elephant poaching has been lower and the problem has persisted (Eckhardt et al., 2000; Robinson et al., 2001; Mapaure & Campbell, 2002; Mosugelo et al., 2002; Cumming, 2005), with a number of reserves resorting to culling of elephants in an attempt to halt woodland loss (Martin et al., 1992).

The impact of elephants on woody vegetation has lead to concern over the possible extirpation of plant species and the loss of animal species whose survival is dependent on forest or woodland habitat (Laws, 1970a; Herremans, 1995; Cumming et al., 1997; Fenton et al., 1998; Lombard et al., 2001; Fritz et al., 2002; Braswell & Slusar, 2005; Botes et al., 2006; O'Connor et al., 2007). Reduction in aesthetic value associated with the decline of mature trees may also result in a loss of tourism potential (Ruess & Halter, 1990). An additional concern is the growing trend in southern Africa of re-establishing elephants in small- to medium- sized (< 1000km^2) reserves, where the threat of elephant-mediated extirpation of vulnerable plant species may be greater than in large protected areas (O'Connor et al., 2007).

Plant and animal species threatened with elephant-related extirpation have previously co-existed with elephants. What then has changed to cause the upsurge in impact to woody vegetation and associated threat to biodiversity? Several possible causes have been put forward, with man's modification of the spatio-temporal pattern of habitat and diet selection of elephants being the over-arching thesis.

The oldest and most widely accepted explanation is the compression hypothesis (Laws, 1970b; Caughley, 1976; Lewis, 1986). Compression results when elephants are forced to remain in reserves and are prevented from making seasonal movements or long migrations in response to changes in the availability of food and water. Under these circumstances, habitats that would normally only be utilised seasonally are occupied year round, and as a result, selected woody species are impacted at unnaturally high frequencies because of longer periods of high probability of encounter with elephants.

The effects of compression on woody plants are potentially greater in reserves with limited herbaceous forage and should be less pronounced in reserves where suitable herbaceous forage is abundant (O'Connor et al., 2007). Herbaceous forage is the mainstay of the wet season diet of elephants, particularly for adult bulls (Buss, 1961; Guy, 1976; Barnes, 1982; Kabigumila, 1993; Osborn, 2004; Codron et al., 2006; Cerling et al., 2006). When herbaceous forage is scarce, either as a result of degradation of grasslands through over grazing or because of drought, elephants are forced to feed on browse for longer periods, resulting in increased impacts on woody plants. Many game reserves originated from livestock areas that had been degraded through over stocking and most are situated in semi-arid regions that experience a high frequency of droughts of long duration (O'Connor et al., 2007). Consequently, because of the indirect effects of man, the woody vegetation of many reserves may be predisposed to heavy impact by elephants.

Provision of artificial surface water in historically waterless parts of reserves has also been put forward as a possible factor leading to the widespread impact on woody plants by elephants (de Beer et al., 2006; O'Connor et al., 2007). Elephants drink on a near daily basis, which restricts foraging to within a maximum distance of about 15 km from water for adult bulls (Conybeare, 2004), and 5 km from water for family units because of the limitations imposed by young calves (Young, 1970). Plants occurring at greater than the maximum foraging distance from water enjoy an absolute refuge from elephants, while plants situated on the fringes of the foraging limit are afforded a partial refuge because they are less likely to be encountered as a result of a greater search area and energetic cost of travel (O'Connor et al., 2007).

Artificial water points have been created in reserves to compensate for loss of access to traditional watering areas, to increase the forage available for water-dependent animals, and to create foci of attraction for animals that provide predictable game viewing for tourists (Weir, 1971; Owen-Smith, 1996). However, this practice has served to reduce the extent of both partial and absolute refugia from elephants and, in many reserves, has eliminated absolute refugia completely (Western, 1975; Owen-Smith, 1996). Consequently, the frequency, timing and duration of utilisation of woody vegetation have been altered, with regions that would have previously only been utilised occasionally by elephants during the wet season now being utilised year round.

During the dry season, ephemeral water sources dry up and elephants are forced to concentrate around the more permanent sources. As food resources in the vicinity of the permanent sources become depleted, density-dependent effects may intensify and become manifested in elephant populations as an increased age of first breeding, a longer inter-calving period (Buss & Savidge, 1966), and an increased rate of calf mortality due to unsustainable energy expenditure, nutritional stress and increased levels of predation (Conybeare & Haynes, 1984; Dudley et al., 2001; Joubert, 2006). These natural effects may serve to reduce the size of elephant populations. By increasing the area and hence the amount of food available to elephants during the dry season, provision of artificial surface water may delay the onset of density-dependent effects and, in so doing, may increase the number of elephants that can be sustained in the short-term (O'Connor et al., 2007). An increase in elephant numbers is concomitant with increased impact to woody vegetation (Cumming, 2005).

Given the above theoretical concepts, restoration of the key determinants of the spatial distribution and diet of elephants to their historic state should result in less widespread and lower levels of impact on woody plants by elephants and a strengthening of the natural controls of elephant populations. This would involve joining existing reserves to create megaparks (van Aarde & Jackson, 2007a), altering reserve boundaries to incorporate key grass areas (O'Connor et al., 2007), and restoration of partial and absolute refugia from elephants by limiting the distribution of surface water to historic sources (Gillson & Lindsay, 2003; O'Connor et al., 2007). However, heavy human settlement outside of reserve boundaries, the limited size of many reserves, and the pressure to provide predictable game viewing associated with numerous artificial water points make this difficult for many protected areas.

Where restoration of the key determinants of habitat and diet selection to their historic state is not practicable, it is important to gain an understanding of how and to what extent anthropogenic factors may have altered the distribution and diet of elephants within a reserve, so that predictions concerning the spatial pattern and degree of man-induced vegetation change and associated biodiversity losses can be made. It is also important to be able to discriminate between elephant impacts that are indirectly caused by man's modification of the landscape, such as compression, grassland degradation through overgrazing or provision of artificial water, and elephant impacts caused by natural phenomena such as drought or variation in the spatio-temporal pattern of rainfall. This information is critical because maximum biodiversity is likely to be achieved by management strategies that aim to curtail man-induced impacts by elephants, but at the same time do not restrict elephant impacts that are indirectly driven by natural phenomena. Consequently, models that predict distribution and diet of elephants under different reserve configurations and patterns of surface water distribution are critical. However, despite their importance, predictive models that operationalize the above theoretical concepts have yet to be developed.

Early elephant-vegetation models were based on simple predator-prey representations of the elephant-tree interaction (Caughley, 1976), but over the past two decades, recognition that the spatio-temporal pattern and intensity of impact on woody vegetation is not only determined by elephants, but also by other ecological and environmental factors acting in concert with elephants, has lead to the development of more complex models (Pellew, 1983; Dublin et al., 1990; Starfield et al., 1993; Baxter & Getz, 2005). Contemporary models include the effects of density dependence on recruitment of tree seedlings, competition from grass, tree demographics, browsing by other herbivores and stochastic environmental variables such as fire and rainfall (see Baxter & Getz, 2005).

Despite the advancement in our understanding of elephant-vegetation systems, current elephant-vegetation models cannot be used to predict the effects of landscape scale factors on habitat and diet selection by elephants because the mechanisms driving elephant foraging behaviour remain undetermined (Owen-Smith et al., 2006) and, consequently, have not been incorporated in the models. This is because research on habitat and diet selection by elephants has been largely descriptive (Buss, 1961; Guy, 1976; Malpas, 1977; van der Merwe et al., 1988; Bowland & Yeaton, 1997; Cerling et al., 1999; de Boer et al., 2000; Babaasa, 2000; Milewski, 2002; Cerling et al., 2004; Codron et al., 2006; Cerling et al., 2006) with little mechanistic modelling of foraging behaviour. There is an urgent need to test possible mechanisms of habitat and diet selection by elephants and, in so doing, provide information that may be used to build the necessary predictive models.

Large herbivores interact with forage resources at several levels of ecological resolution and, consequently, a series of interrelated choices are made during the foraging process, with each choice being associated with a particular spatial scale (Senft et al., 1987). For example, animals first select a home range in which to live and then make subsequent decisions about which habitats to forage in and which foods to eat. Thus foraging can be envisaged as a hierarchical spatial process, from choice of distribution within a region to choice of dietary item (Johnson, 1980; Senft et al., 1987; Orians & Wittenberger, 1991; Rolstad et al., 2000; Morin et al., 2005).

The choices made by elephants at each scale are important determinants of the spatio-temporal pattern and intensity of damage to woody vegetation. At the landscape scale, the pattern of elephant-induced vegetation damage is determined by (1) the habitats elephants choose to feed in (e.g. the woody plants of some habitats may remain undamaged simply because elephants choose not to feed in those habitats); (2) the food types elephants choose to feed from (e.g. the woody plants of some habitats may remain undamaged because elephants choose to feed on food types from the herbaceous layer); and (3) the plant parts elephants choose to consume (e.g. stripping leaves from woody plants causes less damage than the extraction of bark or roots).

To develop an elephant-vegetation model that predicts the effects of landscape-scale factors on habitat and diet selection, existing models need to be integrated with a mechanistic model of foraging by elephants that links the spatio-temporal heterogeneity of vegetation and other landscape features that influence local distribution (e.g. surface water) with the pattern of vegetation utilisation. To have widespread relevance, the foraging model should functionally represent the feeding strategy employed by elephants (Bailey et al., 1996). In addition, because adult bulls have the potential to damage woody vegetation more than members of family units (Guy, 1976; Barnes, 1982; Barnes et al., 1994), it is important that the mechanisms responsible for sex related differences in feeding behaviour (Stokke, 1999; Stokke & du Toit, 2000) and habitat selection (Stokke & du Toit, 2002) be incorporated in the model.

The aim of this chapter is to develop a functional hypothesis for the foraging strategy of elephants that can be used as a theoretical framework for modelling habitat and diet selection by adult bulls and members of family units at the landscape scale. A functional approach to optimal foraging is used to predict (1) the currency that elephants are expected to maximize, and (2) the mechanisms used by adult bulls and members of family units to achieve the optimal foraging goal of maximizing the currency.

1.2. A functional hypothesis of foraging by elephants

1.2.1. *The currency of fitness*

Optimal foraging theory assumes that foraging behaviour and fitness are linked by a particular currency (Pyke, 1984). If elephants are able to rank potential food items according to their contribution to overall fitness and, on the basis of these rankings, select a diet from the available set of food choices that best meets their needs, what then is the currency that elephants use? In this section, a hypothetical framework is developed to predict the currency that elephants use when ranking preference for potential food items. The framework consists of two morphological parametres (1) body size, and (2) type of digestive system (Hanley, 1982; Owen-Smith, 1988).

Body size

Food requirements of animals increase with body mass as a result of increasing costs of maintenance and production (Owen-Smith, 1988). Consequently, because elephants have a very large body size they have a high absolute energy and nutrient requirement relative to smaller animals, and adult bull elephants have a higher daily energy and nutrient requirement than smaller cows and calves. To cope with this constraint, elephants should favour food types that permit a rapid rate of intake of energy and nutrients, and this inclination should be more pronounced for bulls than for members of family units.

Digestive system

Plant cells can be divided into cell solubles contained in the cytoplasm and cell wall material that forms a structural box around the cytoplasm (Lyons et al., 1996). Cell solubles, which include protein, sugars, starch and lipids are rapidly and almost completely digestible. In comparison, the cell wall contains slowly digestible material called fibre, which includes hemicellulose, cellulose and the mostly indigestible lignin (Lyons et al., 1996; Buxton & Redfearn, 1997; Shipley, 1999). Elephants are hindgut fermenters (van Hoven et al., 1981). Unlike ruminants, their digestive system does not have blocking structures that impose a limit on the rate of passage of material through the gut and, therefore, they experience short ingesta retention times, even if the diet is composed of material with high fibre content. Retention time in elephants may be as short as 14 hours (Eltringham, 1982) compared to 70-100 hours in cattle (Owen-Smith, 1988). Because food is retained in the gut for a short time, fermentation of slowly digesting cell wall material, particularly cellulose, is limited (van Hoven et al., 1981; Meissner et al., 1990). It should be noted that the poor digestion of cell wall material shown by elephants is not due to inefficient digestion (i.e. poor digestion per unit time) but rather to the limited time spent digesting (Meissner et al., 1990). Considering that elephants are largely unable to digest and, therefore, utilise cell wall material as a source of energy, they should be more reliant on plant material that is rich in rapidly digestible cell solubles than animals that get energy from digesting cellulose more completely. Due to a longer gut and therefore slower ingesta passage rates, bulls digest fibre better than cows (Clauss et al., 2003b) and, therefore, they are expected to be more tolerant of food with high fibre content (e.g. grass (Shipley, 1999)).

A further consequence of a hindgut digestive system is that very little microbial protein can be recycled (Janis, 1976). In ruminants, fermentation takes place in the fore section of the gut and, consequently, when microflora are washed out of the rumen they pass into the abomasum where they are digested to provide a source of protein (Janis, 1976). Fermentation in elephants takes place in the caecum and colon, which are positioned at the end of the gut. The microflora that pass out of these structures with the flow of digesta are not digested and the potential source of protein is lost with the faeces. The limited ability of elephants to recycle microbial protein may limit their protein uptake relative to what can be achieved by ruminants. To compensate for this elephants should select plant material rich in protein.

In summary, given a short foraging time per unit nutrient, a low level of cell wall digestion, and an inability to recycle microbial protein, it is postulated that elephants must take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time if they are to meet their nutritional demands. The strategy is one of maximum throughput per unit time, which contrasts with the ruminant strategy of maximum digestion per unit feed.

1.3. A functional basis for diet selection

In the above section, it is predicted that elephants optimise fitness by selecting food types that offer the highest rate of intake of cell contents rich in energy and nutrients. In the short-term, the intake rate of energy and nutrients is determined by the distance between patches of food, the speed of travel between patches, the time to gather a trunkload, the mass of a trunkload, the time to chew and swallow a mouthful, the number of trunkloads per patch, and the density of extractable energy and nutrients in the material (Spalinger & Hobbs, 1992; Farnsworth & Illius, 1996; Farnsworth & Illius, 1998; Pastor et al., 1999). Consequently, to maximise the rate of energy and nutrient intake elephants should select food types with cell contents rich in energy and nutrients that occur in closely spaced patches, allow many large trunkloads to be harvested rapidly, and can be chewed and swallowed quickly. Given the above, elephants should select green, actively growing material and avoid senescent material because it is largely devoid of cell contents and therefore has a low density of extractable energy and nutrients.

Seasonal changes in food preference are expected because the level of energy and nutrients in some food types varies more than others over the annual cycle. For example, the protein density of grass declines markedly as the dry season progresses (Field, 1971; Lyons et al., 1996; Osborn, 2004), while the protein density of browse, which is generally higher than that of grass, is more constant over the annual cycle (Topps, 1997). Seasonal variation in patch density, the number of trunkloads that can be harvested per patch and the mass of a trunkload are also expected to cause seasonal changes in diet. For example, during the rainy season all food types are abundant (high patch density), but by the onset of the dry season little green grass is available, and choice of food is restricted to forbs, foliage of woody plants, bark and roots. At the end of the dry season, when most woody plants have shed their leaves, choice is reduced to bark and roots. Consequently, to ensure maximum intake of cell solubles and therefore energy and nutrients, the diet of elephants is expected to change seasonally, with the composition of diet at any point in time being determined by the relative rate of energy and nutrient intake of the food types that are available within the landscape.

1.3.1. *Sex related differences in preference*

Due to a pronounced difference in body size, factors that are important determinants of the rate of energy and nutrient intake for adult bulls may not be as important for members of family units. For example, adult bulls have the ability to take larger trunkloads of food than cows (Stokke & du Toit, 2000) and because large trunkloads can compensate for a low energy or nutrient density, food types that offer a large bite mass should be preferred by adult bulls. Cows and subadults harvest smaller trunkloads than adult bulls (Stokke & du Toit, 2000) and, therefore, they cannot compensate for a low energy or nutrient density by harvesting large trunkloads. Accordingly, other food selection criteria such as the level of extractable energy and nutrients in the food and the density of food patches should increase in importance for members of family units.

1.4. A functional basis for habitat selection

It is hypothesised that elephants optimise fitness by selecting habitats, from the available choice set, such that their rate of intake of cell solubles is maximised. However, habitat selection is also influenced by factors unrelated to food (Bailey et al., 1996). Three important non-dietary factors that influence habitat selection by elephants are safety (Buss, 1961; de Boer et al., 2000), access to drinking water (Young, 1970; Western, 1975; Owen-Smith, 1988; Stokke & du Toit, 2002; Conybeare, 2004; de Beer et al., 2006; Chamaillé-Jammes et al., 2007; Smit et al., 2007), and availability of shade (Owen-Smith, 1988).

1.4.1. *Safety*

It is hypothesised that elephants respond to hunting pressure by selecting closed habitats that provide concealment, such as forest or thickets, in preference to open habitats such as savanna or grassland. During his hunting expeditions, Buss (1961) noted that members of breeding herds in the North Bunyoro region of Uganda appeared nervous when feeding in the open but would noticeably relax and move more slowly when they encountered stands of tall, mature grass or woodlands. De Boer et al. (2000) compared the diet and distribution of elephants in Maputo Elephant Reserve before and after the civil war in Mozambique. Prior to the civil war, when poaching levels were low, elephants preferred open grass plains. In contrast, elephants selected dense forest patches after the civil war when poaching levels were high. Selous (1881) recorded that by 1870, elephants, in what is now Zimbabwe, had retreated into the districts infested by tsetse fly in response to hunting pressure. The tsetse fly afforded some protection to elephants because they prevented hunting from horseback. To hunt elephants on foot was considered by many to be "too fatiguing a pursuit to be followed with much chance of success by Europeans" (Selous, 1881).

1.4.2. *Drinking water*

Water is important for fuelling metabolic processes and, because of the relationship between body mass and energy demand, elephants have a large absolute water requirement. Water is also important for thermoregulation. Although elephants do not have sweat glands, they are able to cool themselves by losing large volumes of water through evaporation from the surface of the skin (Spinage, 1994). To meet the water requirements of metabolism and thermoregulation, elephants drink on a near daily basis (Owen-Smith, 1988), with adult bulls consuming up to 300 litres per drinking session (Spinage, 1994).

The energetic cost of locomotion is much less for large animals than small ones (Taylor et al., 1982) and, consequently, the energetic cost of locomotion for adult bull African elephants is the lowest recorded for any living land animal (Langman et al., 1995). This means that adult bull elephants can afford to walk up to 15 km between food and water (Conybeare, 2004). Due to their smaller body size, cows and calves have higher energetic costs of locomotion than adult bulls. Consequently, members of family units are restricted to a distance of approximately 5 km from water (Young, 1970), primarily because of the energetic limitations of young calves.

1.4.3. *Shade*

The low surface area to mass ratio of elephants means that they have a small surface area to take up heat from the environment, and a large mass to heat up. As a result, elephants do not heat up quickly (Spinage, 1994). However, once they have warmed up, their low surface area to mass ratio prevents them from losing heat rapidly and, therefore, it is important for elephants not to become over heated. Elephants lose most of their heat through radiation to cooler air and, therefore, standing in shaded microclimes is important (Spinage, 1994; Kinahan et al., 2007).

1.4.4. *Importance of a landscape perspective*

In the above section, the short-term rate of intake of cell solubles, safety, distance from surface water, and availability of shade are identified as factors influencing habitat selection by elephants. However, accurate prediction of habitat selection is not only dependent on correct identification of the factors influencing choice but also on correct identification of the scale at which the factors operate (Senft et al., 1987; Turner, 1989; Bailey et al., 1996). Over the past two decades, there has been a growing realisation amongst ecologists that a significant proportion of the local-scale dynamics of ecosystems can be explained by factors that operate beyond the local scale. In other words, the configuration of the landscape surrounding an area is an important determinant of the ecological response within the area. In addition, it has been realised that the temporal features of ecosystems must be understood before the dynamics of ecosystems can be explained. These ideas have become the focus of a new ecological discipline known as landscape ecology.

It is postulated that the factors affecting resource selection by elephants operate at the landscape level. In other words, the attractiveness of a habitat to elephants is not determined by the absolute measure of the factors for the habitat in question, but rather by a measure that is relative to the other habitats in the landscape. A test of this hypothesis forms an important component of this thesis.

1.5. Link between habitat and diet selection

Most published studies of resource selection by animals treat habitat and diet selection as separate processes because habitat selection occurs at the coarse scale whereas choice of diet occurs at the fine scale (Schaefer & Messier, 1995; Ginnett & Demment, 1997; Rolstad et al., 2000; Rettie & Messier, 2000; McLoughlin et al., 2002; Fortin et al., 2003; Martinez et al., 2003; Morin et al., 2005; Friar et al., 2005; Whittingham et al., 2005). However, by treating resource selection as a number of discrete scale-related processes, the cross-scale linkages inherent within the selection process are not represented (Johnson et al., 2004). In reality, resource selection by herbivores is the integrated result of a number of choices made at different scales from components of plants, to plants, to plant communities, to landscapes and upwards. To account for cross-scale linkages in the selection process, Johnson et al. (2004) used a regression approach to develop habitat models that included covariates measured at multiple spatial scales and showed that a multi-scale approach explained a greater percentage of variation in resource selection than a single-scale design. However, regression models do not functionally represent the foraging process and, consequently, the predictive ability of regression type models is limited to the geographic region or season in which they are parameterised (Yearsley et al., 2001). In addition, it is difficult to represent and interpret trade-off between factors when using a regression type model (Chan & Loh, 2004).

In this thesis a novel approach to account for cross-scale linkages in the foraging process is proposed. It is postulated that the nutritional choices made by elephants at different spatial scales are directed towards achieving a common nutritional goal and that the integrated effect of the nutritional choices made during habitat and diet selection can be represented in a statistical model by a single, functionally derived variable, namely the short term rate of intake of digestible energy and nutrients. The effectiveness of this approach for predicting habitat and diet selection by elephants is explored as part of this study.

1.6. Objectives of the thesis

The research conducted in this thesis focuses on determining whether the theoretical concepts proffered above are consistent with the foraging ecology of elephants, and if further insight into the dynamics of elephant-vegetation systems can be gained from these concepts. The specific objectives of the thesis were (1) to develop and parameterise a mechanistic model to describe the short-term rate of intake of digestible energy and nutrients by elephants, (2) to use the model to test whether the short-term rate of intake of digestible energy and nutrients is an important determinant of both habitat and diet selection by adult bull and cow elephants (i.e. maximization of the short-term rate of intake of cell solubles is the currency that links foraging decisions across scales), (3) to test the hypothesis that habitat and diet selection by elephants are influenced by factors that operate at the landscape level, and (4) to discuss the results in terms of the management of elephant-woodland systems.

Chapter 2. Study area

2.1. Introduction

Malilangwe Wildlife Reserve was chosen as the study area. This chapter describes the location, physical geography, past management history, and elephant population of the reserve.

2.2. Location

The 39 378 ha Malilangwe Wildlife Reserve is located in the south-eastern lowveld of Zimbabwe between latitudes 20° 58' and 21° 15' S and longitudes 31° 47' and 32° 01' E (Figure 2.1). The Chipimbi, Chiredzi and Runde Rivers demarcate the western boundary between Maranatha Ranch, Hippo Valley Game Reserve and Matibi II Communal Land respectively. The reserve is bounded to the south by Gonarezhou National Park, to the east by Chizvirizvi Communal Land, and to the north by resettlement land.

A 2.1 m high electrified game fence secures the eastern and northern boundaries. Although a fence exists along the southern boundary with the Gonarezhou National Park, it is poorly maintained and consequently there is some movement of wildlife between the park and the reserve. Wildlife is free to move westwards across the Chiredzi River into the Hippo Valley Game Reserve.

2.3. Climate

2.3.1. *Rainfall*

An estimate of the July to June seasonal mean annual rainfall, derived from a 56 year record (1951 to 2006) collected at Malilangwe Head Quarters is 562 mm. Rain falls seasonally, with approximately 84 % of precipitation occurring in summer between November and March (Figure 2.2). Periods with overcast sky and drizzle are common during the winter months.

The temporal pattern of wet season rainfall accords with the cyclic pattern for Zimbabwe (Makarau & Jury, 1997), with sequences of about nine years above or below the long-term average (i.e. a quasi-periodicity of approximately 18 years), although invariably a number of years are well out of phase (Figure 2.3).

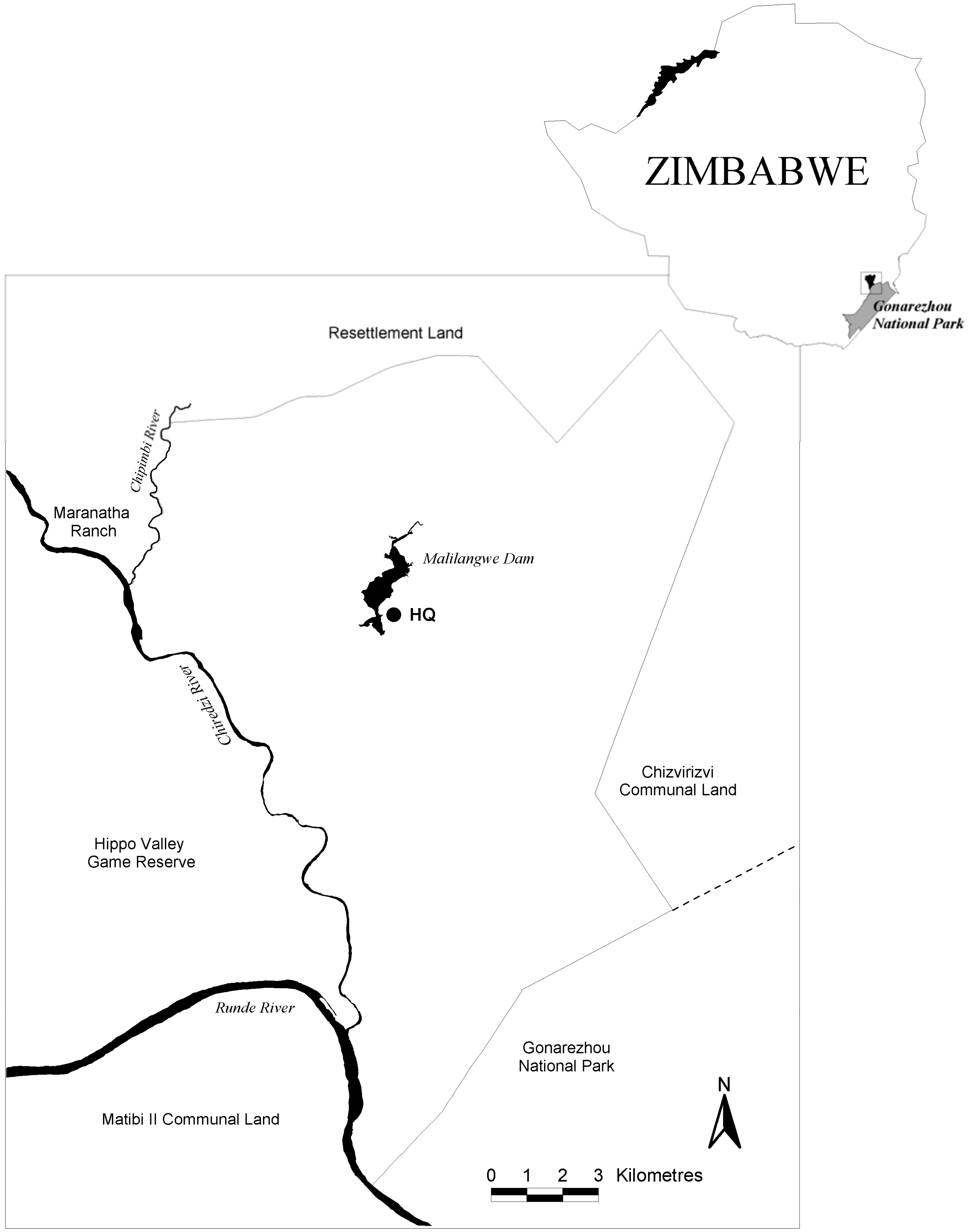


Figure 2.1 Map showing the location of Malilangwe Wildlife Reserve.

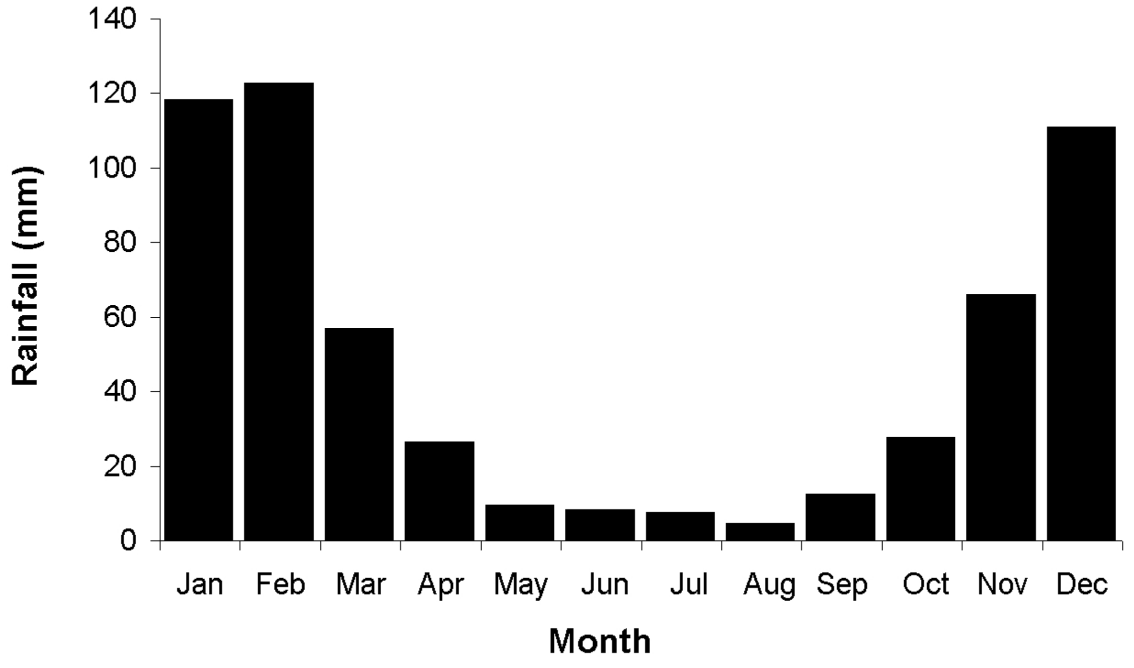


Figure 2.2 Chart showing mean monthly rainfall calculated from a 56 year record (1951 to 2006) collected at Malilangwe Head Quarters. Approximately 84 % of rainfall occurs between November and March.

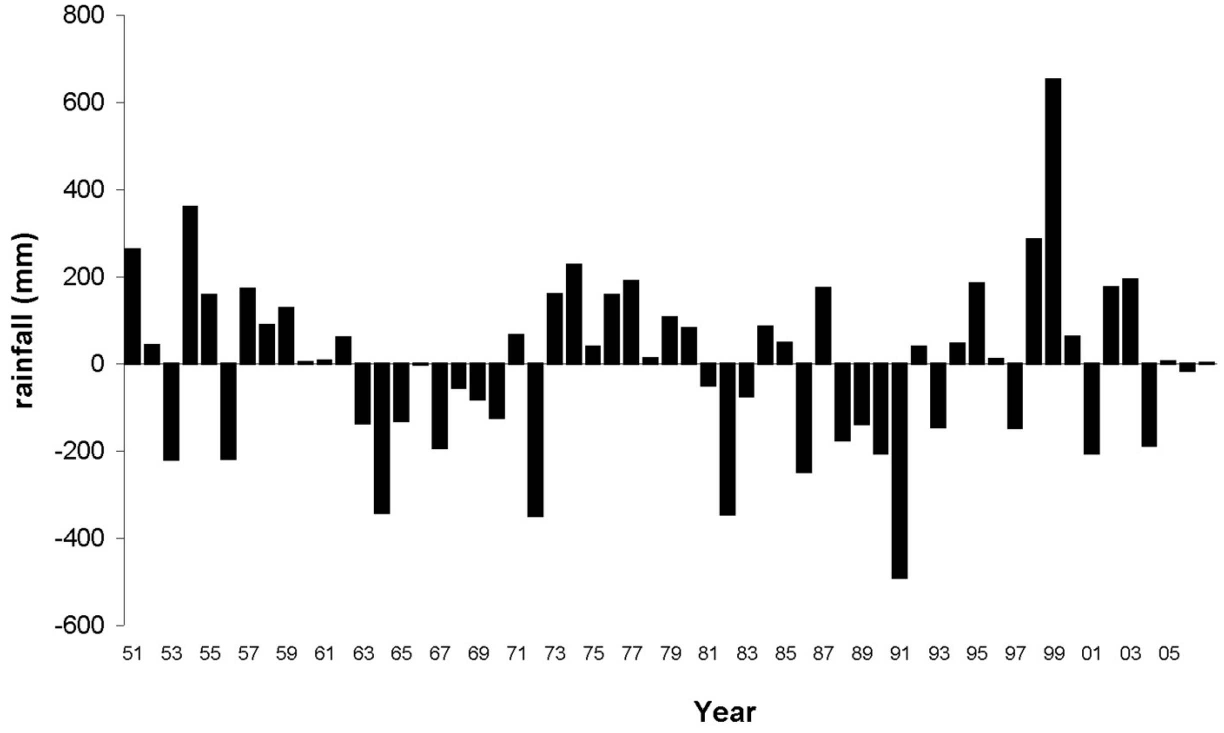


Figure 2.3 Chart showing rainfall deviation from the July to June seasonal mean calculated from a 56 year record (1951 to 2006) collected at Malilangwe Head Quarters.

Inter annual variability in rainfall is high (coefficient of variation 35 %), with severe drought events occurring at roughly 10 year intervals (1964, 1972, 1982, 1991).

2.3.2. *Temperature*

The climate is characterised by a hot wet season from November to March, a cool dry season from March to August, and a hot dry season from September to October. The average minimum monthly temperature ranges from 13.4 °C (July) to 23.7 °C (December), while the average maximum monthly temperature ranges from 23.2 °C (June) to 33.9 °C (November) (Figure 2.4). Frost is virtually absent.

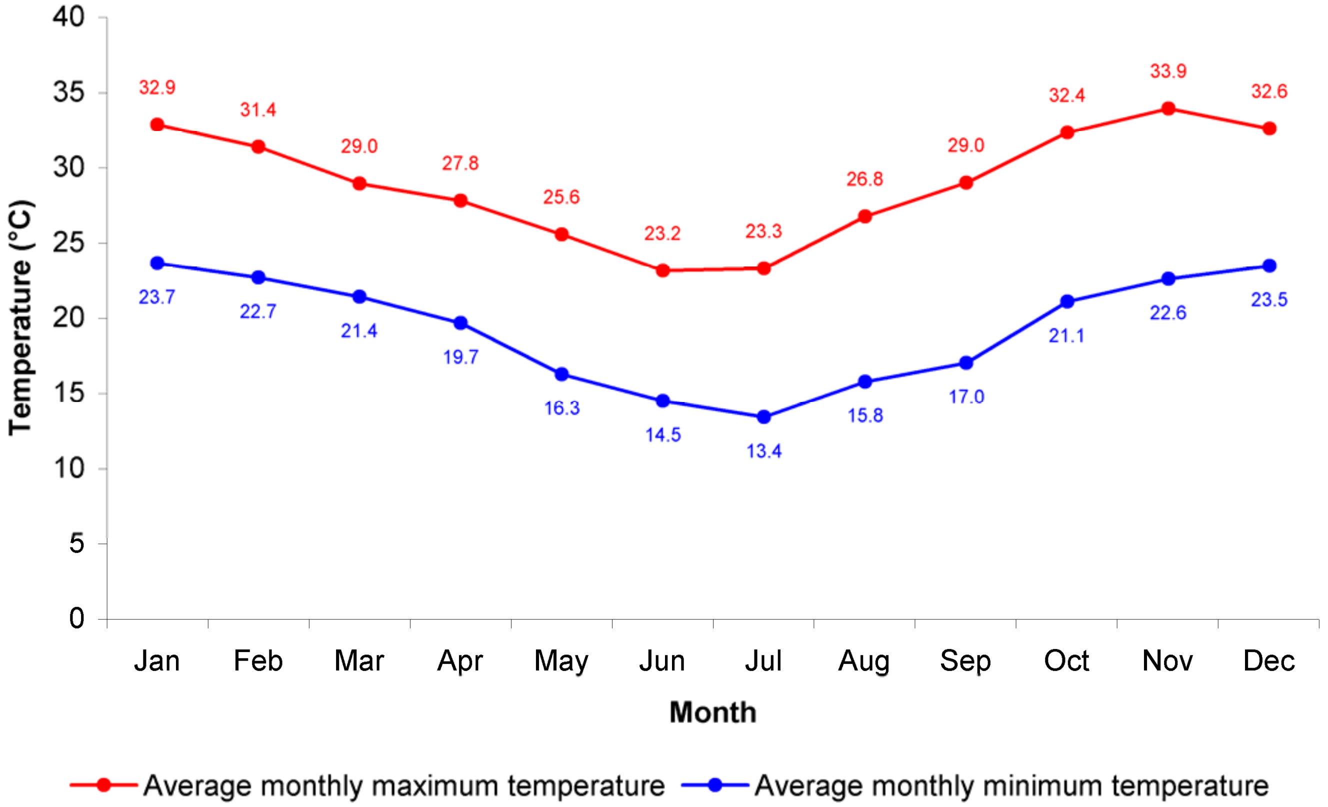


Figure 2.4 Chart showing average monthly maximum and minimum temperatures calculated from a 6 year record (2001 to 2006) collected at Malilangwe Head Quarters.

2.4. Geology and soils

The reserve’s most prominent topographical feature is the Malilangwe Range, an area of very rugged Stormberg sandstone hills that runs roughly east-west, dividing the reserve into northern and southern sections (Figure 2.5). The sandstone occurs in two distinct layers. The lower layer, which was laid down under lacustrine conditions, is red in colour, while the upper layer, which is thought to be of aeolian origin, is white (Swift et al., 1953). Both types weather to produce fine-grained sandy soils with low base status (Clegg, 1999b).

The area to the north of the Malilangwe Range is underlain by acid and basic gneisses, which have been intruded by numerous doleritic dykes. The terrain in this area is gently undulating with moderately shallow, coarse-grained, sandy soils.

Immediately to the south of the Malilangwe Range is a flat to gently sloping region with deep, well-drained, sandy soil derived from Stormberg sandstone. Further south, this gives way abruptly to a moderately flat plain that is underlain by Jurassic basalt of the Upper Karroo system. The soils on the basalt plain vary from deep, self-churning, heavy clays (vertisols) to shallow, sandy loams underlain by rock or by calcareous gravel at depths of less than 40 cm (lithosols). These soils are poorly weathered and essentially unleached (Kelly & Walker, 1976).

A complex mosaic of dolerite, grits, shales and mudstones is found in the west of the reserve between the Malilangwe Range and the Chiredzi River (Swift et al., 1953). The area underlain by dolerite is characterised by shallow, red, loam soils, with numerous rocks and boulders strewn over the surface. The grits are associated with moderately shallow, coarse-grained, sandy soils, and the shales and mudstones with very shallow lithosols. Large areas of alluvium occur in association with the Chiredzi, Runde and Nyamasikana Rivers.

2.5. Relief and drainage

The landsurface of the reserve slopes gently downwards in a south-westerly direction towards the Chiredzi and Runde Rivers, with altitude ranging from 510 m a.s.l. at Hunyugwe in the Malilangwe Range, to 300 m a.s.l. at the Chiredzi - Runde confluence (Figure 2.6).

The Chipimbi, Gananda, and Nyamasikana Rivers, which flow into the Chiredzi River, drain the west, north and central regions of the reserve, while the eastern and southern parts are drained by the Nyamsaan, Mulovele, Mahande and Chiloveka Rivers, which flow into the Runde in the south. The Chiredzi and Runde are the only rivers with a permanent supply of surface water during the dry season.

2.6. Vegetation

The vegetation, which is predominantly tree/bush savanna, is described in detail in chapter 3.

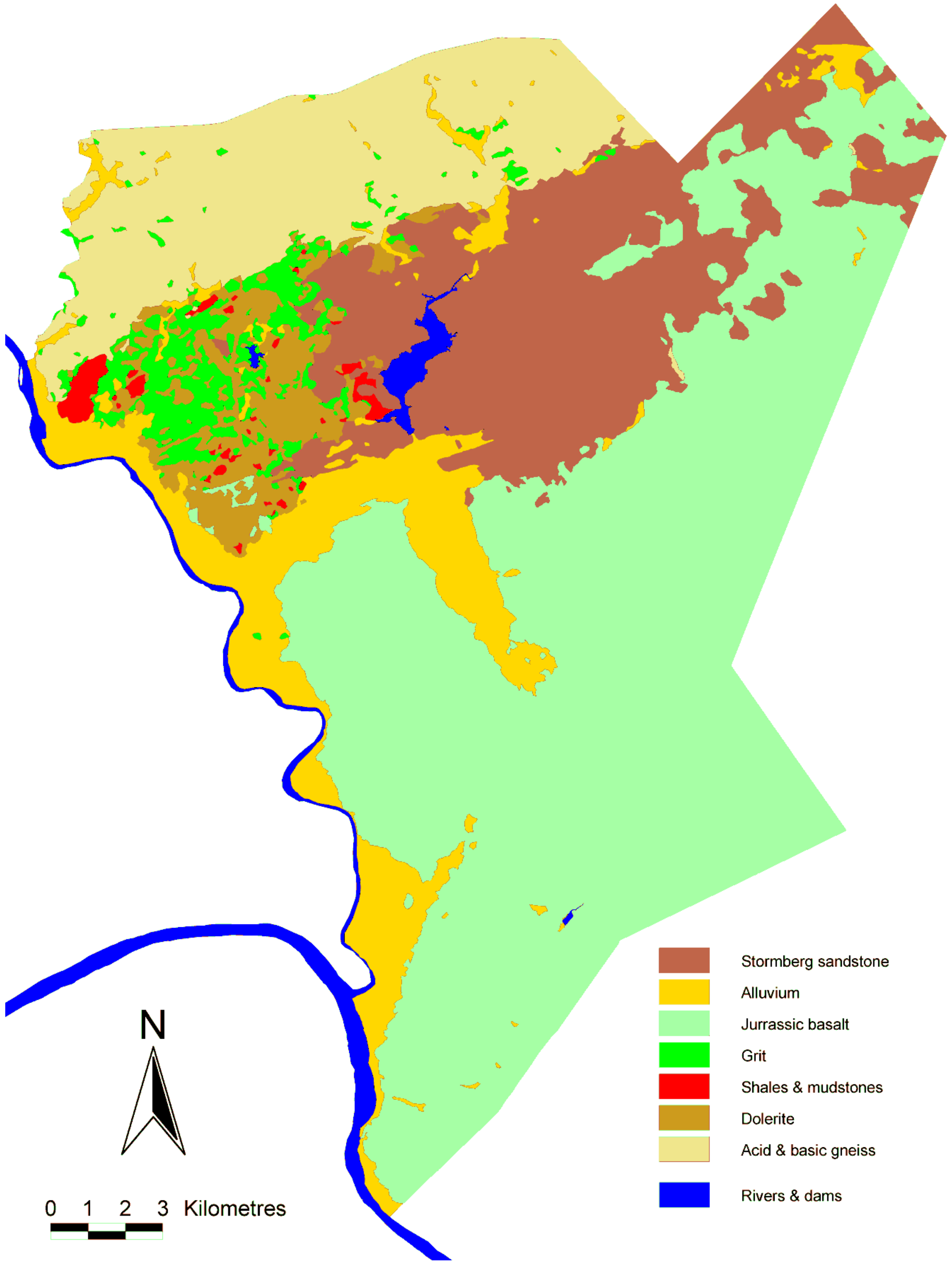


Figure 2.5 Geological map of Malilangwe Wildlife Reserve.

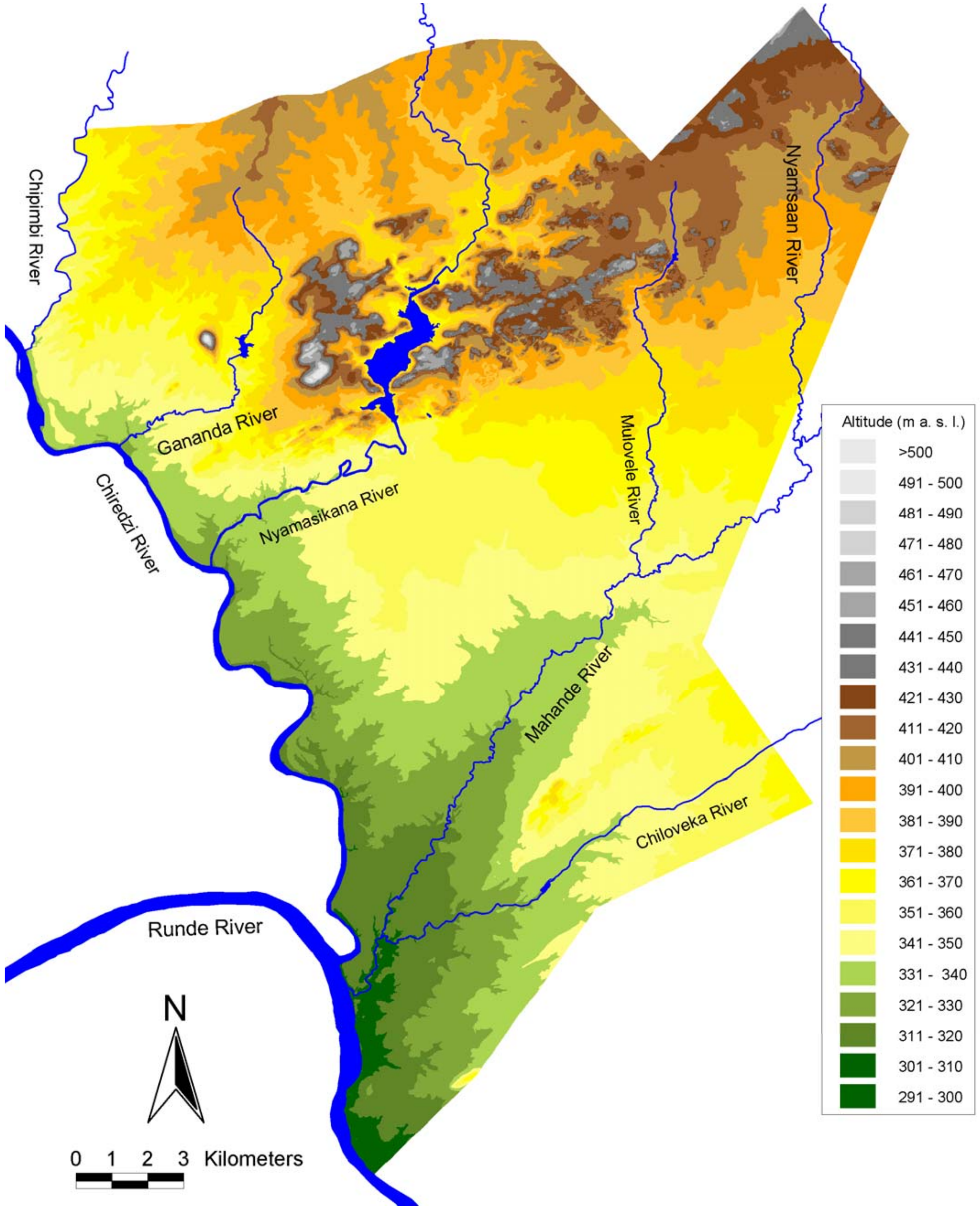


Figure 2.6 Relief and main drainage systems of the Malilangwe Wildlife Reserve.

2.7. Management history

Prior to the arrival of European settlers, parts of the Malilangwe Range and the areas in close proximity to the Chiredzi and Runde Rivers were occupied by Hlengwe agro-pastoralists. In 1949, a large portion of the study area was given over to Mr. R. L. Sparrow, where he pioneered Lone Star Ranch and raised cattle until 1985. After 1985, hunting safaris, which had been conducted since 1967, small-scale agriculture, live-sale of game, and photographic safaris, which commenced in 1987, became the sole forms of landuse on Lone Star.

In 1994, The Malilangwe Trust, a donor-funded, non-profit organisation that aims to conserve wildlife and improve social welfare through investment in the surrounding communities, purchased Lone Star and neighbouring Maranatha Ranch to form the Malilangwe Wildlife Reserve. Ecotourism, limited sport hunting and live-sale of surplus game continued to be the primary forms of landuse.

A principal conservation objective of the Trust is to restore and maintain the reserve's historic biodiversity. In accordance with this goal, animal species that had become locally extinct (black rhino, Lichtenstein's hartebeest and roan antelope) were reintroduced and, where necessary, existing wildlife populations were boosted by buying in animals from other reserves. Populations of most species have increased since the introductions, and are at or nearing ecological carrying capacity.

Fire, which had been actively excluded since the 1950's, was reinstated as a management tool in 1994. A portion of the reserve is burnt annually, with the size of the burnt area being determined by the previous year's rainfall.

The legacy of cattle ranching left the reserve well supplied with sources of artificial water. In 1997, the average distance from permanent water sources (dams, rivers, springs and pans) was 789 m, with 0.6 % of the area being more than 2 km from water (Clegg, 1999b). Closure of several artificial sources after 1999 increased the average distance to 863 m, with 1.4 % of the area being greater than 2 km from water.

2.8. Elephant population

Prior to 1949, elephant were locally common in the study area. Conflict between elephants and man increased with the onset of commercial cattle ranching, and by the early 1960's elephants had been largely eliminated from Lone Star Ranch. Adult bulls periodically ventured on to the property, but only for short periods.

From 1967 to 1979, several hundred elephant calves that had been orphaned by culling operations were kept in bomas on Lone Star prior to being exported to international zoos and sanctuaries. When this venture folded in 1983, the remaining 23 elephants (2 from Gonarezhou National Park, 2 from Matusadona National Park, 1 from Gokwe, and 17 from Hwange National Park) were released onto the ranch. The two oldest individuals, a male and female, were 16 and 17 years old respectively, whilst the youngest individual was 12. It is from this initial nucleus, and from immigration from the Gonarezhou National Park, that the current elephant population originated (Kaschula, 2004).

A total area count of the elephant population has been conducted annually using a helicopter since 1999 (Goodman, 2007). The current population estimate is 160 (Figure 2.7).

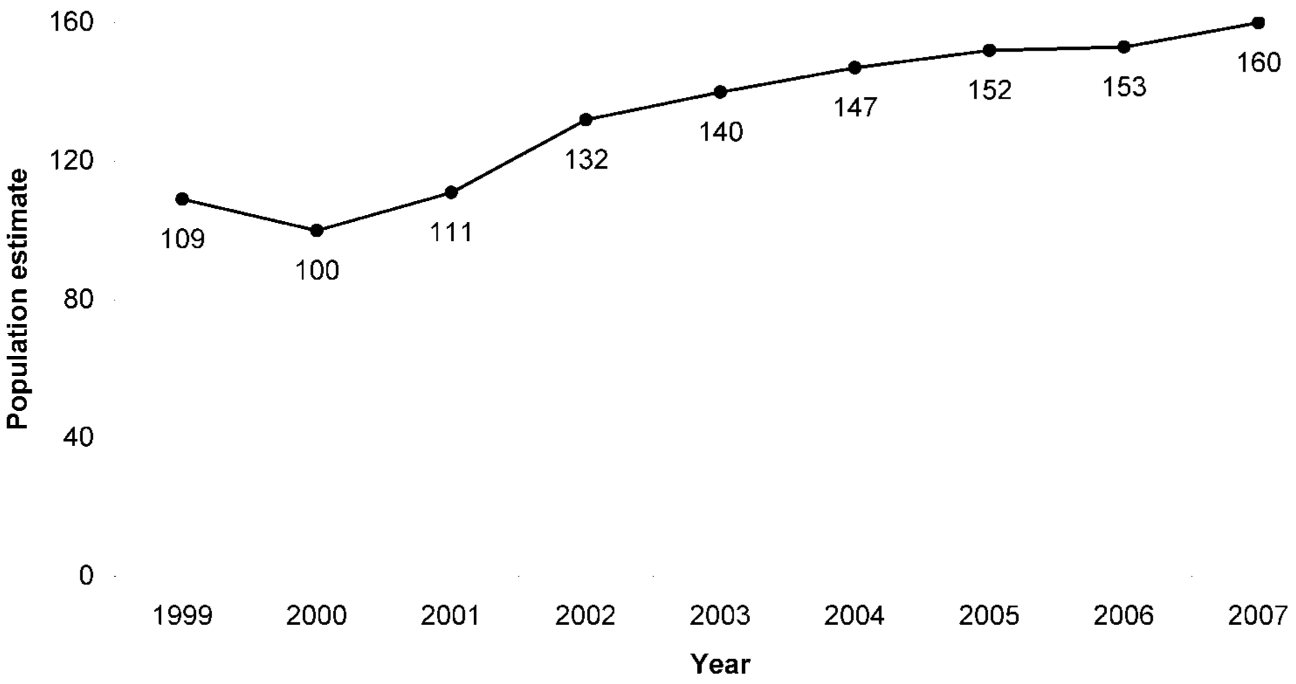


Figure 2.7 Trend in elephant numbers at Malilangwe Wildlife Reserve between 1999 and 2007.

Since 2000, there have been periods when the population increased at a rate in excess of the maximum achievable by elephants. This is explained by immigration of primarily bull elephants from the Gonarezhou National Park.

Chapter 3. Classification and mapping of land cover units applicable to elephants

3.1. Introduction

In Chapter 1, it was hypothesised that elephants select habitats and diets that maximize their short-term rate of intake of digestible energy and nutrients. One of the aims of this thesis was to test this hypothesis at the landscape level. However, before a test could be conducted the spatio-temporal pattern of the short-term rate of protein intake had to first be quantified for the study landscape.

The rate of food intake is the integrated result of several foraging actions (Spalinger & Hobbs, 1992; Sauvant et al., 1996; Pastor et al., 1999; Yearsley et al., 2001) and, consequently, its estimation at the landscape level requires quantification of the phenological and structural characteristics of the vegetation that affect these actions across both space and time. Considering that foraging ultimately involves making choices between species of plants, estimation of the rate of protein intake requires a description of the vegetation at the plant species level.

Although the last decade has seen manifold advancements in the field of remote sensing, the information gained from satellite imagery is still too coarse to provide data on individual plant species (Kerr & Ostrovsky, 2003; Turner et al., 2003). For this reason, the data required to estimate the rate of intake can only be collected using a ground-based approach. Data can be collected by first subdividing the vegetation of the landscape into floristically and structurally homogenous units, and then using the resulting land unit map (Zonneveld, 1989) as a spatial framework for ground-based monitoring of the components of vegetation that influence intake.

Elephants feed from both herbaceous and woody plants (Buss, 1961; Williamson, 1975; Guy, 1976; Barnes, 1982; Owen-Smith, 1988; Cerling et al., 1999; de Boer et al., 2000) and, consequently, land units applicable to elephants should be derived from a classification of the composition of both herbaceous and woody vegetation. Considering that vegetation structure can potentially influence the rate at which food can be harvested by elephants, the classification should also take into account the structure of the woody layer.

Availability of green leaf from woody plants can be estimated by constructing a phenological time series for each woody plant species growing in each land unit. In markedly heterogenous landscapes, it may be difficult to visit each land unit with sufficient frequency to build up a suitably detailed time series for each woody species. Under these circumstances, the temporal resolution of each time series can be improved by pooling data for species across land units where similar phenology is expected. In savannas, plant phenology is largely governed by availability of soil water, which is related to rainfall and topo-edaphic conditions (Monasterio & Sarmiento, 1976; Prins, 1988; Prins & Loth, 1988; Seghieri et al., 1995; de Bie et al., 1998; Shackleton, 1999). Consequently, the topo-edaphic relations among land units should also be investigated as part of the classification process, so that decisions concerning which land units to use when pooling data can be made.

To quantify patterns of resource selection by animals, studies of foraging behaviour at the landscape level use global positioning system (GPS) or satellite collars to collect data on the position of animals over time (Douglas-Hamilton, 1998; Galanti et al., 2000b; Blake et al., 2001; Johnson et al., 2002a; Johnson et al., 2002b; Nielsen et al., 2003; Frair et al., 2005). However, meaningful interpretation of the fine-scale position data from these collars is only possible when spatial databases describing the environment of the landscape are available at an equally fine scale (Guisan & Zimmermann, 2000). To ensure realistic spatial representation of explanatory variables and minimise information loss, overly simplistic division of the landscape should be avoided. As a general rule, the landscape should be described to the highest detail possible with the available resources. The detail with which a landscape can be described in a spatial database is determined by the number of subdivisions generated by the classification process, and the accuracy with which the derived land units can be mapped. Consequently, accuracy assessment is an important part of the mapping process.

This chapter describes how the landscape of the study area was subdivided into land units to create a spatial framework for the forage resource that was applicable to elephants. The specific objectives were (1) to derive a land unit classification for the study area based on vegetation composition and structure, (2) to determine the relationship between the derived land units and the topo-edaphic environment, (3) to map the land units, and (4) to estimate the accuracy of the land unit map.

3.2. Methods

3.2.1. *Vegetation sampling*

A georeferenced 1:25000 aerial photographic mosaic of the reserve was created by individually resampling scanned aerial photographs (300 dpi) to less than 5 m accuracy using a linear or quadratic mapping function and nearest neighbour method, and then concatenating them using Idrisi32 geographic information system (GIS) software (Eastman, 2001). The co-ordinates of trees, obtained from digital georeferenced 1:25000 orthophotos made from the same aerial photographs, were used as control points. The creation of the mosaic was necessary because of the poor picture quality of the orthophotos. Potentially homogenous vegetation units were then delineated on the mosaic by digitising boundaries detected by viewing pairs of aerial photographs through a stereo viewer (10x magnification). After drawing a 50 m buffer around each unit, sampling points were located within each unit, giving 201 sample sites in total, using a stratified random sampling strategy. The co-ordinates of the points were uploaded onto a GPS, which was used to navigate to the sites. On arrival at a sampling point the shrub, tree and herbaceous layers, and soil were sampled using the following methods based on Walker (1976).

Shrub and tree layers

Shrubs were defined as woody plants ≤ 3.0 m in height. However, for thicket forming species (e.g. *Capparis* spp.) and species with numerous stems per individual (> 15), all individuals were classified as shrubs even if they were taller than 3.0 m. Shrubs were sampled in transects of 50 m length and variable width. The sample point formed the south-east corner of a transect, with length laid out to the west and width to the north. If, by adhering to these predetermined directions, a transect was forced to cross a vegetation boundary or road, the length or width was laid out to the east and south respectively. The initial width of a transect was such that at least 15 individuals of the most common species were included, and there were no less than 30 individual shrubs > 0.5 m high regardless of species. A complete shrub was defined as "in" if the centre of its base was included in a transect. However, for multi-stemmed shrubs covering an area of several square metres and for coppice growth on fallen tree trunks, only that portion of the canopy falling within the transect was included. For each shrub in the transect the following was recorded: species, height, maximum canopy diameter, canopy diameter at right angles to the maximum, and canopy shape, which was approximated by one of seven shapes according to Melville et al. (1999). All canopy dimensions were measured to the nearest 0.1 m. Once measurement was complete, the width of a transect was increased to include more individuals of species that were poorly represented. Only these individuals were assessed in the transect extension. The process of increasing the width of a transect was continued until most of the shrub species found at the site were represented. The co-ordinates of the corners of the initial transect, and of each extension, were recorded using a GPS.

Trees, defined as woody plants > 3.0 m in height, were measured in the same way as shrubs except for the following: where a multi-stemmed tree was located at the edge of a transect the tree was considered "in" if half or more of its stems were included; canopy depth and height were measured to the nearest 0.5 m.

Herbaceous layer

At each site a 50 m tape was laid out along the longitudinal bisector of the initial shrub transect. Following the method of Kelly & Walker (1976), a 1 m^2 quadrat was placed at 2 m intervals along the tape, to give a total of 25 quadrats per site, and the aerial cover of each herbaceous species was estimated visually in each quadrat using an eight point scale (0 %; 1 %; 2-10 %; 11-25 %; 26-50 %; 51-75 %; 76-95 %; 96-100 %).

Environmental variables

The topographical position of each site was scored as follows: 1 - rocky outcrop; 2 - upper slope/crest; 3 - mid slope; 4 - lower slope; 5 - flat; 6 - bottom land. The slope at each site was extracted from a digital elevation model (resolution 10 m) that was produced by interpolating between contours at intervals of 10 m. Percent cover of gravel (stones ≤ 5 cm in diameter) and rock (stones > 5 cm in diameter) was assessed (using the eight point scale) in the 25 1 m^2 quadrats used for sampling the herbaceous layer. In every fifth quadrat, a sample was collected from the top 30 cm of soil. These samples were combined to create a composite sample for each site. Once a sample had been taken, the hole was deepened, up to a maximum of 125 cm, to measure soil depth. The soil depth for the site was determined by averaging the five depth measurements. The following were determined for each soil sample: percent sand, silt and clay using the hydrometer method (Bouyoucos, 1936); nitrogen before and after incubation using the sulphuric acid – hydrogen peroxide method ; pH using the calcium chloride method (McLean, 1982); soil water electrical conductivity using a 1:5 soil:water suspension; available phosphorus using the modified resin extraction method; and concentrations of K, Ca, Mg, and Na using atomic absorption. The analyses were done by the Zimbabwe Sugar Association, Private Bag 7006, Chiredzi, Zimbabwe. Total available moisture was calculated for each site using the equations derived by Hutson (1984).

3.2.2. *Land unit classification*

Land units were derived from a five-stage classification of the vegetation of the 201 sample sites. The first stage separated grassland sites from woodland sites. The second stage divided the woodland sites into groups based on the canopy volume (m^3ha^{-1}) of their woody species using a Twinspan classification

(Hill, 1979). The pseudospecies cut levels used in the classification were 0, 50, 1000, 3000, 6000, 10000, 20000, 40000 m^3/ha and their weights were 1, 1, 2, 2, 2, 2, 2, 2 respectively. All pseudospecies, except the two lowest, were available for use as indicators. Groups produced by the second stage that were heterogenous with respect to herbaceous composition were divided further in the third stage by running Twinspan classifications on their herbaceous species cover data. For these classifications, the default pseudospecies cut levels were used with the following weights 1, 2, 2, 2, 2. All pseudospecies, except the lowest, were available for use as indicators. In the fourth stage, sites within each group were checked to determine if they occurred on the same geology and similar topo-edaphic environment. If a discrepancy was found, the offending site was moved to the most closely related group that occurred on the corresponding geology and topo-edaphic environment. The groups derived by the first four stages were considered vegetation types. The types were named after their dominant woody plant species, a woody or herbaceous indicator species, and a description of the structure of the woody layer. The nomenclature used to describe the structure of the woody layer is defined in Table 3.1.

Table 3.1 Nomenclature used to describe the structure of the woody layer. Descriptions for each height class (given in parentheses) are assigned according to the canopy volume (m^3ha^{-1}) of woody species

Height class (m)	Total canopy volume (m^3ha^{-1}) of woody species				
	very low	low	medium	high	very high
0-3.0	<2000	2000-5000	5000-10000 (shrub)	10000-20000 (dense shrub)	>20000 (dense shrub)
3.1-8.0	<1000	1000-2000 (open woodland)	2000-10000 (open woodland)	10000-20000 (woodland)	>20000 (closed woodland)
8.1-14.0	<1000	1000-3000	3000-6000 (open tall woodland)	6000-20000 (tall woodland)	>20000 (tall closed woodland)
14.1-20	<1000	1000-3000	3000-6000	6000-20000	>20000

Note: forest = high or very high in all height classes, grassland = very low in the 0-3.0 m height class and low to very low in the other classes.

It was recognized that fire can modify the structure of woody vegetation in the short-term and, consequently, in the fifth stage, land units were distinguished further on whether the vegetation had been burnt or not within the last year.

3.2.3. *Mapping of land units*

A map of the vegetation types was created by supervised classification of Landsat 7 ETM+ imagery using Idrisi Kilimanjaro GIS software (Eastman, 2003). Spectral signatures were developed for each type by using the vegetation sample points as seed pixels for the delineation of training polygons on a June 2000 Landsat 7 ETM+ satellite image that had been resampled to less than 5 m accuracy using a linear mapping function and nearest neighbour resampling type. Co-ordinates of pans were used as control points. A June image was chosen because spectral differences between most vegetation types are large at this time of the year. The training polygons were digitised using a flood fill method. This technique compares the spectral reflectance of a seed pixel, across all seven bands, to its surrounding pixels, and then automatically digitises a polygon of specified radius, by including contiguous pixels whose reflectance falls within a specified range of similarity (tolerance) to the seed pixel. In an attempt to create homogenous training sites (i.e. sites that included only one vegetation type), a strategy of numerous, small (low similarity tolerance) training polygons was adopted. Signatures were then created for each vegetation type by analysing the range of reflectance of the pixels enclosed in the training polygons. Despite carefully digitised training sites, several vegetation types could not be separated on the basis of spectral reflectance. However, these types were often found in different parts of the reserve, and to include this spatial information in the classification, a prior probability database was created by estimating the cover of the vegetation types within each of the strata created during the aerial photographic interpretation (see section on vegetation sampling). The spectral signatures and the probability database were then used in a maximum likelihood classification to map the vegetation communities from the satellite image. Due to the presence of shadows, it was difficult to create satisfactory spectral signatures for the vegetation type that occurred on the sandstone outcrops and, therefore, the boundaries of this type were digitised from a hill shade model.

A total of 1347 test points were located on the map by placing points in each vegetation type using a stratified random sampling strategy. Each point was visited on the ground and the vegetation type recorded. The ground truth data was compared with the map data and errors of omission and commission for each vegetation type, and the total error for the map were calculated using the Errmat module of Idrisi Kilimanjaro GIS software (Eastman, 2003). A Kappa Index of Agreement was also calculated for each vegetation type.

The management burns implemented in October 2001, just prior to the start of monitoring of food availability, were mapped from a coverage of the road network (burning blocks were demarcated by roads) using Idrisi Kilimanjaro GIS software (Eastman, 2003). The resulting fire coverage was then overlayed onto the vegetation map to create a final land unit map.

3.2.4. *Topo-edaphic environment*

In order to describe variation in the topo-edaphic environment at Malilangwe, the main patterns of variation among the topo-edaphic variables were summarized by a correlation-type principal components analysis (PCA). Discriminant Function Analysis (DFA), using vegetation types as dummy variables in a species file and the topo-edaphic variables as environmental explanatory data, was used to show the position of the vegetation types in the topo-edaphic environment. The significance of the overall DFA and its first axis was tested by a Monte Carlo permutation test. This is a direct test of whether the included environmental variables explain a significant amount of the variation in the topo-edaphic environment among vegetation types. The PCA and DFA analyses were conducted using CANOCO for windows (version 4) software (ter Braak & Šmilauer, 1998).

The data for the topo-edaphic variables did not meet the assumptions of analysis of variance and, consequently, differences between vegetation types were tested with Kruskal-Wallis analysis of variance using Systat 9 (SPSS, 1998).

To show topo-edaphic relations among vegetation types a standardized (standard deviation), matrix of topo-edaphic variables by vegetation type was subjected to hierarchical clustering using an Euclidian distance metric and complete linkage (furthest neighbour) method using Systat 9 (SPSS, 1998). Hierarchical clustering produces clusters that are displayed in a tree such that the most similar vegetation types are closest to each other.

3.3. Results

3.3.1. *Land unit classification*

Thirty-eight vegetation types were derived from the 201 sample sites. Four sites were excluded as outliers. Of these, two were unusual sites on alluvium, one was a dambo grassland that had been encroached by *Colophospermum mopan*e, and one was a disturbed site on sand. Fourteen sites were classified incorrectly with respect to geology and seven sites were incorrectly placed with respect to topo-edaphic environment. These sites were moved into the most closely related vegetation types with the correct geology and topo-edaphic environment.

One grassland vegetation type was identified from the division of grassland from woodland, twenty-nine types from classification of the woody species composition data, and eight types from classifications of the herbaceous species composition (Figure 3.1). The woody and herbaceous species composition for each vegetation type is presented in Table 3.2 and Table 3.3 respectively. Plant nomenclature follows Mapaura and Timberlake (2004).

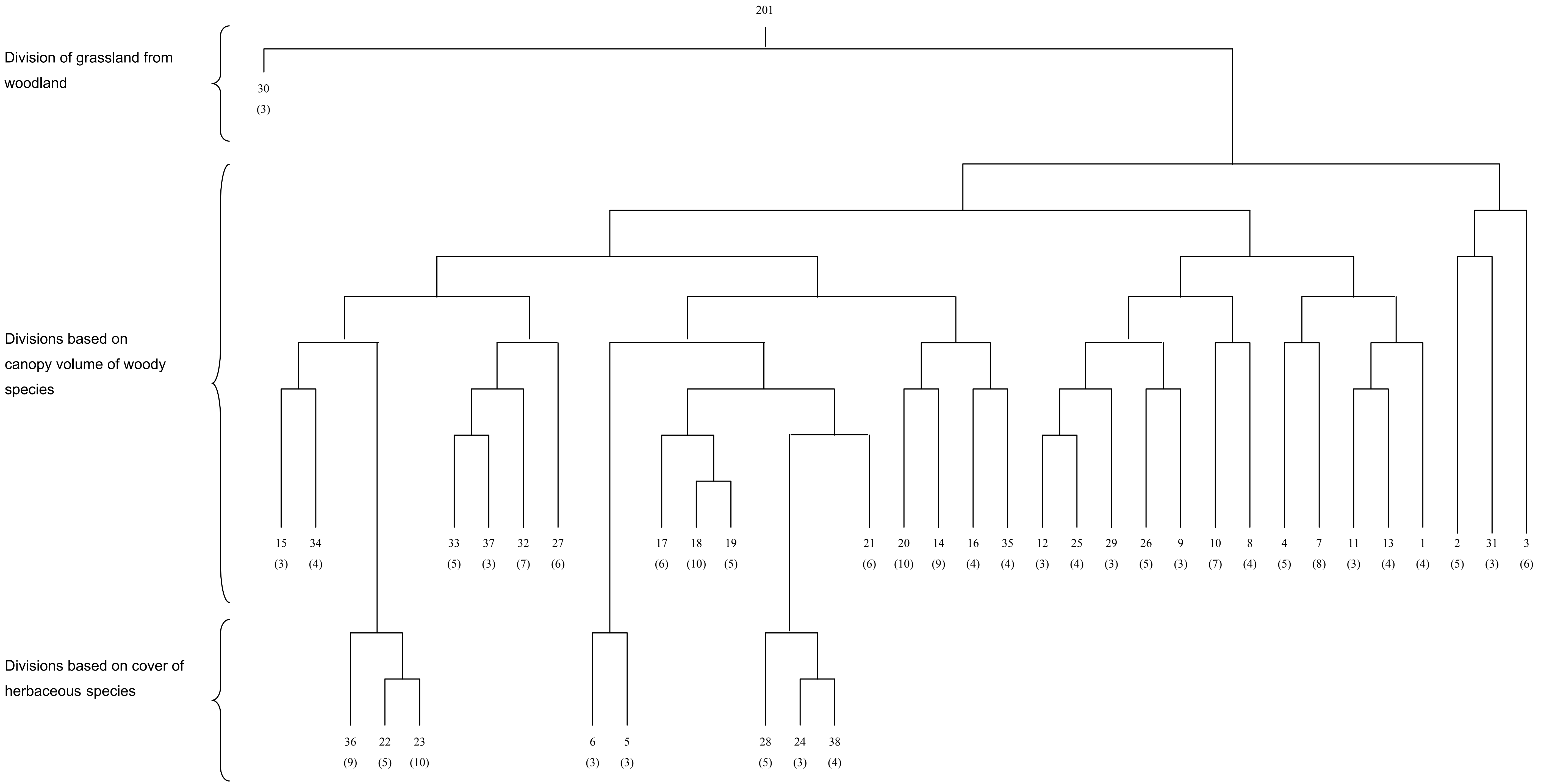


Figure 3.1 Dendogram depicting the sequence of divisions used to derive the 38 vegetation types. The number of sample sites for each type is given in parentheses below the type number. Key to type numbers: 1 - *Acacia welwitschii – Spirostachys africana* dense shrub tall woodland; 2 - *Brachystegia glaucescens – Androstachys johnsonii* dense shrub open tall woodland; 3 - *Julbernardia globiflora – Strychnos madagascariensis* tall woodland; 4 - *Lannea schweinfurthii – Pteleopsis myrtifolia* shrub woodland; 5 - *Colophospermum mopane – Urochloa mosambicensis* shrub open woodland; 6 - *Colophospermum mopane – Leucas glabrata* shrub woodland; 7 - *Albizia petersiana – Strychnos potatorum* shrub open woodland; 8 - *Acacia galpinii – Croton megalobotrys* forest; 9 - *Acacia tortilis* open woodland; 10 - *Acacia tortilis – Philenoptera violacea* shrub tall woodland; 11 - *Acacia tortilis – Thilachium africanum* shrub open tall woodland; 12 - *Combretum imberbe – Sporobolus consimilis* open woodland; 13 - *Acacia welwitschii – Salvadora persica* dense shrub woodland; 14 - *Colophospermum mopane – Pappea capensis* dense shrub tall woodland; 15 - *Colophospermum mopane – Acacia tortilis s*hrub open woodland; 16 - *Colophospermum mopane – Acacia erubescens* dense shrub open woodland; 17 - *Colophospermum mopane – Grewia flavescens* dense shrub tall woodland; 18 - *Colophospermum mopane – Courbonia glauca* shrub open tall woodland; 19 - *Colophospermum mopane – Gardenia volkensii* shrub woodland; 20 - *Colophospermum mopane – Kirkia acuminata* shrub tall woodland; 21 - *Colophospermum mopane – Terminalia pruinoides* dense shrub open tall woodland; 22 - *Colophospermum mopane –- Heteropogon contortus* open woodland; 23 - *Colophospermum mopane – Enneapogon scoparius* open woodland; 24 - *Colophospermum mopane – Panicum maximum* dense shrub woodland; 25 - *Combretum imberbe – Urochloa mosambicensis* wooded grassland; 26 - *Acacia tortilis – Dichrostachys cinerea* shrub open woodland; 27 - *Acacia nigrescens – Combretum apiculatum* shrub open woodland; 28 - *Colophospermum mopane – Commelina kotschyi* shrub open woodland; 29 - *Combretum imberbe – Acacia robusta* open woodland; 30 - *Setaria incrassata* grassland; 31 - *Brachystegia glaucescens – Albizia petersiana* open woodland; 32 - *Acacia nigrescens – Grewia villosa* open woodland; 33 - *Acacia nigrescens – Acacia nilotica* open woodland; 34 - *Dichrostachys cinerea – Dalbergia melanoxylon open* woodland; 35 - *Adansonia digitata – Gyrocarpus americanus* shrub open tall woodland; 36 - *Colophospermum mopane – Brachiaria eruciformis* open woodland; 37 - *Acacia nigrescens – Combretum hereroense* open woodland; 38 - *Colophospermum mopane – Endostemon tenuiflorus* open woodland.

Table 3.2 The mean canopy volume ($m^3\ ha^{-1}$) of each woody plant species in each vegetation type (see Figure 3.1 for a key to type numbers). An entry of – denotes 0

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Acacia borleae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	76.37	-	-	-	-	2.93	-	-	-	163.92	-	0.01	303.03	-
Acacia erubescens	-	-	-	-	-	-	-	-	-	-	-	-	-	227.80	-	6044.79	-	-	-	92.27	-	-	-	-	-	-	455.71	-	-	-	-	-	-	-	498.01	-	-	-
Acacia galpinii	-	-	-	-	-	-	-	19402.78	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	491.50	-	-	-	-	-	-	-	-	-
Acacia gerrardii var. *gerrardii*	-	-	-	-	-	-	-	-	26.16	-	-	-	-	-	-	-	-	-	5.23	-	-	-	-	-	-	-	-	-	-	2.79	-	4.34	-	-	-	-	20.14	-
Acacia nigrescens	-	-	14.89	421.53	-	-	58.92	1208.15	123.04	469.98	-	406.62	189.54	634.56	309.69	-	1.81	20.59	93.22	308.81	167.73	108.83	487.51	3.24	167.38	537.45	3526.17	-	1948.21	7.38	-	4455.95	8523.06	1566.48	1002.54	147.12	1877.51	0.03
Acacia nilotica	-	-	130.13	453.17	324.40	0.46	197.67	-	106.94	-	-	-	-	-	2002.27	-	-	-	6.29	-	-	-	-	-	40.62	-	-	-	-	34.36	-	28.51	531.41	2902.49	-	-	36.20	-
Acacia polyacantha subsp. *campylacantha*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.07	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia robusta subsp. *clavigera*	-	-	-	98.13	-	-	-	3.88	-	-	3.93	-	-	87.32	-	-	-	-	-	-	-	-	-	-	-	515.21	-	-	914.43	-	-	0.61	-	-	-	-	-	-
Acacia schweinfurthii	-	-	-	-	-	-	-	3171.74	-	900.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acacia tortilis	38.54	-	-	234.82	-	-	45.07	4125.91	8624.53	11876.72	10809.90	-	2953.39	62.97	1635.63	154.58	0.10	214.49	-	98.26	-	-	-	-	148.44	9848.04	-	-	145.53	-	-	-	275.93	-	33.96	-	-	-
Acacia welwitschii	11575.28	-	-	0.15	-	-	126.58	-	-	-	325.15	-	4772.89	-	-	110.70	139.52	-	255.61	-	-	-	-	-	-	0.51	-	-	0.03	-	14.11	-	-	-	-	-	-	-
Adansonia digitata	438.43	-	-	-	-	-	-	-	-	-	911.21	-	2382.68	1943.48	-	-	32.49	-	-	1428.39	-	-	-	-	-	461.95	-	-	-	-	-	-	-	-	2387.70	-	-	-
Afzelia quanzensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	275.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	104.33	-	-	-
Albizia anthelmintica	160.91	-	-	286.77	-	1.41	112.27	-	284.95	106.47	569.11	-	433.15	320.78	20.06	57.75	62.61	157.01	30.77	-	0.22	-	-	98.81	-	-	-	-	-	-	-	-	-	10.38	-	-	-	-
Albizia harveyi	-	-	0.03	905.47	-	-	-	-	-	56.36	-	-	-	0.03	-	-	-	-	47.92	-	-	-	-	-	1.51	14.64	-	-	3.17	3.35	-	0.41	0.19	-	-	-	1.08	-
Albizia petersiana subsp. *evansii*	374.52	-	-	2709.73	527.53	3372.04	4842.88	-	-	84.28	-	-	0.31	-	-	18.36	-	-	0.02	-	-	0.53	-	-	-	-	-	-	-	-	1303.75	-	6.60	-	-	-	-	-
Alchornea laxiflora	-	1.27	-	-	-	-	-	0.92	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	-	-	-	-	-	-	-
Allophylus rubifolius	-	-	-	92.47	-	41.00	12.32	8.98	-	651.22	-	-	-	5.03	-	-	-	0.05	-	-	-	-	-	-	-	0.42	-	-	-	-	-	-	5.72	-	-	-	-	-
Ancylobothrys petersiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	-	-	-	-	-
Androstachys johnsonii	-	12136.66	-	-	-	-	-	-	-	-	-	-	-	-	-	79.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	764.97	-	-	-
Anisotes rogersii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	831.52	-	-	-
Artabotrys brachypetalus	-	1117.05	25.17	46.62	-	-	-	-	-	-	-	-	-	-	-	241.53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06	-	-	-
Balanites maughamii	-	11.09	-	-	10.47	1.59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bauhinia tomentosa	54.68	-	-	-	-	-	-	-	-	-	-	-	-	46.34	-	1.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.68	-	-	-
Berchemia discolor	-	-	-	1.72	-	-	124.26	5.02	0.34	207.16	0.18	-	200.46	104.99	-	90.21	-	-	0.01	-	-	-	-	-	-	1.07	372.82	-	0.20	-	-	0.43	-	-	355.24	-	0.02	-
Boscia angustifolia	-	-	-	-	-	0.26	-	-	-	-	-	-	-	-	-	179.59	0.03	-	-	0.61	0.03	0.79	-	-	-	-	0.08	-	-	-	-	-	-	-	58.85	-	-	-
Brachystegia glaucescens	-	19885.48	-	1.49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10500.53	-	-	-	1469.36	-	-	-
Bridelia cathartica	-	-	-	0.23	-	-	-	4.61	-	3.89	-	1.64	-	-	-	3.53	-	-	-	-	-	-	-	-	-	0.32	-	-	-	-	-	-	-	-	-	-	-	-
Bridelia mollis	-	2.31	-	6.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-	-
Cadaba termitaria	0.02	-	-	-	-	-	-	-	-	0.03	-	-	0.14	0.05	-	-	0.08	5.67	-	-	-	-	-	4.03	0.21	-	-	-	-	-	0.10	-	-	-	3.33	-	-	-
Canthium glaucum subsp. *frangula*	-	5.69	-	-	-	-	-	-	-	-	0.53	-	-	61.74	-	1178.09	-	-	-	-	-	-	-	-	-	-	-	-	-	-	59.89	-	-	-	59.04	-	-	-
Canthium racemulosum var. *racemulosum*	-	30.84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Canthium setiflorum subsp. *setiflorum*	0.35	9.95	0.45	-	-	-	13.76	-	-	-	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Capparis sepiaria var. *subglabra*	594.09	-	-	96.69	-	-	179.44	0.15	246.74	1542.90	2601.22	-	728.63	35.45	-	-	5.97	26.77	-	-	-	-	-	-	-	-	18.47	-	-	-	-	-	-	-	-	-	-	-
Capparis tomentosa	19.99	-	-	0.29	-	-	0.02	1490.50	-	-	1.63	1.45	12.74	-	-	-	0.51	42.89	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cardiogyne africana	-	-	-	-	-	-	-	7018.85	-	25.76	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.98	-
Cassia abbreviata	-	-	-	42.12	-	-	-	-	-	0.03	-	-	-	-	-	229.15	-	-	-	44.28	0.08	15.37	-	-	-	-	0.09	-	-	-	-	16.52	-	-	1.13	-	-	39.31
Catunaregam swynnertonii	115.26	-	8.39	24.87	22.98	0.24	37.79	-	-	-	-	-	0.31	0.60	-	-	-	-	47.90	6.72	6.27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cephalocroton mollis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.74	-	-	-	-	6.35	-	-	-	-	-	-	-	-	-	2.32	-	-	-	-
Cissus cornifolia	-	6.36	2.54	26.41	53.84	119.31	38.18	-	-	-	-	-	-	54.98	-	33.18	6.16	18.27	13.29	47.94	48.93	9.37	29.93	-	-	12.37	261.03	17.81	-	-	-	3.57	-	-	26.04	3.95	0.75	55.48
Cissus integrifolia	-	-	-	-	0.28	98.02	-	26.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cissus quadrangularis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cissus rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	89.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cleistanthus schlechteri	-	-	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	105.72	-	-	-	-	-	-	-
Cleistochlamys kirkii	-	-	-	-	-	-	-	375.95	-	-	3.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clerodendrum eriophyllum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22.44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clerodendrum ternatum	-	-	-	-	-	-	4.33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cocculus hirsutus	-	-	-	-	-	-	-	1141.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Coffea racemosa	1.67	6.60	49.18	125.78	29.12	158.00	178.13	4.06	-	0.69	10.86	-	-	-	-	2.67	-	-	8.26	-	-	-	-	-	-	-	-	-	-	-	106.38	-	-	-	-	-	-	-
Colophospermum mopane	-	-	-	0.02	3506.84	16341.69	1118.06	176.86	0.02	352.29	-	469.84	155.40	18066.98	6113.90	4537.77	26092.56	23819.71	25455.16	13748.18	23118.87	3404.88	5514.64	19643.31	156.93	248.41	178.33	9932.40	186.04	41.77	-	245.63	135.80	887.36	-	3934.52	7.71	6658.46
Combretum adenogonium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	58.73	-	-	-	-	34.15	-
Combretum apiculatum	-	396.18	-	656.26	138.38	-	29.01	-	-	-	-	-	-	27.88	-	776.45	-	-	-	164.19	809.83	358.45	0.28	0.62	-	42.37	2081.02	0.48	51.61	-	-	119.44	-	-	117.62	2.05	-	695.29
Combretum celastroides	-	-	-	-	-	-	-	1.33	-	-	-	-	89.74	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	275.17	-	-	-
Combretum hereroense	-	-	-	209.75	201.15	-	55.29	397.97	-	91.84	1.73	32.80	-	90.26	-	-	-	-	-	101.16	0.50	124.43	6.58	2.89	-	-	232.99	0.33	329.47	259.29	-	122.60	23.50	57.52	22.34	52.17	777.56	-
Combretum imberbe	-	-	-	1929.78	-	-	45.99	3774.16	6.90	1498.73	-	3127.69	-	75.84	-	-	36.66	140.39	91.36	3.96	2.46	111.48	22.22	-	525.13	908.45	1032.27	-	2764.25	516.76	-	474.53	561.68	62.08	400.31	71.90	268.39	125.21
Combretum microphyllum	-	-	-	0.01	-	-	-	6075.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Combretum zeyheri	-	457.75	230.55	1666.84	149.31	16.92	15.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	39.55	-	-	-	-	-	-	-
Commbretum mossambicense	23.90	0.01	34.05	24.01	173.16	113.79	170.12	277.29	-	224.64	-	-	0.44	-	23.16	-	-	2.20	0.97	-	35.90	0.29	-	2.62	10.91	0.58	1.43	0.21	6.27	-	7.25	1.03	1.13	-	288.98	-	-	7.23
Commiphora africana	-	-	-	-	3.05	13.64	2.50	-	-	-	-	-	-	0.15	-	-	-	-	-	15.06	80.82	19.72	59.89	20.24	6.66	-	62.95	8.55	-	-	-	0.30	-	-	-	141.68	-	-
Commiphora edulis	-	0.01	-	0.22	-	-	0.04	75.98	-	0.09	-	-	493.81	5.49	-	13.55	-	-	-	214.43	2.26	-	-	-	-	-	0.02	0.79	-	-	-	0.02	0.05	-	265.68	-	0.20	-
Commiphora glandulosa	-	-	-	-	2120.12	624.57	1036.91	-	18.29	-	-	-	-	60.05	110.98	-	22.19	-	1.22	951.17	2.05	47.48	18.72	-	-	-	210.43	65.80	-	-	-	35.91	11.99	42.59	34.21	8.39	55.01	242.01
Commiphora mollis	36.79	-	-	156.11	-	-	71.24	-	-	-	-	-	-	404.48	-	111.55	-	-	-	1104.49	57.25	386.50	-	-	-	-	1043.42	-	-	-	-	401.70	-	-	2200.40	-	-	0.64
Commiphora pyracanthiodes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	37.86	-	-	-	-	0.34	-	-	-	-	-	-	-	-	-	-
Coptosperma littorale	-	0.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cordia monoica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.95	-	-	-	-	-
Cordyla africana	-	-	-	-	-	-	-	0.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Courbonia glauca	1.06	-	-	-	-	-	-	-	-	-	-	-	92.00	0.06	-	-	1.28	45.97	-	-	-	-	-	-	-	-	-	-	-	-	0.24	-	-	-	0.97	-	-	-
Crossopteryx febrifuga	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	207.13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Croton megalobotrys	-	-	-	-	-	-	-	9785.14	-	1206.82	-	-	8.46	-	-	-	-	0.02	-	-	-	-	-	-	0.28	-	-	-	-	-	-	-	-	-	-	-	-	-
Croton pseudopulchellus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	53.96	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dalbergia arbutifolia	-	-	-	59.15	-	-	-	765.79	-	17.62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dalbergia melanoxylon	-	-	533.12	44.71	374.18	1288.45	103.43	-	-	-	-	1.41	-	6.18	77.12	-	-	12.59	106.83	2.04	1.97	0.21	11.82	1198.54	5.48	-	37.76	3.69	9.36	-	-	76.08	39.50	700.86	-	296.73	85.35	-
Deinbollia xanthocarpa	-	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dichrostachys cinerea subsp. *africana*	244.19	-	63.93	435.08	69.89	457.12	1010.50	1434.33	76.79	1494.18	436.09	8.60	163.36	36.45	209.15	584.37	9.52	11.39	120.37	31.96	52.12	12.93	32.60	15.38	84.51	1998.61	603.13	10.20	143.84	7.42	56.69	123.21	462.46	1064.50	5.42	4.55	657.51	30.71
Diospyros loureiriana subsp. *loureiriana*	-	-	105.78	134.41	-	-	8.90	-	-	-	-	-	-	-	-	-	-	-	42.81	-	-	-	-	-	-	-	-	-	-	-	2.97	0.02	-	-	-	-	-	-
Diospyros lyciodes	-	2.79	3.65	60.53	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diospyros mespiliformis	1.53	-	44.78	98.02	-	-	-	4789.43	0.79	25.07	-	7.01	-	-	-	-	-	-	-	0.66	-	13.84	-	-	-	31.16	184.48	-	-	-	-	1.01	2.09	4.50	-	-	-	-
Diospyros senensis	-	-	-	-	-	-	-	-	-	-	32.20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diospyros squarrosa	-	-	-	0.11	0.71	5.15	0.55	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.27	0.02	-	-	-	-	0.07	-	-	-	-	-	-	0.35	-	-	-	0.26
Dombeya kirkii	33.24	-	-	-	-	-	-	-	-	-	-	-	15.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dovyalis hispidula	-	0.10	-	502.34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Drypetes mossambicensis	1069.99	-	6.22	134.12	-	68.71	8.06	-	-	0.85	-	-	60.21	96.42	-	84.93	49.53	-	264.11	-	-	-	-	-	-	-	-	-	0.02	-	21.11	-	-	-	-	-	-	-

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Ehretia amoena	59.22	-	0.03	3.12	21.39	84.53	36.53	-	-	27.70	4.14	0.70	-	13.70	1.76	0.81	0.75	2.37	9.99	-	1.67	0.13	1.29	8.38	0.92	6.52	0.86	-	-	-	-	3.33	41.41	26.85	61.82	2.38	22.25	-
Elaeodendron schlechterianum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elephantorrhiza goetzei subsp. *goetzei*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.51	-	-	-
Entada chrysotachys	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.56	-	-	-
Erythrococca trichogyne var. *trichogyne*	-	0.65	-	4.60	-	1.94	68.76	-	-	-	-	-	-	-	-	-	-	-	2.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euclea divinorum	18.49	-	49.03	30.09	-	-	14.15	625.09	-	0.34	-	25.54	-	0.01	2.43	-	25.47	4.79	94.81	-	11.40	-	-	54.52	0.11	-	0.07	-	0.16	-	-	0.20	0.14	66.68	-	0.07	4.85	-
Euclea natalensis	-	5.92	7.45	3.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Faidherbia albida	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus abutilifolia	-	449.56	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus capreifolia	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ficus tettensis	-	534.97	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Flacourtia indica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.20	-	-	-	-	0.71	-
Flueggea virosa subsp. *virosa*	-	-	0.07	171.85	-	-	0.08	289.71	-	45.14	-	21.63	-	1.18	0.89	-	-	1.45	0.28	0.91	5.62	0.09	0.77	4.08	0.93	-	9.06	-	21.71	-	-	138.61	17.21	-	-	1.56	8.51	0.44
Friesodielsia obovata	-	-	-	0.48	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Garcinia livingstonei	-	-	20.60	82.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gardenia resiniflua subsp. *resiniflua*	292.48	0.36	-	0.34	-	-	0.14	0.10	0.08	-	0.51	-	191.93	932.97	-	212.30	127.28	-	5.48	24.06	117.04	-	-	-	-	1.31	0.86	-	-	-	-	-	-	-	370.43	-	-	46.47
Gardenia volkensii subsp. *volkensii*	0.01	0.45	258.45	225.69	282.93	550.02	88.40	0.01	19.64	-	-	-	-	-	-	0.57	-	-	218.29	-	-	-	-	-	-	9.57	0.06	-	119.46	-	93.67	0.05	-	-	-	-	-	-
Grewia bicolor	2078.94	-	-	20.68	1807.29	1492.84	863.09	831.20	80.77	1276.11	1526.10	-	4824.79	13969.14	438.47	1151.16	5194.18	694.28	203.82	1985.94	4637.30	33.57	37.92	2.31	-	1578.06	1177.24	17.09	578.04	3.32	28.98	45.66	5.18	10.19	377.63	178.11	21.70	327.86
Grewia caffra	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	90.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grewia flavescens	345.57	35.27	3.78	313.73	2.95	73.52	513.57	240.92	17.27	452.80	169.79	-	211.14	1146.76	48.64	287.86	576.90	64.69	409.95	187.99	174.94	67.20	-	-	-	285.67	1743.07	-	203.93	-	2.69	64.48	3.77	7.65	630.38	-	2.20	9.34
Grewia inaequilatera	-	-	-	5.68	-	-	-	826.92	-	548.08	6.20	-	0.80	0.05	-	-	14.47	5.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.15	-	-	-
Grewia lepidopetala	123.17	-	-	0.37	-	-	36.10	20.99	-	8.64	1.33	-	19.73	71.26	-	33.78	0.88	0.59	-	2.90	8.10	-	-	-	-	-	-	-	-	-	-	-	-	-	255.96	-	-	-
Grewia monticola	79.43	40.74	7.84	51.09	352.61	4.75	58.63	274.88	28.97	225.51	86.29	0.47	93.91	41.80	46.57	482.87	170.16	329.74	97.26	1472.87	1197.74	89.58	31.94	-	-	2351.96	7476.19	-	1700.20	-	-	314.54	32.17	0.56	137.25	-	13.00	77.90
Grewia sp.	0.79	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Grewia sulcata	-	-	-	202.35	-	-	-	181.21	-	6.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.87	-	-	-	-	-	-	-	-	-	-	-	-
Grewia villosa	0.64	-	-	-	-	-	-	6.86	-	38.53	-	-	-	0.31	-	-	-	-	-	5.14	-	4.78	45.21	-	3.90	-	5.94	-	-	-	-	145.94	76.43	185.35	-	57.17	15.46	-
Gymnosporia pubescens	-	-	-	-	0.08	-	-	-	-	-	-	-	-	252.25	-	-	77.64	-	-	111.90	271.02	-	250.95	857.03	-	-	-	0.30	-	-	-	53.31	-	0.15	-	5.62	-	-
Gymnosporia putterlickioides	624.92	-	-	1.72	-	-	212.76	496.38	-	8.49	-	-	1117.68	1200.11	-	158.22	639.83	-	-	105.54	9.20	10.58	0.39	-	-	-	4.48	-	-	-	0.53	5.40	8.44	-	77.79	-	0.45	-
Gynosporia senegalensis	-	-	9.56	5.90	-	-	0.07	387.18	-	8.26	-	35.78	-	-	-	-	-	-	-	-	-	-	-	-	11.03	-	-	-	-	59.16	-	0.13	1.78	-	-	-	417.33	-
Gyrocarpus americanus subsp. *africanus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2220.95	-	-	-
Heinsia crinita subsp. *parvifolia*	-	5.71	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.71	-	-	-	-	-	-	-
Heteromorpha stenophylla var. *transvaalensis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hibiscus ovalifolius	6.73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	86.46	-	-	-
Hippocratea africana	3.98	-	-	-	-	-	-	-	-	0.57	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hippocratea crenata	-	47.01	-	0.80	-	-	1249.43	345.87	-	-	24.33	-	49.48	-	-	8.81	-	-	-	-	-	-	-	-	-	-	-	-	-	-	99.91	-	-	-	0.49	-	-	-
Hippocratea indica	34.22	-	0.13	10.13	-	49.61	358.03	739.18	-	11.38	8.84	-	77.98	93.46	-	148.05	-	18.13	0.73	-	-	-	-	-	-	-	-	-	-	-	304.04	-	-	-	-	-	-	-
Hipprocratea buchananii	-	-	-	4.13	33.59	286.69	14.82	-	-	302.11	2.29	-	-	2.91	-	-	1.97	0.55	-	0.53	2.35	9.02	15.32	6.87	-	0.37	1.47	0.48	-	-	-	0.49	1.91	-	-	1.01	-	7.70
Hymenocardia ulmoides	-	5.38	-	-	-	-	-	-	-	-	-	-	-	-	-	72.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyphaene petersiana	-	-	-	362.89	-	-	-	0.70	-	47.94	-	254.35	-	-	-	-	-	19.46	-	-	-	-	-	-	77.02	-	-	-	-	-	-	-	-	-	-	-	-	-
Julbernardia globiflora	-	1001.70	14076.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kigelia africana	-	-	-	-	-	-	-	5694.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kirkia acuminata	-	-	-	-	-	-	-	-	0.01	-	281.99	-	-	1982.65	-	486.04	-	-	-	5286.54	152.63	347.60	-	-	-	-	346.93	-	-	-	-	74.67	-	-	2305.03	0.41	-	391.53
Lagynias dryadum	-	0.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lannea schweinfurthii var. *stuhlmannii*	167.88	-	89.35	3558.28	665.55	324.07	863.26	-	-	36.37	1382.99	-	2869.25	738.67	-	622.10	203.53	22.42	2.28	742.45	67.87	60.66	-	-	-	-	648.76	-	-	-	-	55.11	-	-	1146.63	-	-	-
Lecaniodiscus fraxinifolius	26.38	160.94	-	89.05	-	-	141.39	1069.34	-	71.90	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Maerua angolensis	1.18	-	-	-	-	-	-	-	-	-	-	-	-	12.02	-	67.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15.66	-	-	-
Maerua parvifolia	0.98	-	0.30	0.19	53.36	36.29	99.83	-	0.86	66.15	3.45	-	6.22	19.87	604.70	0.29	4.27	24.21	3.22	2.54	16.46	-	-	6.83	-	10.27	-	-	-	-	264.34	-	1.25	-	7.08	-	-	-
Manilkara mochisia	457.68	305.39	-	2.84	-	-	-	-	-	0.03	-	-	4.61	-	-	716.50	-	28.18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Margaritaria discoidea var. *nitida*	-	63.85	285.78	83.92	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.48	-	-	-	-	-	-	-	-	-	-	-	4.34	-	-	-	-	-	-	-
Markhamia zanzibarica	-	-	-	0.28	0.79	1.64	88.05	-	-	-	-	-	-	2.26	-	-	-	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	91.08	-	-	108.15
Millettia usaramensis subsp. *australis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14.39	-	-	-
Monodora junodii var. *junodii*	0.24	14.35	-	23.44	-	12.71	107.15	244.82	-	0.35	146.21	-	138.04	14.25	-	442.75	5.37	-	0.17	5.37	4.56	-	-	-	-	-	-	-	-	-	110.77	-	-	-	16.74	-	-	-
Mundulea sericea	-	-	-	-	-	-	-	-	-	-	-	-	0.23	-	-	240.85	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Newtonia hildebrandtii var. *hildebrandtii*	7634.66	-	-	-	-	-	-	-	-	-	-	-	2083.30	352.34	-	55.01	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ochna barbosae	-	136.09	18.63	29.74	-	-	0.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	73.40	-	-	-	-	-	-	-
Ochna inermis	-	-	-	-	-	-	-	-	-	-	-	-	-	9.11	-	-	-	-	-	1.04	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.91	-	-	-
Olax dissitiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ormocarpum trichocarpum	-	-	-	0.17	-	-	-	-	3.77	-	-	-	-	-	-	-	-	-	-	-	-	2.01	0.28	-	-	-	-	-	-	-	-	5.39	-	5.65	-	-	11.38	-
Pappea capensis	-	-	-	-	-	-	-	-	-	-	-	-	-	875.74	-	40.31	-	-	5.67	-	14.25	-	-	-	-	-	29.72	-	-	-	-	-	-	-	-	-	-	-
Pavetta gracillima	-	0.21	-	0.81	-	-	5.51	11.74	-	0.64	-	-	-	-	-	0.77	1.07	-	-	0.62	-	-	-	-	-	-	-	-	-	-	1.61	0.03	-	-	-	-	-	-
Philenoptera violacea	-	0.15	289.63	289.93	104.44	5.13	361.39	3959.93	0.11	4484.36	2.67	1156.63	-	0.03	-	-	-	5.47	-	103.76	20.16	22.50	27.68	-	146.07	24.87	25.75	106.51	25.16	283.73	147.68	55.25	41.45	32.76	1373.82	9.44	558.48	-
Phyllanthus pinnatus	1083.63	-	0.47	-	-	14.09	48.18	-	-	2.96	-	-	52.75	200.05	-	609.64	60.50	-	-	674.18	105.51	3.68	-	-	-	122.74	4.00	-	1.52	-	-	-	-	-	329.36	-	-	-
Phyllanthus reticulatus	-	-	-	0.18	-	-	-	13.35	-	0.25	0.05	9.36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	39.70	-	-	-	-	-	-	-	8.05	-
Psydrax livida	-	14.40	4.19	1.56	-	-	3.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.82	-	-	-	-	-	-	-
Ptaeroxylon obliquum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	202.82	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteleopsis myrtifolia	-	15.20	177.36	479.17	-	-	5.83	-	-	-	-	-	-	-	-	138.43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	246.76	-	-	-	-	-	-	-
Pterocarpus brenanii	42.18	-	-	-	11.02	-	-	-	-	-	-	-	-	-	0.85	-	-	0.87	-	239.21	0.66	15.30	-	-	-	-	-	12.33	-	-	-	48.36	21.94	2.53	0.57	0.87	-	57.16
Pterocarpus lucens subsp. *antunesii*	13.56	17.69	-	-	-	-	-	-	-	-	-	-	-	-	-	235.62	-	-	-	-	-	-	27.10	-	-	-	-	-	-	-	-	-	-	-	1029.29	-	-	-
Rhigozum zambesiacum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	227.80	-	-	-	26.73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhoicissus revoilii	-	-	-	-	-	-	-	-	-	-	-	-	-	43.37	-	-	148.98	-	-	71.19	195.11	-	-	-	-	-	57.73	-	-	-	-	-	-	-	77.30	-	-	-
Rhus gueinzii	-	-	-	105.69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salvadora persica	-	-	-	-	-	-	-	-	-	-	40.64	-	1347.73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schrebera trichoclada	-	-	59.85	196.49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sclerocarya birrea	-	-	-	642.76	102.82	-	140.50	-	-	-	-	-	-	0.31	-	-	-	-	237.27	361.12	457.30	188.16	14.86	-	0.03	0.01	646.11	0.02	325.57	-	-	660.09	0.35	-	8.94	0.12	61.87	181.85
Senna petersiana	-	-	0.32	44.48	-	-	36.52	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	270.01	-	-	-	-	-	2.92	-
Spirostachys africana	6579.01	-	-	3680.85	10.49	280.30	1490.33	1399.15	-	118.39	82.52	-	506.47	151.31	-	-	188.82	-	86.65	-	3.76	-	-	-	-	153.43	-	-	96.70	-	-	-	-	-	-	-	-	-
Stadmannia oppositifolia subsp. *rhodesica*	-	487.94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Steganotaenia araliacea var. *araliacea*	-	238.93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-
Sterculia rogersii	-	-	-	-	-	-	-	-	-	-	-	-	-	38.13	-	-	-	-	-	543.52	490.27	17.78	-	-	-	77.47	166.65	-	-	-	-	-	-	-	-	-	-	-
Strophanthus kombe	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25.99	-	-	-	-	-	-	-
Strychnos decussata	5.33	-	-	0.47	-	-	1.73	-	-	-	-	-	246.92	-	-	238.95	-	-	-	-	-	-	-	-	-	0.04	-	-	-	-	0.09	-	-	-	104.60	-	-	-
Strychnos madagascariensis	111.02	24.24	323.55	613.35	699.69	862.58	498.95	-	-	-	103.28	-	-	-	-	17.59	-	-	3.82	-	58.89	5.22	-	0.19	-	-	9.62	-	-	-	345.74	-	-	-	-	-	-	-
Strychnos potatorum	-	-	-	296.99	47.92	635.48	1224.88	39.38	-	35.76	524.98	-	82.77	-	-	-	-	-	-	-	-	-	-	-	-	-	13.19	-	-	-	-	-	-	-	67.98	-	-	-
Strychnos spinosa	-	-	4.58	0.80	70.70	25.21	11.55	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-
Synaptolepis kirkii	-	-	8.71	-	-	-	-	-	-	3.92	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Tabernaemontana elegans	-	-	-	1.28	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.08	-	-	-	-	-	-	-
Terminalia prunioides	-	-	-	-	37.04	-	-	-	-	0.19	-	-	298.97	3853.06	-	-	191.20	0.08	-	723.78	3916.35	54.45	-	-	-	-	513.73	-	-	-	-	1.76	-	-	290.92	60.70	0.20	53.74
Terminalia sericea	-	-	108.56	263.77	49.76	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thilachium africanum	728.34	-	0.48	0.08	-	-	53.30	292.49	-	23.42	524.39	-	774.37	290.31	-	316.71	362.72	2.98	24.76	-	-	-	-	-	-	5.89	-	-	-	-	7.36	-	-	-	130.90	-	-	-
Tinnea rhodesiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14.82	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triclaysia allenii	-	-	-	0.09	74.28	21.87	0.06	-	-	-	-	-	-	1.41	2.22	75.07	-	-	96.55	26.75	5.45	2.16	2.34	0.29	-	0.47	21.67	-	-	-	-	-	-	-	42.66	-	-	124.70
Vangueria infausta subsp. *infausta*	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vitex ferruginea subsp. *amboniensis*	-	-	-	4.76	-	-	-	-	-	-	-	-	3.53	10.90	-	2.87	-	-	-	4.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.44	-	-	-
Vitex mombassae	-	407.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xanthocercis zambesiaca	42.11	-	-	0.10	-	-	-	1333.41	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Xeroderris stuhlmannii	-	420.55	1087.61	716.55	63.53	0.13	374.47	-	-	-	-	-	-	-	-	36.66	-	-	-	-	-	-	-	-	-	-	-	-	-	-	23.16	2.35	-	-	15.48	-	-	-
Ximenia americana var. *microphylla*	-	-	-	0.21	-	-	-	-	-	-	-	-	-	-	-	-	24.66	-	17.62	12.10	-	-	1.59	-	-	-	-	-	-	-	-	0.15	-	-	-	-	-	-
Ximenia caffra var. *caffra*	-	1.22	9.95	56.99	-	-	0.02	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.28	-	-	-
Xylia torreana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1661.49	-	-	-
Zanthoxylum capense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.34	4.80	-	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ziziphus mucronata	0.19	-	-	35.63	-	-	-	1916.94	9.09	0.25	-	249.12	2.28	-	-	4.82	3.25	0.01	-	0.68	1.31	-	-	-	12.01	29.42	122.54	-	314.35	2.81	-	11.36	14.06	9.65	-	-	17.43	-

Table 3.3 The mean aerial cover (%) of each herbaceous plant species in each vegetation type (see Figure 3.1 for a key to type numbers). An entry of – denotes 0

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Abutilon angulatum	-	-	-	-	-	-	-	-	-	0.033	-	-	-	0.044	-	-	-	0.071	-	0.124	-	-	-	-	-	0.008	-	-	-	0.013	-	-	-	-	0.020	-	-	-
Abutilon austro-africanum	0.020	-	-	-	-	-	-	0.010	0.053	0.133	-	0.093	0.050	0.120	-	0.020	0.100	0.018	0.032	0.296	0.033	-	0.056	0.293	1.280	-	-	2.856	-	0.067	-	0.495	0.806	1.120	0.100	2.862	0.413	0.070
Abutilon indicum subsp. *guineense*	-	-	-	-	-	-	-	0.300	-	-	-	0.413	0.030	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.034	0.940	-	-	-	-
Abutilon lauraster	0.010	-	-	-	-	-	-	0.010	-	-	-	-	-	0.004	-	-	0.253	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Abutilon ramosum	-	-	-	-	-	-	0.005	-	-	0.013	-	-	-	0.484	-	0.010	-	-	-	0.215	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Acalypha ciliata	-	0.144	-	-	-	-	-	-	-	-	-	-	-	0.004	-	0.040	-	-	-	0.007	-	-	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-
Acalypha fimbriata	0.010	0.184	-	-	-	0.107	0.060	-	-	0.040	-	0.040	0.010	0.173	-	-	0.200	0.009	0.008	0.047	0.080	0.008	0.028	0.027	0.110	0.032	0.025	0.024	-	0.133	-	0.035	0.017	0.010	0.020	0.036	0.013	0.100
Acanthospermum hispidum	0.010	-	-	-	-	-	-	-	-	0.007	0.650	-	-	-	-	0.010	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Achyranthes aspera var. *pubescens*	-	-	-	-	-	-	-	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.048	0.008	-	-	-	-	-	-	-	-	-	-	-
Achyranthes aspera var. *sicula*	0.710	0.048	-	0.016	0.040	2.133	0.075	0.780	-	0.660	0.250	-	0.440	0.956	-	0.730	1.047	0.098	0.024	0.337	0.287	-	0.032	0.040	-	0.192	0.008	-	-	-	-	0.005	0.051	-	0.040	0.009	-	0.020
Acrachne racemosa	-	0.016	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.020	-	-	-
Agathisanthemum bojeri	-	-	-	0.032	-	-	-	-	-	-	-	-	-	-	-	0.780	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ageratum conyzoides	-	-	-	-	-	-	-	0.990	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alternanthera pungens	3.010	-	-	-	-	-	-	-	-	-	1.490	-	0.020	-	-	0.520	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alysicarpus rugosus	-	-	-	-	-	-	-	-	-	-	-	0.253	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amaranthus thunbergii	-	-	-	-	-	-	-	-	-	-	0.010	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Ampelocissus africana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.080	-	-
Ancylobotrys petersiana	-	-	0.040	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Andropogon fastigiatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.476	-	0.336	3.020	-	-	-	-	0.496	-	-	-	-	-	-	-	0.369	-	2.040
Anisotes formosissimus	5.575	-	-	-	-	-	-	-	-	-	-	-	0.060	0.524	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aptosimum lineare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	-	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aptosimum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aristida adscensionis	0.100	0.192	-	-	0.427	1.347	0.135	-	-	0.007	0.010	-	1.330	1.484	-	2.510	1.553	1.084	0.328	3.179	2.407	0.168	3.608	0.160	0.370	1.880	1.219	0.544	0.133	-	-	1.515	1.486	0.750	2.730	4.284	0.200	5.880
Aristida congesta subsp. *barbicolis*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	0.032	-	-	0.384	-	-	-	-	-	-	-	-	-	-	-	-
Aristida congesta subsp. *congesta*	-	-	2.803	-	0.027	-	0.095	-	-	-	-	-	0.010	-	0.027	0.060	2.640	0.907	0.008	0.993	0.107	-	0.044	-	-	1.520	-	-	0.027	-	0.560	0.135	-	-	-	-	-	0.935
Aristida rhiniochloa	0.010	-	-	-	-	-	-	-	-	-	-	-	0.020	-	-	-	0.027	-	-	0.193	0.253	0.008	0.220	-	-	-	-	0.008	-	-	-	-	-	-	-	0.004	-	0.270
Aristida sciurus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.560	-	-	-	-	-	-	-
Aristolochia albida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.035	-	-	-	-	-	-
Asparagus suaveolens	-	0.144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aspilia natalensis	-	-	0.527	-	0.093	1.067	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asystasia gangetica	-	-	0.047	-	-	-	0.205	4.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.387	-	-	-	-	-	-	-
Barleria elegans	0.070	-	-	-	-	-	-	-	-	0.547	-	-	-	-	-	-	0.073	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barleria lancifolia subsp. *lancifolia*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.508	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barleria lugardii	-	-	-	-	-	-	-	-	-	-	-	-	-	0.049	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Barleria prionitis subsp. *ameliae*	1.050	-	-	-	-	-	-	-	0.200	-	-	-	0.310	0.600	-	0.010	0.947	-	0.744	0.149	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.060	-	-	-
Barleria spinulosa	-	-	-	-	-	-	0.125	-	-	-	-	-	-	0.347	-	0.020	0.053	-	0.072	1.933	0.053	-	-	-	-	-	-	-	-	-	0.160	-	-	-	0.070	-	-	-
Barleria taitensis	0.040	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bidens pilosa	-	0.016	-	-	-	-	-	-	-	-	-	-	-	0.049	-	0.020	-	-	-	0.127	0.093	-	0.012	-	-	-	-	-	-	-	-	0.005	-	-	-	0.004	-	-
Bilbostylis hispidula	-	0.260	-	0.120	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.712	-	-	-	-	-	-	-	-	-	-	-	0.053	-	-	-	-	-	-	-
Blainvillea gayana	0.130	0.008	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-
Blepharis diversispina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blepharis maderaspatensis	-	0.480	-	0.408	0.080	-	0.005	-	-	-	0.010	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	1.200	-	-	-	0.110	-	-	-
Blepharis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.176	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Blumea viscosa	-	-	-	0.016	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.168	-	-	-	-	-	-	0.010	-	-	-
Boerhavia erecta	0.200	-	-	-	-	-	-	0.010	0.173	0.067	0.390	-	0.810	0.071	-	0.400	0.467	0.080	0.056	0.131	0.080	-	-	-	-	0.184	-	-	-	-	-	0.050	0.006	-	-	-	-	-
Bothriochloa radicans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.440	-	-	1.724	0.660	0.392	7.342	-	-	-	-	-	-	0.093	-	1.030	-	-	-	0.311	-	1.140
Brachiara deflexa	0.210	0.208	0.040	-	0.053	4.267	0.085	0.840	0.013	1.787	0.810	0.107	0.590	3.556	0.053	6.650	3.007	0.467	0.208	1.575	1.707	0.048	1.580	3.547	0.010	1.244	0.199	0.240	-	-	0.013	0.930	0.880	1.010	2.420	0.787	-	1.240
Brachiaria eruciformis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	2.556	3.420	0.490	-	-	14.444	-	-	-	3.343	16.649	18.500	-	24.811	0.427	1.880
Calostephane divaricata	-	-	0.007	-	-	-	-	-	-	-	-	-	-	0.196	-	-	-	0.022	-	0.102	0.100	-	0.052	-	-	-	-	0.016	-	-	-	-	0.046	0.050	0.130	-	0.080	0.010
Cardiospermum halicacabum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	0.104	-	-	-	0.010	0.120	0.080	-	0.044	0.107	-
Celosia trigyna	0.070	-	0.107	0.032	0.053	0.107	0.725	0.060	0.013	0.073	0.410	-	0.240	0.004	-	0.050	-	0.022	0.008	-	-	-	-	-	-	0.008	-	-	-	-	1.080	0.005	-	-	0.140	-	-	-
Cenchrus ciliaris	-	-	-	-	-	-	-	-	-	-	-	-	-	0.169	-	-	-	-	-	-	-	-	0.492	0.960	3.300	-	-	-	-	-	-	7.488	1.980	5.800	-	2.676	0.333	-
Chamaecrista absus	-	0.064	-	-	0.013	0.240	0.120	-	-	-	-	-	-	-	-	-	-	-	-	0.022	0.020	-	-	-	-	-	0.017	-	-	-	-	-	-	-	-	-	-	-
Chamaecrista mimosoides	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	0.007	0.040	-	-	-	-	-	-	-	-	-	0.005	-	-	-	-	-	0.020
Chamaesyce gracillima	-	0.096	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	0.033	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chamaesyce tettensis	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-	-	0.020	-	-	-	0.016	-	-	-	-	0.010	0.006	0.010	-	-	-	-
Chloris mossambicensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.111	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chloris roxburghiana	-	-	-	-	-	-	-	-	-	-	-	-	-	0.169	-	-	-	0.027	-	0.069	-	0.144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chloris virgata	0.500	-	0.007	-	-	-	-	-	0.373	0.020	1.210	-	8.970	0.018	-	0.380	-	0.036	0.016	0.011	-	-	0.032	-	-	0.088	-	-	0.093	-	-	-	-	-	0.020	0.004	-	-
Cissampelos mucronata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cleome hirta	-	-	-	-	-	-	0.035	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cleome macrophylla	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Cleome monophylla	-	-	-	-	-	0.040	0.155	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Clerodendrum ternatum	-	-	0.020	-	-	0.147	0.060	-	-	-	-	-	-	-	-	-	-	-	0.040	0.007	0.127	0.248	0.028	-	-	-	0.050	-	-	-	-	0.005	-	-	-	-	-	-
Coccinia adoensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.006	-	-	-	-	-
Coleochloa setiferaa	-	3.888	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Commelina benghalensis	0.390	0.624	0.127	0.112	0.027	0.720	0.480	0.020	0.053	0.753	0.420	-	0.375	0.154	0.013	0.230	0.367	0.004	0.272	0.047	0.013	-	-	-	-	0.352	-	-	0.093	-	0.280	-	-	-	1.860	-	-	-
Commelina erecta	-	0.088	0.007	-	-	-	0.005	-	-	-	-	-	-	0.009	-	-	-	-	-	0.029	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Commelina kotschyi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	-	-	0.164	-	0.010	-	-	6.344	-	0.027	-	0.115	0.509	0.360	-	1.347	0.107	-
Conyza albida	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-
Conyza sumatrensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Corbichonia decumbens	0.070	-	-	-	-	-	-	-	-	-	-	-	0.070	-	-	0.060	0.007	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	0.280	-	-	-
Corchorus asplenifolius	0.130	0.056	0.133	0.032	-	0.080	0.090	0.010	0.013	0.007	0.100	-	0.450	0.711	0.307	0.010	0.160	0.116	0.104	0.616	1.247	0.048	0.100	-	-	0.176	0.678	0.008	0.707	-	0.053	0.010	-	-	0.020	-	-	0.040
Corchorus confusus	-	0.008	-	-	-	-	0.005	-	0.067	-	-	0.160	-	-	-	-	-	0.080	-	0.011	-	0.008	0.244	0.427	0.030	0.152	-	0.160	-	0.080	-	0.530	0.291	0.310	-	0.284	0.453	-
Corchorus longepedunculatus	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	0.008	-	-	-	-	-	-	-	0.010	-	-	0.010
Crabbea velutina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.720	-	-	-	0.007	0.160	-	-	-	-	-	0.150	-	-	-	-	-	-	-	-	-	-	-
Crossandra mucronata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crotalaria pisicarpa	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-
Crotalaria senegalensis	-	-	0.007	-	0.253	0.400	0.055	-	-	0.007	0.010	-	-	-	-	0.010	-	-	-	0.011	0.007	0.024	0.044	-	-	-	-	-	-	-	-	0.095	-	-	-	-	-	-
Crotalaria sphaerocarpa subsp. *sphaerocarpa*	-	0.136	0.040	0.008	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	0.373	-	-	-	-	-	-	0.010
Cucumis metuliferus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-
Cucumis zeyheri	-	-	-	-	0.027	0.933	0.210	-	-	0.013	0.060	-	-	-	-	0.070	0.007	-	-	0.018	0.007	0.008	-	-	-	0.032	0.008	-	0.027	-	-	-	0.069	0.140	-	0.170	0.093	0.060
Cyamopsis dentata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyathula lanceolata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.720	-	-	-	-	-	-	0.510	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyathula orthacantha	0.045	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyperus involucratus	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyperus rotundus subsp. *rotundus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyphostemma subciliatum	0.010	-	-	-	-	-	-	0.070	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dactyloctenium aegyptium	-	-	-	-	-	-	-	-	-	-	1.170	0.107	0.030	-	0.013	0.010	-	-	-	0.004	-	-	-	-	-	0.008	-	-	0.013	-	-	-	-	-	-	-	-	-
Dactyloctenium giganteum	0.030	-	-	-	0.013	-	0.050	0.010	-	2.167	0.240	-	0.190	-	-	0.010	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Danthoniopsis pruinosa	-	0.416	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Decorsea schlechteri	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	0.009	-	0.040	0.447	0.064	0.172	-	-	-	-	-	-	-	-	0.200	-	-	-	0.191	-	0.100
Dicerocaryum eriocarpum	-	-	0.200	-	0.107	-	0.350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.000	-	-	-	-	-	-	-
Dichanthium annulatum	-	-	-	-	-	-	-	-	-	-	-	2.547	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.120	-	-	-	-	-	-	-	-
Dicliptera spinulosa	-	-	-	-	-	-	-	1.060	-	0.160	-	-	-	0.009	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicoma tomentosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.011	-	-	0.788	-	-	-	-	-	0.013	-	-	-	-	-	-	-	-	-
Digitaria eriantha	0.790	1.432	21.550	40.128	3.600	0.013	17.000	1.080	-	3.967	2.500	-	0.070	0.440	0.013	2.240	0.007	-	-	0.004	0.267	0.008	0.112	-	-	-	3.060	-	-	0.773	13.520	1.470	-	2.000	-	-	4.273	-
Digitaria sp.	-	-	-	-	-	-	-	0.010	-	-	0.020	-	-	0.013	-	-	0.047	-	-	0.309	0.007	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Dinebra retroflexa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-
Duosperma quadrangulare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.700	-	-	-	-	-	-	-	0.291	8.410	-	1.209	-	-
Echinochloa colona	-	-	-	-	-	-	-	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Elytraria acaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	0.036	0.040	-	0.180	0.120	0.064	0.258	0.573	-	-	0.013	-	-	0.091	-	-	-	-	-	-	-	-	0.027	-	0.010
Endostemon obtusifolius	0.210	-	-	-	-	-	0.005	0.150	0.080	0.240	0.030	-	-	0.267	-	-	0.027	-	0.088	0.782	1.100	-	-	-	-	0.048	0.058	-	-	-	-	-	-	-	0.020	-	-	2.610
Endostemon tenuiflorus	0.260	-	-	-	-	-	-	-	0.853	-	-	-	0.250	0.013	-	3.030	0.007	0.031	-	0.556	0.007	-	-	-	-	0.280	-	-	-	-	-	0.005	-	-	0.020	-	-	4.110
Enicostema axillare	-	-	-	-	-	-	-	-	-	-	-	0.107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.200	-	-	-	-	-	-	-	-
Enneapogon cenchroides	-	0.016	0.073	-	0.013	0.013	0.030	-	-	-	-	-	0.020	1.089	-	0.020	0.027	0.049	-	0.619	0.167	0.072	4.692	1.053	-	0.272	0.096	0.504	-	-	-	0.115	-	-	0.240	0.098	-	1.630
Enneapogon scoparius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.696	0.367	0.496	11.582	0.027	-	-	-	0.152	-	-	-	2.940	-	-	-	-	-	0.120
Enteropogon macrostachyus	0.010	0.392	-	-	-	-	-	-	-	-	-	-	-	0.062	-	0.150	0.013	0.160	0.056	2.596	0.020	-	0.028	0.267	-	-	0.058	-	-	-	-	-	-	-	4.300	-	-	-
Epaltes gariepina	-	-	-	0.496	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis aethiopica	0.030	0.056	-	-	-	-	-	-	-	-	-	-	0.060	-	-	0.260	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis aspera	0.260	-	-	-	-	-	-	-	-	-	-	-	0.010	0.098	-	-	0.007	-	-	0.007	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis cilianensis	0.010	-	-	-	-	-	-	-	-	-	0.080	-	0.070	0.018	-	0.090	0.007	0.004	0.016	0.015	-	-	-	-	-	0.112	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis ciliaris	-	-	-	-	-	-	-	-	-	-	-	-	0.060	-	0.080	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis cylindriflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis lehmanniana	-	-	1.503	0.008	2.413	-	3.305	-	-	-	-	-	-	-	-	-	-	0.164	4.544	-	0.292	-	-	-	-	0.144	0.225	-	-	-	-	-	-	-	-	-	-	-
Eragrostis rigidior	2.775	0.016	-	4.084	-	-	-	-	1.367	0.007	3.375	-	0.200	0.004	0.027	4.815	0.047	0.076	2.016	0.091	-	-	-	-	-	0.664	-	-	0.027	-	-	-	-	-	-	-	-	-
Eragrostis rotifer	-	-	-	-	-	-	-	-	-	-	0.150	-	-	-	-	-	-	-	0.344	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis sp.	-	0.144	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.040	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis superba	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-	0.007	-	-	-	2.090	-	-	-	0.030	-	0.490	-	-	-	-	0.865	-	-	-	-	-	-
Eragrostis trichophora	-	-	-	-	0.480	7.427	1.013	-	-	-	0.020	-	0.300	-	-	-	-	-	-	-	1.060	-	-	-	-	0.072	-	-	-	-	-	-	-	-	-	-	-	-
Eragrostis viscosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eriochloa fatmensis	-	-	-	-	-	-	-	-	-	-	-	0.107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eriochloa stapfiana	-	-	-	-	-	-	-	-	-	-	-	1.147	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Evolvulus alsinoides	0.030	0.176	-	0.008	-	-	-	-	-	-	-	-	0.020	0.036	0.667	0.110	0.040	0.018	0.008	0.019	0.061	0.024	0.024	-	-	0.072	0.016	0.048	0.107	-	-	0.010	-	-	-	-	-	0.070
Fuirena pubescens	-	-	-	2.528	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gisekia pharnaceoides var. *pharnaceoides*	-	0.016	-	-	-	-	0.155	-	-	-	0.070	-	0.020	-	-	-	-	-	-	-	-	-	-	-	-	0.240	-	-	-	-	0.013	-	-	-	-	-	-	-
Gloriosa superba	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heliotropium ciliatum	-	0.248	-	0.008	-	-	-	-	0.080	-	0.080	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.240	-	0.104	-	-	-	-	-	0.010	-	0.018	-	0.020
Heliotropium steudneri	-	-	-	-	-	-	-	-	-	0.013	-	-	0.200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heliotropium strigosum	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	0.008	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Hemizygia bracteosa	-	-	0.053	-	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-
Hemizygia elliottii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.240	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hermannia glanduligera	0.020	-	0.107	0.272	0.320	0.427	2.650	-	-	-	0.560	-	0.010	-	-	-	-	-	-	-	0.007	-	0.012	-	-	0.016	0.016	0.040	-	-	1.587	-	-	-	-	-	-	0.010
Hermbstaedtia odorata var. albi-rosea	-	-	0.007	-	1.280	0.560	0.670	-	0.253	0.027	0.380	-	0.010	-	0.280	0.160	0.067	0.062	0.288	0.025	-	-	-	-	-	0.664	-	-	0.013	-	0.200	-	-	-	-	-	-	-
Heteropogon contortus	-	0.024	-	-	-	-	-	-	-	-	-	0.747	-	-	0.013	-	-	0.027	-	3.462	1.284	22.144	7.474	-	-	-	1.538	0.616	-	-	-	3.940	-	-	-	-	0.120	1.910
Heteropogon melanocarpus	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hewittia scandens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.006	0.020	-	-	-	-
Hibiscus caesius	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hibiscus micranthus	0.080	0.016	0.013	0.008	0.013	0.187	0.005	-	-	-	-	-	-	0.084	0.280	0.040	0.147	0.196	0.296	0.187	0.153	0.128	0.068	0.093	0.010	0.048	0.082	-	-	-	-	0.065	-	-	0.220	0.004	-	0.040
Hibiscus physaloides	-	-	-	-	0.027	0.040	0.035	-	-	-	-	-	-	-	-	-	-	0.004	-	0.004	-	-	-	-	-	-	-	-	-	-	-	0.005	-	-	-	-	-	-
Hibiscus schinzii	-	-	0.060	-	-	-	-	-	-	-	0.070	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.080	-	0.109	-	-	-	-	-
Hibiscus sidiformis	-	0.024	-	-	-	0.013	0.005	-	-	0.020	0.010	-	-	0.018	-	0.010	-	-	0.016	0.011	0.033	0.008	0.024	-	0.010	0.016	-	-	-	-	-	0.010	-	-	0.020	0.004	-	0.060
Hibiscus trionum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	0.010	-	-	-	0.009	-	-
Hybanthus enneaspermus var. *enneaspermus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	0.064	-	-	-	-	0.017	-	-	0.004	-	-
Indigofera astragalina	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Indigofera brachynema	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.040	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.005	-	-	-	-	-	-
Indigofera daleoides var. *daleoides*	-	-	-	-	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	0.055	-	-	1.418	-	-	-	-	0.008	-	-	-	0.155	-	-	0.010	-	-	0.240
Indigofera delagoaensis	-	-	0.007	0.064	-	-	0.225	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Indigofera holubii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	0.028	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-
Indigofera lupatana	-	0.016	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Indigofera parviflora var. *crispidula*	-	-	-	-	-	-	0.035	-	-	-	-	-	-	-	-	-	-	-	0.016	-	-	-	-	-	-	-	-	0.008	-	-	0.013	-	-	-	-	-	-	-

Species	Vegetation type																																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Indigofera schimperi var. *schimperi*	-	-	-	-	-	-	-	-	-	-	-	0.080	-	-	-	-	0.047	0.004	-	-	0.027	-	0.392	0.040	-	-	-	0.288	-	-	-	0.030	0.331	0.230	-	1.289	-	0.640
Indigofera trita subsp. *subulata*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	1.507	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Indigofera viciodes	-	0.008	0.027	0.008	-	-	0.005	-	-	-	-	-	-	0.009	-	0.030	0.020	0.004	-	0.037	0.147	0.032	-	-	-	-	0.025	-	0.067	-	-	-	-	-	0.010	-	-	0.260
Ipomoea coptica var. *coptica*	0.080	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ipomoea coscinosperma	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.212	-	0.010	-	-	0.048	-	-	-	0.030	0.034	0.540	-	0.022	0.187	-
Ipomoea dichroa	-	-	-	-	0.027	-	0.010	-	-	-	-	-	-	0.009	-	0.010	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	0.005	-	-	0.010	-	-	-
Ipomoea lapathifolia	-	-	-	-	-	-	-	-	-	-	-	0.093	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.053	-	-	0.034	-	-	-	0.133	-
Ipomoea pes-tigridis	-	0.008	0.007	0.024	0.040	0.013	0.150	-	-	0.047	-	-	-	0.009	-	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	0.067	0.005	-	-	0.050	-	-	-
Ipomoea plebeia subsp. *africana*	0.010	-	-	-	-	-	-	0.010	0.013	-	-	-	-	0.049	-	-	-	0.004	-	0.196	0.401	0.056	0.004	-	-	0.080	0.200	-	0.027	-	-	0.005	-	-	0.020	-	-	-
Ipomoea shirambensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.049	-	-	-	-	-	-	-	-	-	-	-	-	-	0.180	-	-	-
Ipomoea sinesis subsp. *blepharosepala*	-	-	-	0.032	-	-	-	-	-	0.007	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	-	0.032	-	-	-	-	-	0.040	-	-	0.020	-	-	0.020
Ischaemum afrum	-	-	-	-	-	-	-	-	-	-	-	14.120	-	-	-	-	-	-	-	-	-	-	-	0.160	-	-	-	-	-	32.973	-	0.820	-	1.380	-	-	1.173	-
Jacquemontia tamnifolia	0.010	0.016	-	0.008	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Jamesbrittenia micrantha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.180	-	-	-	-
Jatropha campestris	-	-	-	-	-			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.224	-	0.020	-	-	0.008	-	-	-	0.035	0.006	0.020	-	0.053	0.080	-
Jatropha sp.						0.013	0.045																															
Justicia anagalloides	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.147	-	-	-	0.080	-	-	-	-	0.011	0.010	-	-	-	-
Justicia flava	0.790	-	-	0.032	-	-	0.100	0.020	0.027	0.560	0.750	-	0.050	0.253	0.240	0.720	1.047	0.431	0.352	0.091	0.327	-	-	0.107	-	0.040	0.008	-	0.013	-	-	-	-	-	-	-	-	-
Justicia matammensis	0.010	-	-	-	-	-	0.005	-	-	0.107	0.010	-	0.030	0.093	-	0.010	0.013	0.009	0.008	0.077	0.053	-	-	-	-	0.176	0.008	-	0.027	-	-	-	-	-	0.350	-	-	-
Justicia striata subsp. striata	-	0.536	-	-	-	-	-	-	-	0.020	-	-	-	0.036	-	-	-	-	-	0.042	0.027	0.040	-	-	-	-	0.008	-	-	-	-	0.015	-	-	-	-	-	-
Kalanchoe lanceolata	0.170	0.064	-	-	-	-	-	-	0.013	0.093	0.260	-	0.210	0.004	-	-	0.113	0.027	0.056	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Kohautia virgata	0.100	-	-	0.024	-	-	-	-	-	-	0.060	-	0.040	0.089	-	0.050	0.053	0.009	0.024	0.069	-	0.008	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-	-	-
Kyllinga alba	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.070	-	-	-	-	-	-	-	-	-	0.616	-	-	-	-	-	-	-	-	-	-	-	-
Kyphocarpa angustifolia	-	0.312	-	-	-	-	-	-	-	-	-	-	-	-	-	0.030	-	-	-	0.015	0.020	-	-	-	-	0.096	-	-	-	-	-	-	-	-	-	-	-	-
Lagenaria sphaerica	-	-	-	-	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Laggera decurrens	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.070	-	-	-
Launaea cornuta	-	-	-	-	-	-	-	-	0.040	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	0.013	0.040	-	-	0.048	-	0.093	-	0.080	-	2.470	-	-	0.013	-
Lepidagathis scabra	0.450	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.150	0.040	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.180	-	-	-
Leptocarydion vulpiastrum	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Leptochloa chinensis	-	-	-	-	-	-	-	0.200	-	-	-	-	-	-	-	-	-	-	0.016	-	-	-	-	-	0.030	-	-	-	-	-	-	-	-	-	-	-	-	-
Leucas glabrata var. *glabrata*	0.520	-	0.253	0.016	0.187	8.573	2.235	-	-	-	0.500	-	0.850	0.587	-	0.010	0.260	0.111	0.280	0.018	-	-	-	-	-	-	-	0.072	-	-	0.013	-	-	-	-	-	-	-
Lintonia nutans	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	2.544	-	-	-	-	0.457	-	-	2.460	-	-
Lippia javanica	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	0.192	0.004	-	-	0.024	-	-	-	-	-	-	-	-	0.065	-	-	-	-	-	-
Mariscus sumatrensis	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-	-	-	-
Marsdenia macrantha	-	-	-	0.008	-	0.013	0.155	-	0.013	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Megalochlamys revoluta subsp. *cognata*	1.230	-	-	-	-	-	-	-	-	-	-	-	-	0.169	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melhania acuminata	0.060	0.304	0.013	0.024	0.347	1.107	1.240	-	-	0.140	0.090	-	-	0.653	0.333	0.110	0.400	0.631	0.536	1.211	0.574	0.512	0.296	0.027	-	0.016	0.659	-	-	-	-	0.533	-	-	0.080	0.004	-	0.600
Melhania sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010
Melhania sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.084	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melinis repens	-	0.624	0.007	-	-	-	-	-	-	-	-	-	-	0.004	-	0.080	0.013	-	-	0.320	-	-	0.128	0.013	-	-	0.074	0.080	-	-	-	0.025	0.006	-	-	0.222	-	0.680
Melinis tenuissima	0.060	0.016	0.007	0.408	0.013	0.267	0.690	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.040	-	-	-	-	-	-	-
Merremia kentrocaulos	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	0.107	-	0.228	-	0.070	0.016	0.158	0.200	-	-	-	0.200	-	-	-	0.107	-	-
Merremia pinnata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Merremia tridentata	-	-	-	0.016	0.053	-	0.040	-	-	-	0.020	-	-	-	0.013	-	-	-	0.008	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Momordica balsamina	-	-	0.007	0.016	-	-	0.100	-	-	-	-	0.080	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.053	-	-	-	-	-	-	-	-	-
Monechma debile	-	-	-	-	0.080	0.253	0.065	-	-	-	-	-	-	0.173	-	-	0.007	0.004	-	0.051	0.027	-	0.160	0.120	-	-	-	-	-	-	-	0.010	-	-	0.130	0.284	-	-
Neorautanenia brachypus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.284	-	-	-	-	0.400	-	-	-	0.070	0.069	0.150	-	0.462	0.173	-
Nidorella resedifolia subsp. *microcephala*	0.020	-	-	-	-	-	-	-	-	-	0.690	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ocimum americanum var. *americanum*	0.110	-	-	-	-	-	-	-	0.013	-	0.260	-	0.040	-	-	-	-	0.009	0.056	0.025	0.027	-	-	-	-	-	0.008	-	-	-	-	0.005	-	-	-	-	-	-
Ocimum gratissimum subsp. *gratissimum*	0.060	-	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.707	-	-	-	-	-	-	-	-	-
Ocimum obovatum	0.250	-	-	-	-	-	-	-	0.013	-	-	-	0.570	0.058	-	-	-	-	-	0.004	-	0.016	0.080	-	-	0.008	-	1.176	0.013	-	-	0.005	-	-	-	-	-	0.270
Oropetium capense	-	0.968	0.013	-	-	-	-	-	-	-	-	-	0.020	0.076	-	0.370	0.087	0.178	0.008	0.011	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Otoptera burchellii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-
Oxygonum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.573	-	-	-	-	-	-	-
Panicum coloratum	-	-	-	-	-	-	-	-	-	-	-	10.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Panicum maximum	9.820	1.736	10.287	7.936	7.247	0.387	6.523	28.665	3.427	47.217	1.740	0.600	11.850	0.031	0.800	0.390	0.007	10.542	9.720	2.097	1.148	1.240	-	5.173	7.050	0.592	4.973	-	11.767	0.787	0.973	7.223	20.311	2.270	14.840	3.591	9.160	-
Pavonia leptocalyx	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pavonia procumbens	0.230	-	-	0.008	-	0.533	0.010	-	-	-	-	-	-	0.142	0.027	-	0.040	0.004	0.128	0.325	0.353	0.016	0.492	0.027	-	-	0.450	-	-	-	0.013	0.075	-	-	0.110	-	-	-
Pergularia daemia var. *daemia*	-	-	-	0.008	-	-	-	-	-	0.053	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Perotis patens	-	-	0.493	0.016	0.507	-	0.700	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.373	-	-	-	-	-	-	-
Phyllanthus maderaspatensis	-	-	0.007	0.008	0.027	0.013	0.025	-	0.013	-	0.030	0.120	-	0.031	0.013	-	0.020	0.022	-	0.113	0.053	-	0.056	0.053	0.310	-	0.016	0.352	0.107	0.507	-	0.080	-	0.130	-	0.142	0.080	0.090
Phyllanthus parvulus var. *parvulus*	-	0.112	-	0.032	-	-	-	-	0.027	0.013	-	-	-	0.089	0.013	0.040	0.053	0.004	0.008	0.204	0.227	0.104	0.740	0.173	-	0.056	0.171	0.032	0.013	-	0.067	0.150	0.080	0.330	0.050	0.284	0.240	0.190
Plumbago zeylanica	-	-	-	-	-	-	-	0.140	-	0.907	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.056	-	-	-	-	-	-	-	-	-	-	-	-
Pogonarthria squarrosa	0.210	2.064	1.553	1.112	17.173	-	1.605	-	-	-	-	-	-	-	-	-	-	-	0.208	0.004	-	-	-	-	-	-	-	-	-	-	5.040	-	-	-	-	-	-	-
Polygala erioptera subsp. *erioptera*	-	0.032	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.080	0.011	0.208	-	0.008	0.240	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Portulaca foliosa	-	-	-	-	-	-	-	-	-	-	-	-	0.030	-	-	-	-	-	-	-	-	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-
Portulaca kermesina	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	0.240	-	0.027	-	-	-	-	-	-	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-
Pupalia lappacea var. *velutina*	1.240	0.064	0.253	0.344	2.333	18.453	3.535	0.560	0.307	1.413	0.550	-	3.140	3.524	0.080	1.270	6.310	1.987	1.192	3.287	4.787	-	0.120	1.133	0.010	2.256	1.209	-	0.013	-	0.760	0.590	0.749	0.190	1.720	0.342	-	-
Pyrenacantha kaurabassana	-	-	0.087	-	0.080	-	-	-	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Raphionacme monteiroae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rhynchosia albissima	-	-	-	-	-	-	-	-	-	-	-	1.240	-	-	-	-	-	-	0.008	-	-	-	-	0.053	-	-	-	-	-	1.800	-	0.600	0.480	1.870	-	0.009	5.160	-
Rhynchosia minima	-	-	-	-	-	-	-	-	-	0.007	-	-	-	0.196	-	-	-	-	0.008	0.568	0.860	0.296	2.720	-	0.010	-	0.083	-	-	-	-	0.915	-	-	-	0.027	-	0.370
Rhynchosia totta var. fenchelii	-	-	-	-	0.173	-	-	-	-	-	-	-	-	-	-	-	0.020	-	0.016	0.207	0.280	0.056	0.004	-	-	-	0.250	-	-	-	-	-	-	-	-	-	-	0.060
Rottboellia cochinchinensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.064	-	-	-	-	0.954	3.200	-	2.360	7.347	-
Ruellia bignoniiflora	-	-	-	-	-	-	0.005	-	-	-	-	-	-	0.004	-	-	-	-	0.008	0.091	0.087	-	0.136	-	-	-	-	-	-	-	-	0.090	-	-	0.010	-	-	-
Ruellia patula	0.540	-	0.027	0.064	-	0.147	0.005	-	0.480	-	0.030	-	1.740	0.402	0.040	0.370	0.433	0.107	0.632	0.440	1.395	0.072	0.028	-	-	0.152	0.138	-	0.013	-	-	0.030	-	-	-	0.004	-	-
Ruspolia decurrens	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.140	-	-	-
Sansevieria hyacinthoides	-	-	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-
Schmidtia pappophoroides	-	2.872	3.893	0.208	1.347	-	-	-	-	-	-	-	-	-	0.267	-	-	-	0.904	0.138	-	-	1.860	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.070
Secamone parvifola	-	-	-	-	-	-	0.035	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Seddera suffruticosa var *suffruticosa*	-	-	-	-	-	-	-	-	-	-	-	-	-	0.276	-	0.010	0.147	0.013	-	0.418	0.133	0.024	1.680	-	-	-	-	-	-	-	-	0.290	-	-	-	-	-	0.050
Seddera suffruticosa var. *hirsutissima*	-	-	-	-	-	-	-	-	-	-	0.010	-	-	0.018	0.227	-	0.053	0.013	0.008	0.007	0.301	-	-	-	-	0.016	0.040	-	0.013	-	-	0.040	-	-	-	-	-	-
Sehima galpinii	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.742	0.013	0.060	-	-	31.540	-	-	-	0.010	19.254	20.945	-	18.398	9.460	0.080
Selaginella dregei	-	3.308	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sesamum alatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sesbania leptocarpa	-	-	-	-	-	-	-	-	-	-	-	0.333	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sesbania tetraptera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Setaria incrassata	-	-	-	-	-	-	-	-	-	-	-	4.640	-	-	-	-	-	-	-	-	-	-	0.072	0.080	0.270	-	-	-	-	36.393	-	0.205	0.223	2.990	-	0.524	32.920	-
Setaria sagittifolia	0.010	0.072	-	-	-	0.053	0.005	0.370	-	0.353	0.150	-	0.010	1.378	-	0.050	-	0.333	-	0.048	-	-	-	0.013	-	0.056	0.008	-	-	-	-	-	-	-	0.150	-	-	-

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Sida alba	0.080	-	-	-	0.013	0.080	0.030	-	-	-	0.050	0.067	0.030	0.062	-	0.050	-	0.004	-	0.037	0.013	0.056	0.072	-	0.020	0.004	0.008	-	0.013	0.040	-	0.078	0.006	0.040	-	-	0.027	0.010
Sida cordifolia	0.120	-	0.007	0.168	-	-	0.290	-	0.080	-	0.070	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.760	-	-	-	-	-	-	-
Sida hoepfneri	-	-	0.047	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solanum catombelense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.100
Solanum incanum	0.090	-	0.053	0.024	-	-	-	0.010	-	0.053	-	0.120	-	0.258	0.253	0.030	-	0.080	-	0.229	-	-	0.004	-	0.040	-	0.088	-	-	-	0.080	0.255	0.080	0.020	0.010	-	0.133	-
Solanum nigrum	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorghum bicolor	-	-	-	-	-	-	-	0.090	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.080	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sorghum versicolor	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	0.098	0.013	0.032	2.672	0.013	-	-	-	0.304	-	-	-	0.040	-	0.010	-	0.191	0.093	0.130
Spaeranthus peduncularis	0.060	-	-	-	-	-	-	0.090	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Spermacoce arvensis	0.090	0.072	0.453	0.040	0.707	0.493	0.820	-	-	-	1.290	-	0.010	0.022	-	0.030	-	-	0.120	0.004	-	-	-	0.013	-	0.008	-	-	-	-	0.200	-	-	-	-	-	-	-
Sporobolus africanus	-	-	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sporobolus consimilis	-	-	-	-	-	-	-	-	-	-	-	22.180	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sporobolus fimbriatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.022	0.460	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	-
Sporobolus iocladus	-	-	-	-	-	-	-	-	-	-	-	10.680	-	-	-	-	-	3.240	3.480	-	-	-	-	-	-	-	-	-	3.520	-	-	-	-	-	-	-	-	-
Sporobolus panicoides	-	-	-	-	-	-	-	-	-	-	-	-	-	0.062	-	2.430	0.033	-	-	0.040	-	-	-	-	-	-	0.280	-	-	-	-	-	-	-	-	-	-	0.030
Sporobolus stapfianus	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	0.040	0.080	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stapelia gigantea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia forbesii	-	-	0.053	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia longipes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.777	-	-	-	-	0.155	-	-	-	-	-	-
Tephrosia purpurea	-	0.200	-	0.032	-	-	0.730	-	-	0.013	0.020	0.013	0.130	0.049	1.693	0.140	0.067	-	0.024	0.022	-	-	-	-	0.040	0.512	-	-	-	-	0.067	-	-	-	0.030	-	0.013	0.340
Tephrosia purpurea subsp. *leptostachya*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tephrosia purpurea subsp. *leptostachya var. pubescens*	0.130	-	1.000	0.088	0.267	0.040	0.320	-	-	-	0.230	-	0.210	0.018	-	0.020	-	0.053	-	0.116	0.167	0.280	0.088	-	-	0.296	0.381	-	0.133	-	0.013	0.035	-	-	-	0.004	-	0.510
Tephrosia uniflora subsp. *uniflora*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.320
Tephrosia villosa subsp. *ehrenbergiana*	-	-	-	-	-	-	-	-	-	-	-	-	-	0.058	-	0.190	-	-	-	0.247	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.960
Tetrapogon tenellus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.173	-	-	0.007	-	-	0.265	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tragia okanyua	-	-	-	-	-	0.987	0.225	-	-	-	-	0.133	0.010	-	-	-	-	-	-	0.040	-	0.096	-	0.213	-	-	0.281	0.008	-	-	-	0.100	-	-	-	-	-	0.020
Tragus berteronianus	0.020	0.040	0.040	0.008	-	-	0.045	-	-	-	0.260	-	0.220	0.013	0.160	0.110	0.020	0.027	0.024	0.011	0.007	-	-	0.040	-	0.168	-	-	-	-	0.027	-	-	-	-	-	-	0.020
Tribulus terrestris	0.010	-	-	-	-	-	0.005	-	-	-	0.200	-	0.010	0.004	0.027	-	-	-	-	-	-	-	-	-	-	0.032	-	-	-	-	-	-	-	-	-	-	-	-
Trichodesma zeylanicum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	0.004	0.013	0.008	0.024	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-
Tricholaena monachne	-	0.216	0.737	0.488	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.756	-	-	1.412	-	-	-	0.964	-	-	-	2.427	0.005	0.320	-	-	-	-	-
Tridax procumbens	0.010	-	-	-	-	-	-	-	-	-	0.010	-	-	0.027	-	-	0.007	-	-	0.004	0.007	-	-	-	-	-	-	-	-	-	-	0.010	0.006	0.010	-	0.004	-	-
Tripogon minimus	-	-	-	-	-	-	-	-	-	-	-	-	-	0.004	-	1.150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Triumfetta pentandra	-	0.096	0.020	0.048	-	0.333	0.390	-	-	0.027	0.010	-	0.050	0.124	-	0.330	0.040	-	-	0.089	0.020	-	-	-	-	0.096	-	-	-	-	0.067	-	-	-	0.100	-	-	-
Urochloa mosambicensis	7.495	0.104	1.333	3.632	36.393	2.160	15.468	4.510	75.960	4.680	19.615	-	5.210	-	46.480	0.070	0.100	25.002	5.480	7.278	12.453	40.604	5.564	0.133	53.540	29.328	60.716	0.008	63.153	0.093	0.013	45.258	21.043	0.060	5.410	1.653	9.747	5.720
Urochloa oligotricha	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.016	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Urochloa panicoides	-	-	-	-	-	-	-	-	-	-	0.730	-	0.050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.005	0.006	-	-	-	-	-
Vernonia poskeana	-	0.144	-	0.016	-	-	-	-	-	-	-	0.013	0.010	-	0.027	0.030	-	-	0.016	0.156	-	0.016	0.296	0.080	0.120	-	0.050	0.184	-	-	-	0.055	0.086	0.220	-	0.169	0.147	-
Vernonia steetziana	-	0.016	0.093	0.008	0.240	-	0.065	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.747	-	-	-	-	-	-	-
Vigna unguiculata subsp. *dekindtiana*	-	0.016	0.093	0.024	0.120	0.267	0.315	-	-	-	-	-	-	-	-	-	-	-	0.008	0.053	0.013	-	-	-	-	-	-	-	-	-	0.053	0.010	-	-	0.010	-	-	-
Vigna vexillata var. *angustifolia*	-	-	-	-	-	-	-	-	-	-	-	0.027	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Waltheria indica	0.080	0.552	0.648	0.712	0.840	0.027	0.835	-	-	0.013	-	-	0.130	0.169	-	0.300	-	-	0.016	0.004	-	-	-	0.013	-	-	-	-	-	-	5.173	-	-	-	-	-	-	-
Withania somnifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.080	-	-	-	-	-	0.020	-	-	-
Zaleya pentandra	-	-	-	-	-	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Zehneria minutiflora	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.060	-	-	-	-	-	-	-	-	-	-	-	-	-
Zornia glochidiata	0.010	0.136	-	0.008	-	-	-	-	-	-	-	-	0.010	-	-	0.070	-	-	-	-	-	-	-	-	-	0.080	-	-	-	-	0.053	-	-	-	-	-	-	-

3.3.2. *Vegetation mapping and accuracy assessment*

The map of the vegetation types is shown in Figure 3.2.

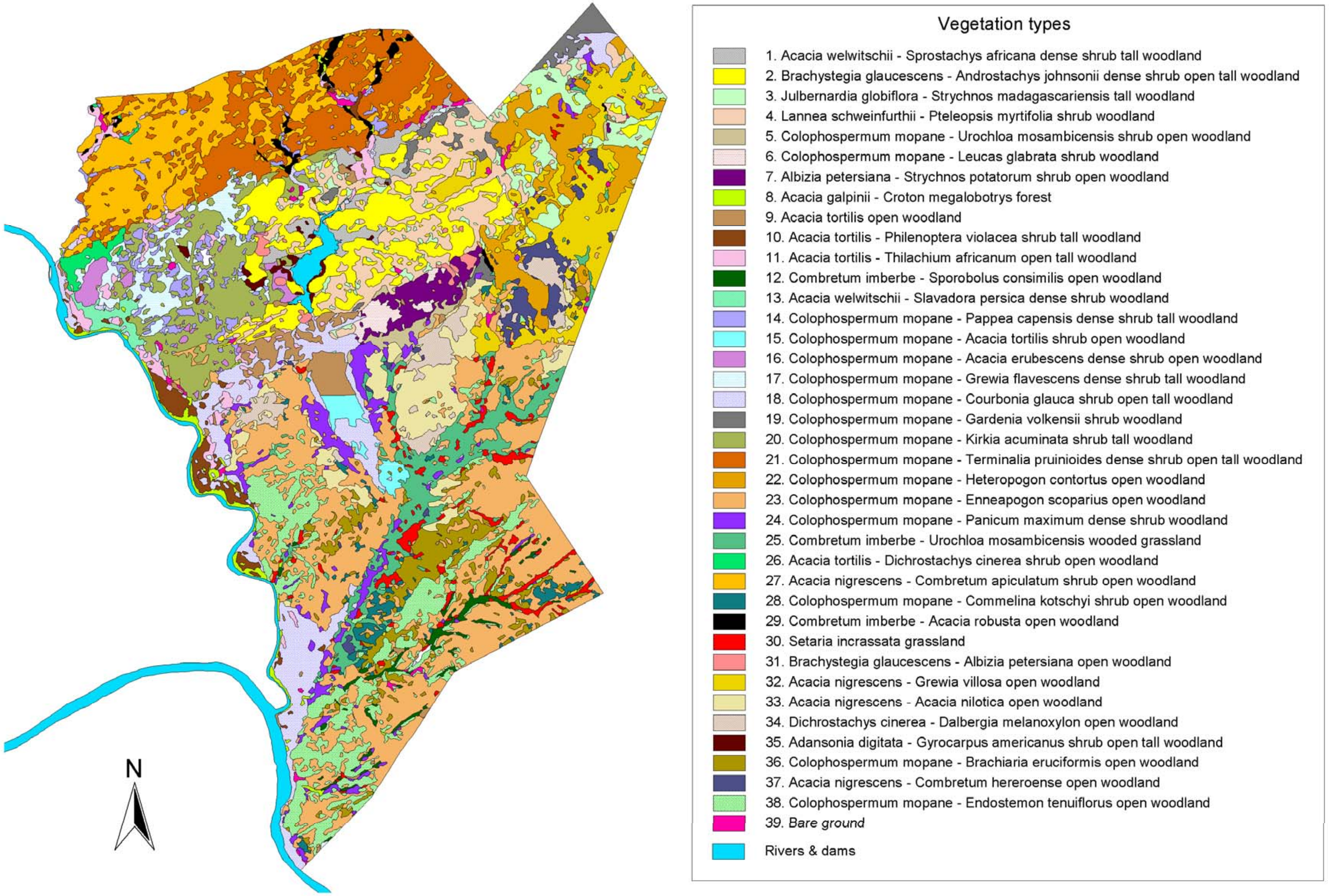


Figure 3.2 Vegetation map of Malilangwe Wildlife Reserve.

The total proportional error for the map was 0.1 with a 99 % confidence interval of ± 0.02 (Table 3.4).

Table 3.4 Error matrix describing the accuracy of the vegetation map. Columns represent the ground truth data, and the rows the mapped data. Error of omission describes the proportion of sample points that have been mistakenly excluded from a vegetation type, and error of commission describes the portion that has been mistakenly included in a vegetation type. The total proportional error for the map is given in the bottom right hand corner of the matrix

		Vegetation types from ground truth data																																						Total no. sample pnts.	Error of commission
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38		
Vegetation types from map	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
	1	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	25	0.04
	2	0	24	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0.04
	3	0	0	20	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	24	0.17
	4	0	0	4	40	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	45	0.11
	5	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	27	0.07
	6	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0.00
	7	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0.00
	8	0	0	0	0	0	0	0	27	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0.04
	9	0	0	0	0	0	0	0	0	46	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	47	0.02
	10	0	0	0	0	0	0	0	0	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48	0.00
	11	0	0	0	0	0	0	0	0	1	1	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	0.05
	12	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0.00
	13	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0.00
	14	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0.38
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49	0.00
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	26	0.04
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0.19
	18	0	0	0	0	0	0	0	2	2	0	2	0	0	0	1	0	0	50	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	0.14
	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0.00
	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	28	0.11
	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	30	0.07
	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	41	0.07
	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51	2	1	0	0	1	0	1	0	0	1	0	0	2	0	0	59	0.14
	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	0.02
	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53	0	0	0	0	30	0	0	0	0	0	0	0	0	83	0.36
	26	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	28	0.11
	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	22	0.05
	28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0	0	0	10	0	0	25	0.40
	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	0	0	24	0.00
	30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	15	0	0	0	0	0	1	0	0	18	0.17
	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	24	0.00
	32	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	51	1	0	0	0	0	0	54	0.06
	33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	46	9	0	0	0	0	56	0.18
	34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	36	0	0	0	0	45	0.20
	35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	16	0.00
	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	7	0	3	0	0	0	0	0	40	0	2	54	0.26
	37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	24	0	25	0.04
	38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	55	57	0.04
	40	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1.00
Total no. sample pnts.		25	24	24	45	25	25	30	30	49	50	41	25	30	11	50	25	19	50	20	25	29	40	55	63	55	25	23	23	25	50	25	55	57	45	20	53	24	57	1347	
Error of omission		0.04	0.00	0.17	0.11	0.00	0.00	0.00	0.10	0.06	0.04	0.15	0.00	0.00	0.27	0.02	0.00	0.32	0.00	0.05	0.00	0.03	0.05	0.07	0.10	0.04	0.00	0.09	0.35	0.04	0.70	0.04	0.07	0.19	0.20	0.20	0.25	0.00	0.04		0.1039

3.3.3. *Topo-edaphic environment*

There was substantial variation in topo-edaphic conditions at Malilangwe. The primary gradient, as identified by the first two components of the PCA of the topo-edaphic variables (accounting for 52.2 % of the variance), was represented by changes in total available moisture, soil texture and base status, with pH, conductivity, Mg, Ca, and K positively correlated with high clay, silt, and available moisture and negatively correlated with sand (Figure 3.3). The transition from shallow soils with high rock and gravel cover on steep slopes to deep soils on low lying topographical positions formed a secondary gradient.

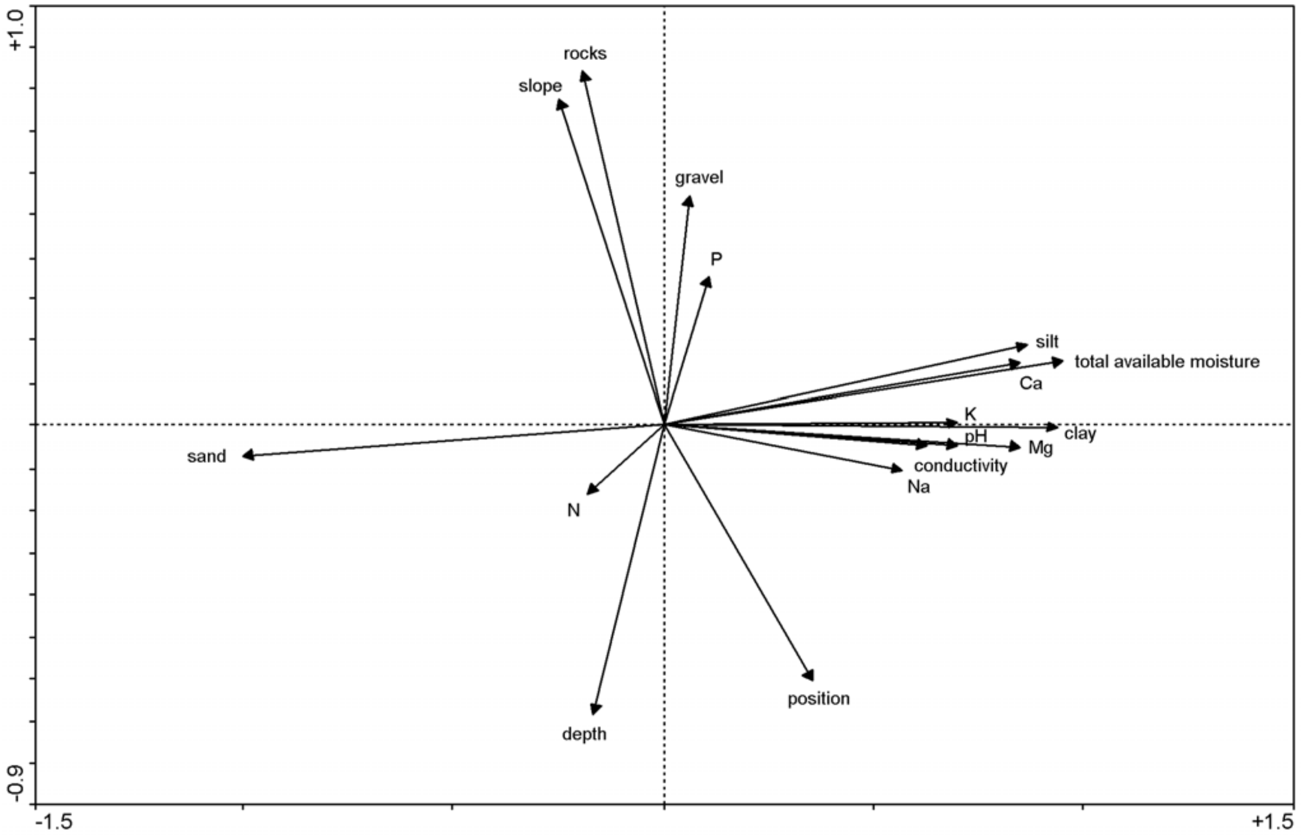


Figure 3.3 The first two axes of a correlation-type PCA of the topo-edaphic variables (eigenvalues: axis 1 = 0.375, axis 2 = 0.147; 52.2 % of the variance).

The first run of a DFA showed that the environmental conditions of the *Brachystegia glaucescens* – *Androstachys johnsonii* dense shrub open tall woodland that occurred on sandstone outcrops with steep slopes and very high rock cover, and the *Combretum imberbe* – *Sporobolus consimilis* open woodland that occurred on soils with a very high sodium content were markedly different from those of the other vegetation types. To more clearly represent topo-edaphic conditions in the remaining vegetation types, these two were deleted and the analysis re-run. The second analysis showed that the topo-edaphic environment differed between types, with clear separation in most cases (Figure 3.4). Descriptions of the topo-edaphic environment for each vegetation type are provided below in the section where each vegetation type is described. The sum of all unconstrained eigenvalues (35.0) was much larger than the sum of all constrained eigenvalues (4.567) indicating that important environmental variables had been omitted. Despite this, tests of the first DFA axis and all DFA axes together were significant (P<0.001). This showed that the measured topo-edaphic variables explained a significant, albeit low, proportion of the variation. An important feature was the presence of high eigenvalues for up to eight axes (Table 3.5). This indicated that differences in vegetation types were not represented by a few primary gradients, but by many smaller, independent gradients.

Table 3.5 Summary of discriminant function analyses (DFA) for vegetation types of Malilangwe: a) DFA – all communities included, axes 1-4, b) DFA – all communities included, axes 5-8, c) DFA – two communities deleted, axes 1-4, d) DFA – two communities deleted, axes 5-8

		Axis order			
		1	2	3	4
a)	DFA – all vegetation types, axes 1-4				
	Eigenvalue	0.890	0.852	0.786	0.643
	Species-environment correlation	0.943	0.923	0.887	0.802
	Cumulative percent variance of:				
	Species data	2.4	4.7	6.8	8.6
	Species environment	17.0	33.2	48.2	60.5
b)	DFA – all vegetation types, axes 5-8				
	Eigenvalue	0.458	0.427	0.324	0.291
	Cumulative percent variance of:				
	Species data	1.4	2.6	3.6	4.4
c)	DFA – deleted veg. types, axes 1-4				
	Eigenvalue	0.886	0.830	0.596	0.493
	Species-environment correlation	0.941	0.911	0.772	0.702
	Cumulative percent variance of:				
	Species data	2.5	4.9	6.6	8.0
	Species environment	19.4	37.5	50.5	61.3
d)	DFA – deleted veg. types, axes 5-8				
	Eigenvalue	0.401	0.346	0.306	0.263
	Cumulative percent variance of:				
	Species data	1.2	2.3	3.3	4.1

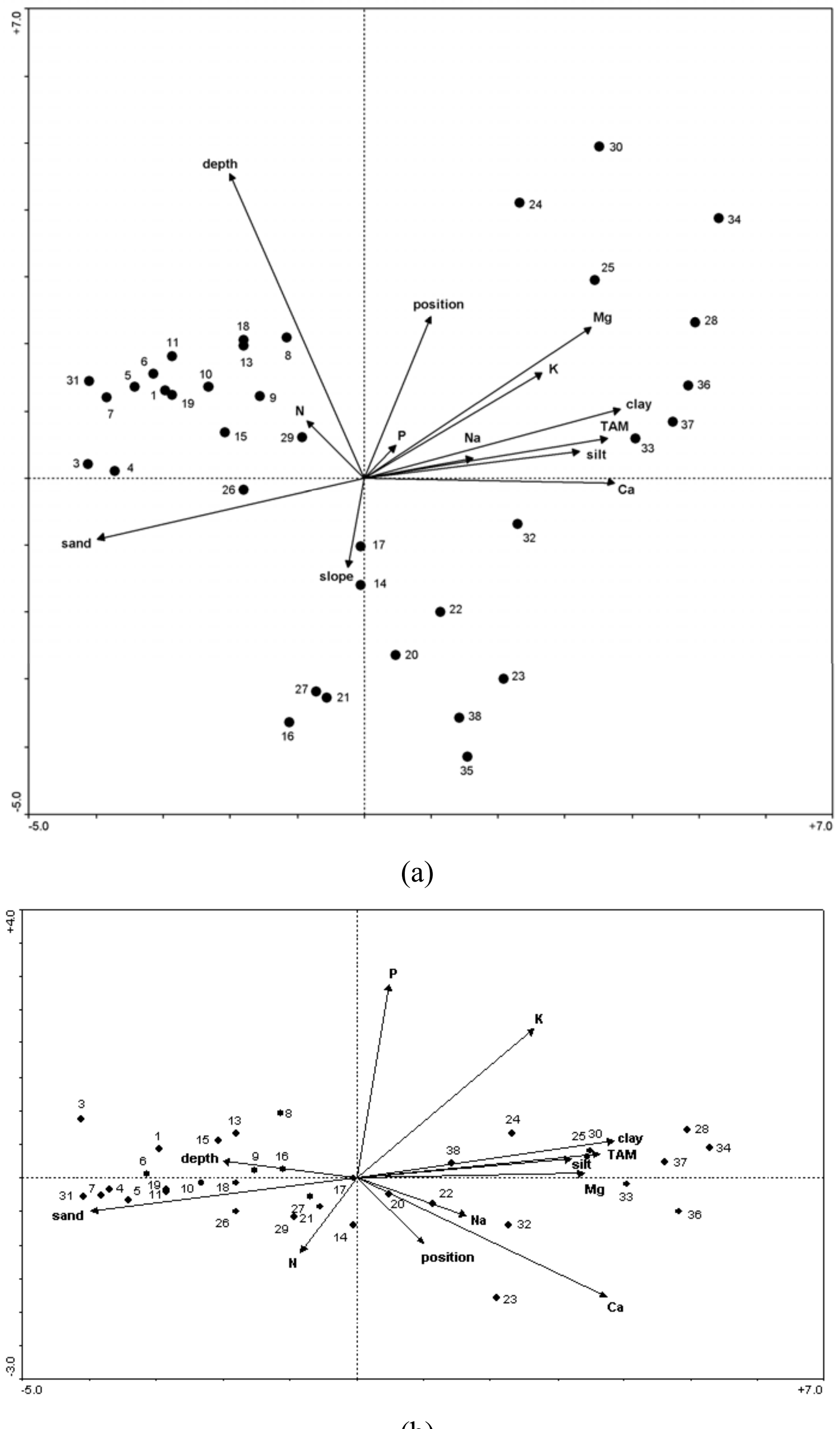
The vegetation types differed ($P<0.01$) for all of the topo-edaphic variables (Table 3.6) and for the woody canopy volume (m^{3}ha^{-1}) in each of the four height classes (Table 3.7). However, differences were sometimes due to only a few vegetation types.

Table 3.6 Mean value of topo-edpahic variables for each vegetation type (see Figure 3.1 for a key to type numbers). Sample sizes are given in parentheses below the types

Topo-edaphic variable	Vegetation type																																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
	(4)	(5)	(6)	(5)	(3)	(3)	(8)	(4)	(3)	(6)	(4)	(3)	(4)	(9)	(3)	(4)	(6)	(9)	(5)	(11)	(6)	(5)	(10)	(3)	(4)	(5)	(5)	(5)	(3)	(3)	(3)	(8)	(7)	(4)	(4)	(9)	(3)	(4)
Sand (%)	79.0	90.8	89.7	90.4	89.3	88.7	90.5	71.0	78.0	84.7	85.0	54.0	72.0	76.7	80.7	80.5	75.0	75.8	85.6	74.2	75.7	70.0	66.2	58.7	56.0	82.0	76.4	45.6	80.7	50.7	90.7	61.0	44.9	42.0	66.5	47.1	44.0	67.5
Silt (%)	11.0	4.4	6.3	3.2	2.7	3.3	4.5	13.5	9.3	5.7	6.5	14.7	9.0	7.3	6.7	6.5	7.0	7.1	4.0	9.6	8.7	13.2	13.4	10.7	18.0	6.8	6.8	17.2	6.0	18.0	2.7	13.0	14.9	16.5	11.0	17.8	16.0	16.0
Clay (%)	10.0	4.8	4.0	6.4	8.0	8.0	5.0	15.5	12.7	9.7	8.5	31.3	19.0	16.0	12.7	13.0	18.0	17.1	10.4	16.2	15.7	16.8	20.4	30.7	26.0	11.2	16.8	37.2	13.3	31.3	6.7	26.0	40.3	41.5	22.5	35.1	40.0	16.5
pH	5.6	5.6	5.7	5.5	5.6	5.9	5.5	5.8	5.9	5.4	5.9	8.4	5.7	6.9	6.1	5.4	6.8	6.4	6.1	6.6	6.4	6.3	7.4	6.9	6.9	6.1	6.0	6.7	6.2	7.1	5.3	6.8	7.2	6.6	5.7	7.1	6.2	6.6
Conductivity (µS cm^{-1})	45.5	51.0	50.2	42.4	47.3	56.3	46.8	79.3	84.0	79.2	53.8	574.3	94.5	120.7	63.7	43.5	123.8	130.2	42.8	119.5	81.2	144.4	150.2	99.3	83.5	120.0	44.8	126.6	102.7	136.0	18.7	148.1	161.3	155.8	95.3	164.9	121.3	123.5
Gravel (%)	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.8	0.9	0.0	3.3	0.8	0.0	0.0	0.7	0.2	0.7	0.9	0.5	0.2	0.4	0.1	0.2	0.1	0.1	0.0	1.0	0.0	0.0	3.7	0.3	0.1	2.0
Rocks (%)	0.1	43.2	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	3.7	0.3	0.0	0.0	6.2	6.2	0.2	0.0	0.2	0.0	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	10.9	0.0	0.0	11.4
Slope	1.9	14.3	3.2	1.2	0.6	1.6	1.1	2.8	1.4	0.5	0.2	0.6	1.0	0.9	1.7	1.8	0.7	0.7	1.2	1.3	0.8	0.6	0.2	0.7	0.0	0.6	1.7	0.9	0.2	0.6	0.7	0.8	0.8	1.2	12.2	0.4	0.3	2.6
Depth (cm)	125.0	11.4	116.7	110.8	125.0	125.0	125.0	125.0	110.6	116.4	125.0	123.7	125.0	53.3	105.0	19.4	60.3	125.0	117.3	34.7	31.1	31.3	25.2	125.0	96.7	83.0	35.5	74.4	89.2	116.5	125.0	56.8	67.1	107.4	13.6	66.8	64.9	17.0
Position (mean rank)	3.5	1.0	2.8	3.2	4.3	5.0	4.0	4.8	4.3	4.7	5.0	6.0	4.5	4.3	5.0	4.5	4.0	4.6	4.2	3.2	3.5	5.0	3.5	5.0	5.0	4.6	3.6	5.0	5.7	6.0	3.7	4.8	4.3	5.3	3.0	5.1	5.0	2.8
TAM (mm m^{-1})	103.0	84.5	88.9	82.2	81.6	83.2	84.8	111.5	100.0	89.7	91.3	121.2	101.9	96.5	93.5	93.2	96.6	96.5	85.9	102.3	99.7	111.3	113.3	111.0	127.1	93.1	95.6	129.9	92.1	129.4	81.0	114.8	125.5	130.0	108.3	130.4	128.2	118.1
N (ppm)	26.5	31.0	27.3	24.8	25.0	25.7	27.4	26.8	25.7	25.5	26.8	19.7	28.5	27.6	25.3	27.5	27.8	27.8	28.6	26.0	24.0	26.4	25.2	26.7	23.5	29.2	24.8	23.0	25.7	39.3	31.7	25.6	25.9	22.0	22.0	25.0	21.3	26.3
P (ppm)	23.8	76.6	53.0	16.4	19.7	12.3	32.5	47.5	36.0	64.0	65.0	19.3	69.0	19.8	45.0	20.0	67.2	31.2	12.4	52.3	26.5	65.6	22.2	19.0	127.5	37.6	9.4	63.8	19.7	159.3	14.7	11.1	7.7	27.8	102.5	33.8	37.0	90.5
K (meq 100 g^{-1})	0.6	0.3	0.2	0.5	0.5	0.5	0.5	0.9	0.9	1.1	0.9	0.9	1.0	0.7	1.1	0.4	1.1	1.1	0.7	0.8	0.8	1.1	1.0	2.1	2.1	0.7	0.4	1.7	1.1	1.9	0.6	1.2	1.2	1.4	1.7	1.2	1.7	1.1
Ca (meq 100 g^{-1})	4.2	9.7	2.8	3.2	3.3	4.0	2.9	11.4	8.9	6.5	3.5	18.6	8.7	17.1	5.6	2.6	13.7	8.7	6.0	16.3	8.6	12.1	29.4	19.7	19.0	7.2	10.3	28.2	8.6	24.6	0.9	25.9	30.5	30.3	10.7	29.7	26.6	19.8
Mg (meq 100 g^{-1})	2.0	1.5	0.8	1.6	2.2	1.8	1.7	5.1	5.4	2.2	1.9	10.7	2.7	2.2	2.2	1.1	4.3	7.7	4.1	5.0	3.7	5.5	6.7	16.5	20.3	2.3	5.4	17.4	3.3	24.3	1.7	7.8	16.0	25.3	4.0	18.5	16.2	7.8
Na (meq 100 g^{-1})	0.1	0.2	0.1	0.2	0.2	0.1	0.2	0.2	0.3	0.2	0.2	3.0	0.2	0.2	0.4	0.2	0.3	0.6	0.3	0.2	0.4	0.3	0.5	0.4	0.5	0.2	0.5	0.4	0.2	0.8	0.1	0.4	0.6	0.5	0.3	0.3	0.6	0.5

Table 3.7 Mean woody canopy volume (m^3 ha^{-1}) in 4 height classes for each vegetation type (see Figure 3.1 for a key to type numbers). An entry of – denotes 0. Sample sizes are given in parentheses below the types

Height class (m)	Vegetation type																																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
	(4)	(5)	(6)	(5)	(3)	(3)	(8)	(4)	(3)	(6)	(4)	(3)	(4)	(9)	(3)	(4)	(6)	(9)	(5)	(11)	(6)	(5)	(10)	(3)	(4)	(5)	(5)	(5)	(3)	(3)	(3)	(8)	(7)	(4)	(4)	(9)	(3)	(4)
0.0-3.0	10008	10575	2341	9392	6895	9449	9212	23223	3068	8220	7576	1685	11439	20101	7568	12278	11269	6630	8762	8951	11148	2032	4611	14315	966	7922	9723	5620	3494	678	3396	3333	2732	4945	7352	3645	3454	4747
3.1-8.0	17886	23291	12283	12759	4929	14016	8577	22285	6469	8898	10063	3230	11468	19406	5356	9843	17127	14285	16687	15504	18413	3167	1744	7622	477	9179	8384	3229	5117	545	7941	4399	2392	2852	12070	1316	1764	4392
8.1-14.0	7613	4743	3531	2429	374	4021	944	28812	139	11058	3059	895	2958	6867	153	731	6088	4480	2110	6208	4575	351	261	-	35	2046	1360	-	1339	2	2941	593	244	16	4737	19	80	102
14.1-20.0	-	-	-	-	-	-	-	12466	-	515	-	-	-	155	-	-	9	327	-	456	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	-	-	-



(a)

(b)

Figure 3.4 Plot of vegetation types (●) in relation to (a) the first and second and (b) first and third axes of discriminant function analysis (DFA). See Figure 1 for a key to the numbers for vegetation types.

The joining history for the hierarchical clustering of vegetation types by topo-edaphic environment is given in Table 3.8, and the tree diagram in Figure 3.5.

Table 3.8 Joining history for the hierarchical clustering of vegetation types using an Euclidian distance metric and complete linkage (furthest neighbour) method

Cluster containing vegetation type	and	Cluster Containing vegetation type	Were joined at distance	No. of members in new cluster
6		5	0.229	2
11		10	0.258	2
15		9	0.321	2
7		4	0.324	2
37		28	0.334	2
6		19	0.391	3
27		21	0.392	2
36		33	0.403	2
17		14	0.435	2
11		15	0.441	4
3		7	0.455	3
29		26	0.456	2
13		8	0.469	2
32		23	0.48	2
34		37	0.492	3
17		20	0.506	3
29		18	0.51	3
3		1	0.583	4
11		6	0.598	7
34		36	0.635	5
17		22	0.658	4
13		29	0.701	5
3		31	0.717	5
17		32	0.803	6
11		3	0.844	12
24		34	0.872	6
13		27	0.894	7
17		38	1.082	7
13		11	1.106	19
25		24	1.165	7
13		16	1.335	20
17		25	1.566	14
35		2	1.879	2
17		30	2.011	15
13		35	2.386	22
17		12	2.589	16
17		13	3.59	38

The vegetation types at the top of Table 3.8 were joined first (i.e. were most similar with respect to topo-edaphic environment) while the last entry represents the joining of the largest two clusters to form one cluster for all 38 vegetation types.

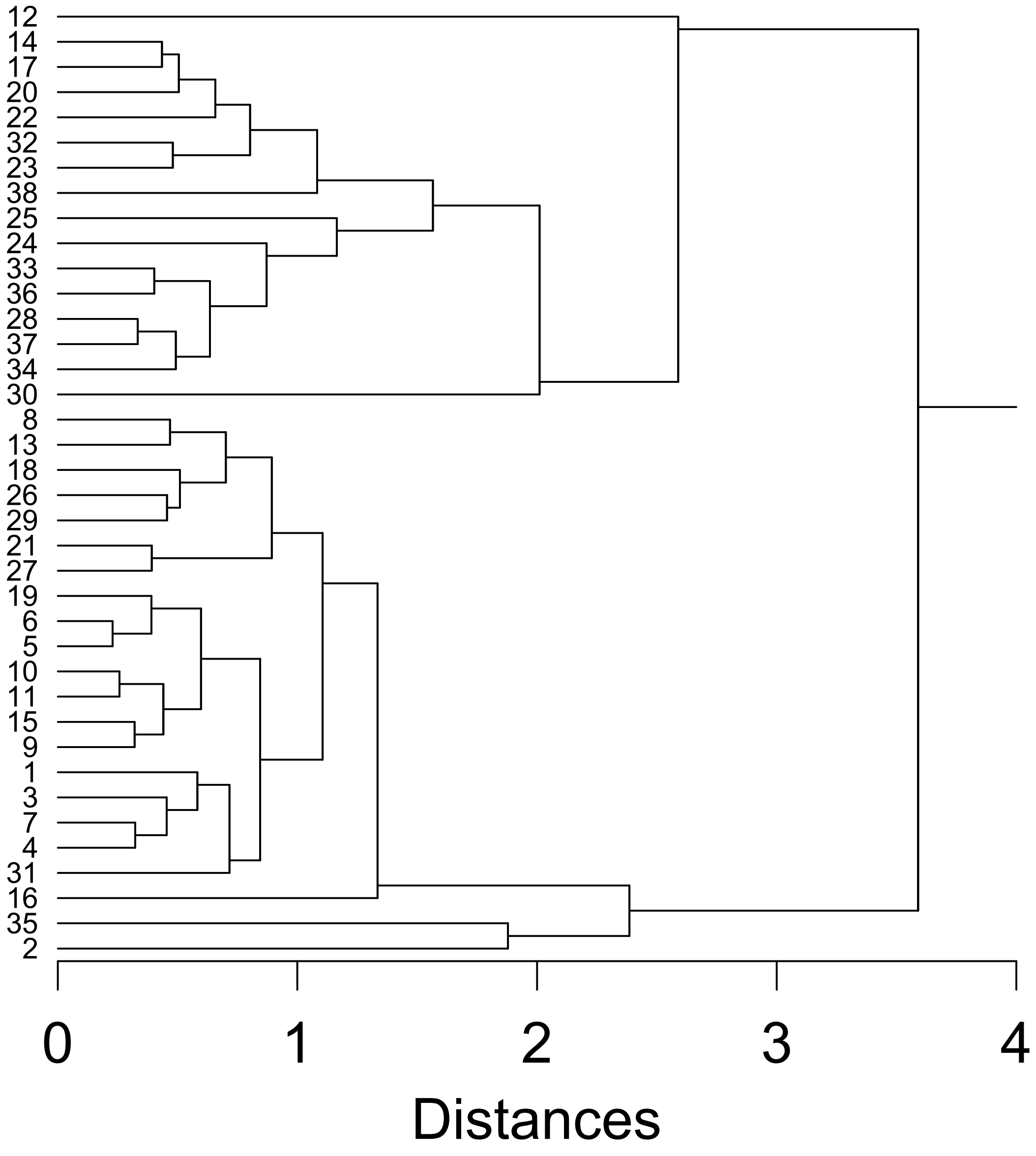


Figure 3.5 Tree diagram showing the relationship between vegetation types in terms of topo-edaphic environment. The tree is arranged such that vegetation types with the most similar topo-edaphic conditions are positioned closest to each other. The scale below the tree is graduated in Euclidian distance units and can be used to measure the distance at which vegetation types or clusters are joined. For example, types 6 and 5 are the most closely related and were joined at a distance of 0.229, while types 12 and 2 were the most unrelated and were joined at a distance of 3.590.

3.3.4. *Descriptions of the vegetation types*

1. *Acacia welwitschii – Spirostachys africana* dense shrub tall woodland

This vegetation type is best represented in two relatively broad, flat-bottomed valleys that are found on either of side Malilangwe dam (Figure 3.2). The valleys have gentle slopes, and are flanked by sandstone hills. The soil is deep (> 125 cm) and has higher silt and clay concentrations than other soils in the reserve that are derived from Stormberg sandstone. The enrichment could be due to the accumulation of silt and clay particles that have been washed down into the valleys from the surrounding hills. Common trees include *Acacia welwitschii*, *Newtonia hildebrandtii*, *Spirostachys africana*, and *Drypetes mossambicensis*. Many of the trees and, in particular *Spirostachys africana* trees, were killed during the 1992 drought. The shrub layer is dominated by *Grewia bicolor*, *Phyllanthus pinnatus*, *Capparis sepiaria* var. *subglabra*, *Gymnosporia putterlickioides*, and *Thilachium africanum*. Approximately 41 % of the soil surface is covered by herbaceous vegetation. The dominant grass species are *Panicum maximum* (9.8 % cover), *Urochloa mosambicensis* (7.5 % cover), and *Eragrostis rigidior* (2.8 % cover). *Anisotes formosissimus* (5.6 % cover) is the dominant herb, with *Alternanthera pungens* (3.0 % cover) also being common.

2. *Brachystegia glaucescens – Androstachys johnsonii* dense shrub open tall woodland

This vegetation type is found on the sandstone hills and kopjes of the Malilangwe Range. Slopes are often steep, and approximately 43 % of the surface is bare rock. Where soil has formed, it is shallow and very sandy, with a noticeably high level of phosphorus. The dominant trees are tall spreading *Brachystegia glaucescens* and shorter, thicket forming *Androstachys johnsonii*. Taller specimens of *A. johnsonii* are found in deep, well-watered ravines. Other common trees include *Ficus tettensis*, *Ficus abutilifolia*, *Stadmania oppositifolia*, *Combretum zeyheri*, *Xeroderris stuhlmannii*, *Vitex mombassae*, and the climber *Artabotrys brachypetalus*. The shrub layer is dominated by *A. johnsonii.* Other common shrub species include *Ochna barbosae*, *Lecaniodiscus fraxinifolius*, *Margaritaria discoidea*, *Hippocratea crenata*, *Grewia monticola*, *Grewia flavescens*, *Monodora junodii*, and *Psydrax livida*. Herbaceous cover is sparse (25 %) with the sedge *Coleochloa setifera* (3.9 % cover) being dominant.

3. *Julbernardia globiflora – Strychnos madagascariensis* tall woodland

This vegetation type occurs on gentle but noticeable slopes, at sites with moderately deep, sandy, dystrophic soils derived from Stormberg sandstone. The tree layer is dominated by *Julbernardia* *globiflora* (on average 78 % of the total canopy volume) with *Xeroderris stuhlmannii*, *Strychnos madagascariensis*, *Philenoptera violacea* and *Combretum zeyheri* also being common. The shrub layer is poorly developed, giving the woodland an open park-like appearance. *Dalbergia melanoxylon* contributes most to the shrub canopy volume, with *Margaritaria discoidea*, *Gardenia volkensii* and *Diospyros loureiriana* subsp. *loureiriana* also being important.

On average the herbaceous layer covers 49 % of the surface. The dominant grasses are *Digitaria eriantha* (21.6 % cover), *Panicum maximum* (10.3 % cover) and *Schmidtia pappophoroides* (3.9 % cover).

4. *Lannea schweinfurthii – Pteleopsis myrtifolia* shrub woodland

This vegetation type is found in association with moist, sandy, moderately deep soils that occur in valleys between the sandstone hills of the Malilangwe Range, and on flat terrain in the north-east of the reserve. The sandstone bedrock is not far below the soil surface (average soil depth is 111 cm) and, consequently, water that infiltrates the soil is prevented from percolating to depth. Water collects in the soil layers above the rock barrier, and in the rainy season the water table often intercepts the soil surface forming numerous springs and seeps.

The tree layer is of diverse composition with *Lannea schweinfurthii* var. *stuhlmannii*, *Spirostachys africana*, *Albizia petersiana*, *Combretum imberbe*, *Combretum zeyheri*, *Albizia harveyii*, *Xeroderris stuhlmannii*, *Combretum apiculatum*, *Sclerocarya birrea*, *Strychnos madagascariensis*, *Pteleopsis myrtifolia*, and *Terminalia sericea* being common. The shrub layer is also of diverse composition with *Dichrostachys cinerea*, *Dovyalis hispidula*, *Hyphaene petersiana*, *Grewia flavescens*, *Gardenia volkensii*, *Grewia sulcata*, *Flueggea virosa*, *Diospyros loureiriana subsp. loureiriana*, *Coffea racemosa*, *Rhus gueinzii*, *Allophylus rubifolius*, *Lecaniodiscus fraxinifolius*, and *Margaritaria discoidea* being common.

Herbaceous cover is 64 % on average. *Digitaria eriantha* (40 % cover), *Panicum maximum* (7.9 % cover), *Eragrostis rigidior* (4.0 % cover) and *Urochloa mosambicensis* (3.6 % cover) are the dominant grass species, and *Waltheria indica* (0.7 % cover), *Epaltes gariepina* (0.5 % cover), *Blepharis maderaspatensis* (0.4 % cover), *Pupalia lappacea* (0.3 % cover) and *Hermannia glanduligera* (0.3 % cover) are the dominant forb species.

5. *Colophospermum mopane – Urochloa mosambicensis* shrub open woodland

This vegetation type occurs on deep, sandy soil, in a narrow strip along the contact between the sandstone and basalt geologies to the south of the Malilangwe Range. Trees are relatively widely spaced with *Colophospermum mopane*, *Commiphora glandulosa*, *Strychnos madagascariensis*, *Lannea schweinfurthii* var. *stuhlmannii* and *Acacia nilotica* accounting for most of the canopy volume. The shrub layer is moderately well developed, with *Grewia bicolor*, *Dalbergia melanoxylon*, *Grewia monticola*, *Gardenia volkensii*, *Combretum mossambicense*, *Tricalysia allenii*, *Dichrostachys cinerea* and *Maerua parvifolia* being common.

The herbaceous layer is well developed (78 % cover), with *Urochloa mosambicensis* (36.4 % cover), *Pogonarthria squarrosa* (17.2 % cover), *Panicum maximum* (7.2 % cover) and *Digitaria eriantha* (3.6 % cover) being the dominant grass species. Common forb species include *Pupalia lappacea* (2.3 % cover), *Hermbstaedtia odorata* (1.3 % cover), *Spermacoce arvensis* (0.7 % cover), *Melhania acuminata* (0.3 % cover), *Hermannia glanduligera* (0.3 % cover), *Crotalaria senegalensis* (0.3 % cover) and *Tephrosia purpurea* subsp. *leptostachya* var. *pubescens* (0.3 % cover).

6. *Colophospermum mopane – Leucas glabrata* shrub woodland

This vegetation type occurs as a small patch at the eastern end of the airstrip. The soil, which is derived from the lower red Stormberg sandstone (Swift et al., 1953), is deep, very sandy, and red in colour. The red sandstone is poorly exposed at Malilangwe (Swift et al., 1953), and this possibly explains the limited distribution of this vegetation type. Tall *Colophospermum mopane* trees dominate the tree layer (60 % of total woody canopy volume). Other important tree species include *Albizia petersiana*, *Strychnos madagascariensis*, *Strychnos potatorum*, and *Commiphora glandulosa*. The shrub layer is well developed. Important shrub species include *Grewia bicolor*, *Dalbergia melanoxylon*, *Gardenia volkensii*, *Dichrostachys cinerea*, *Hippocratea buchananii*, *Coffea racemosa*, *Cissus cornifolia*, and *Combretum mossambicense*.

Herbaceous cover is on average 54 %. Grass cover is poor, with *Eragrostis trichophora* (7.4 % cover), *Brachiaria deflexa* (4.3 % cover) and *Urochloa mosambicensis* (2.2 % cover) contributing most to cover. In contrast, forbs are abundant, with *Pupalea lappacea* (18.4 % cover), *Leucas glabrata* (8.6 % cover), *Achyranthes aspera* (2.1 % cover), *Aspilia natalensis* (1.1 % cover), *Melhania acuminata* (1.1 % cover), *Tragia okanyua* (1.0 % cover), *Cucumis zeyheri* (0.9 % cover), *Commelina benghalensis* (0.7 % cover), *Hermbstaedtia odorata* (0.6 % cover), *Spermacoce arvensis* (0.5 % cover), *Pavonia* *procumbens* (0.5 % cover), *Hermannia glanduligera* (0.4 % cover) and *Crotalaria senegalensis* (0.4 % cover) being the most common species.

7. *Albizia petersiana – Strychnos potatorum* shrub open woodland

This vegetation type occurs on deep, sandy soils derived from white Stormberg sandstone. Trees are relatively widely spaced. *Albizia petersiana* is the dominant tree species, with *Strychnos potatorum*, *Spirostachys africana*, *Colophospermum mopane*, *Commiphora glandulosa*, and *Lannea schweinfurthii* var. *stuhlmannii* also being important. The shrub layer, which is moderately well developed, is of diverse composition. Species, in order of importance, that contribute most to shrub canopy volume include *Hippocratea crenata*, *Dichrostachys cinerea*, *Grewia bicolor*, *Grewia flavescens*, *Hippocratea indica*, *Gymnosporia putterlickioides*, *Capparis sepiaria* var. *subglabra*, *Coffea racemosa*, *Combretum mossambicense*, *Lecaniodiscus fraxinifolius*, *Monodora junodii*, *Dalbergia melanoxylon*, and *Maerua parvifolia*.

Total herbaceous cover is on average 65 %. Grass cover is relatively low, with *Digitaria eriantha* (17 % cover), *Urochloa mosambicensis* (15.5 % cover), *Panicum maximum* (6.5 % cover) and *Eragrostis lehmanniana* (3.3 % cover) contributing most to grass cover. Herbs are abundant with *Pupalea lappacea* (3.5 % cover), *Hermannia glanduligera* (2.7 % cover), *Leucas glabrata* (2.2 % cover), *Melhania acuminata* (1.2 % cover), *Spermacoce arvensis* (0.8 % cover), *Hermbstaedtia odorata* (0.7 % cover), *Celosia trigyna* (0.7 % cover), *Tephrosia purpurea* (0.7 % cover), *Commelina benghalensis* (0.5 % cover), *Dicerocaryium eriocarpum* (0.4 % cover), *Triumfetta pentandra* (0.4 % cover), and *Sida cordifolia* (0.3 % cover) contributing most to cover.

8. *Acacia galpinii – Croton megalobotrys* forest

This vegetation type occurs on the deep alluvial soils of the lowest terrace of the Chiredzi River and along parts of the Nyamasikana River. The tree layer is characterised by very tall *Acacia galpinii*, *Acacia tortilis*, *Combretum imberbe*, *Diospyros mespiliformis*, *Kigelia africana*, and *Philenoptera violacea* trees, their canopies frequently overlapping to form a continuous cover. *Croton megalobotrys* and woody climbers such as *Acacia schweinfurthii*, *Cardiogyne africana*, and *Combretum microphyllum* dominate the shrub layer, which is often dense.

On average, herbaceous cover is 45 %, with *Panicum maximum* (28.7 % cover) being the dominant grass species and *Asystasia gangetica* (4 % cover), *Dicliptera spinulosa* (1 % cover), *Ageratum conyzoides* (1 % cover) and *Acyranthes aspera* (0.8 % cover) being common forb species.

It should be noted that this vegetation type was partially cleared in the 1960’s in an attempt to eradicate tsetse fly and that the current vegetation has developed in response to this disturbance.

9. *Acacia tortilis* open woodland

This vegetation type is associated with old agricultural lands on deep alluvial soils. The tree layer is characterised by widely spaced *Acacia tortilis* of medium height. The shrub layer is poorly to moderately well developed with *Capparis sepiaria* var. *subglabra*, *Grewia bicolor* and *Dichrostachys cinerea* being dominant. The herbaceous layer is well developed, and is dominated by *Urochloa mosambicensis* (76 % cover).

10. *Acacia tortilis – Philenoptera violacea* shrub tall woodland

This vegetation type occurs on the deep alluvial soils of the second lowest terrace of the Chiredzi River. The dominant trees are tall *Acacia tortilis* and *Philenoptera violacea*, with *Combretum imberbe* and *Croton megalobotrys* also being common. The species, in order of importance, that contribute most to the canopy volume of the shrub layer are *Capparis sepiaria* var. *subglabra*, *Dichrostachys cinerea*, *Grewia bicolor*, *Acacia schweinfurthii*, *Allophylus rubifolius*, *Grewia inaequilatera* and *Grewia flavescens*.

Panicum maximum (47.2 % cover) dominates the herbaceous layer, which is well developed. Common forb species include *Pupalea lappacea* (1.4 % cover), *Commelina benghalensis* (0.8 % cover), *Achyranthes aspera* (0.6 % cover), *Justicia flava* (0.6 % cover), and *Barleria elegans* (0.5 % cover).

11. *Acacia tortilis – Thilachium africanum* shrub open tall woodland

This vegetation type occurs on the deep alluvial soils of the highest terrace of the Chiredzi River. Much of the original vegetation was cleared by tsetse control operations in the 1960’s and has since recovered to open woodland dominated by tall *Acacia tortilis*, with *Lannea schweinfurthii* var. *stuhlmannii* also being common. The shrub layer is moderately well developed with *Capparis sepiaria* var. *subglabra*, *Grewia bicolor*, and *Thilachium africanum* contributing most to canopy volume. Soil surface conditions are poor, with a large proportion of the surface being capped and, consequently, herbaceous cover is sparse.

12. *Combretum imberbe – Sprobolus consimilis* open woodland

This vegetation type occurs in association with the shallow, linear valleys of the Chiloveka drainage system. The soil, which is generally deeper than 1 m, is characterised by light coloured, fine, sandy loam to sandy clay surface horizons over dark, reddish brown clay subsoils. The clay fraction is dominated by the non-expanding lattice minerals illite and kaolinite and, consequently, the soil exhibits limited swelling and cracking during wetting and drying phases (Low et al., 1984). A striking characteristic of the soil is its very high concentration of sodium, which is an order of magnitude larger than that of the other soils of the study area.

The tree layer is dominated by widely spaced *Combretum imberbe* and *Philenoptera violacea*. The shrub layer is poorly developed with *Ziziphus mucronata* and *Hyphaene petersiana* contributing most to shrub canopy volume. In some areas, gully erosion has resulted in bush encroachment by *Colophospermum mopane* and *Acacia nigrescens* (Clegg, 1999a). The grass layer is well developed with *Ischaemum afrum* (14.1 % cover), *Setaria incrassata* (4.6 % cover), *Dicanthium annulatum* (2.5 % cover) and *Eriochloa stapfiana* (1.1 % cover) growing at poorly drained sites and the halophyte-like *Sporobolus consimilis* (22.2 % cover), *Sporobolus iocladus* (10.7 % cover), and *Panicum coloratum* (10.0 % cover) occurring at sites with better drainage.

13. *Acacia welwitschii – Salvadora persica* dense shrub woodland

This vegetation type occurs on alluvium along a localised stretch of the upper Chiredzi River. The tree layer, which is of medium height, is dominated by *Acacia welwitschii*, *Acacia tortilis*, *Lannea schweinfurthii* var. *stuhlmannii*, *Adansonia digitata*, and *Newtonia hildebrandtii*. The shrub layer is moderately well developed, with *Grewia bicolor*, *Salvadora persica* and *Gymnosporia putterlickioides* contributing most to shrub canopy volume.

Soil surface conditions are generally poor, with bare ground and rill and gully erosion being common. Consequently, herbaceous cover is sparse with *Panicum maximum* (11.9 % cover), *Chloris virgata* (9 % cover), and *Urochloa mosambicensis* (5.2 % cover) being the dominant grasses. Common forb species include *Pupalia lappacea* (3.1 % cover), and *Ruellia patula* (1.7 % cover).

14. *Colophospermum mopane – Pappea capensis* dense shrub tall woodland

This vegetation type is found between the western edge of the Malilangwe Range and the Chiredzi River on shallow (53 cm deep on average), coarse-grained, sandy soils derived from grits and conglomerates. The tree layer is dominated by tall, relatively closely spaced, *Colophospermum mopane*, with *Terminalia prunioides*, *Kirkia acuminata*, *Adansonia digitata*, and *Pappea capensis* also being common. The shrub layer is exceptionally well developed with *Grewia bicolor*, *Grewia flavescens* and *Gymnosporia putterlickioides* forming near impenetrable thickets in places.

Grass cover is low, with the annuals *Brachiaria deflexa* (3.6 % cover), *Aristida adscensionis* (1.5 % cover), *Setaria sagittifolia* (1.4 % cover) and *Enneapogon cenchroides* (1.1 % cover) being the dominant species. Forbs that contribute most to herbaceous cover include *Pupalia lappacea* (3.5 % cover), *Achyranthes aspera* (0.96 % cover), *Corchorus asplenifolius* (0.71 % cover), *Melhania acuminata* (0.65 % cover), and *Leucas glabrata* (0.59 % cover).

15. *Colophospermum mopane – Acacia tortilis* shrub open woodland

This vegetation type occurs on alluvium between Banyini and the Mahande River. A portion of it was cleared for cotton production in the late 1980's. The tree layer, which is of medium height, is composed of widely spaced *Colophospermum mopane*, *Acacia nilotica* and *Acacia tortilis*. The dominant shrubs are *Maerua parvifolia*, and *Grewia bicolor*.

The grass layer is well developed and is dominated by *Urochloa mosambicensis* (46.5 % cover). *Evolvulus alsinoides* (0.67 % cover) and *Tephrosia purpurea* (1.7 % cover) are the dominant forb species.

16. *Colophospermum mopane – Acacia erubescens* dense shrub open woodland

This vegetation type is found in association with very shallow soils (19 cm deep on average) derived from shales and mudstones. The tree layer is dominated by relatively widely spaced *Colophospermum mopane* and *Acacia erubescens*. The shrub layer, which is moderately well developed, is dominated by *Canthium glaucum* subsp. *frangula*, *Grewia bicolor*, *Phyllanthus pinnatus*, and *Monodora junodii*. Woody species which are relatively common in this vegetation type, but are uncommon elsewhere in the reserve, include *Afzelia quanzensis*, *Androstachys johnsonii*, *Boscia angustifolia*, *Croton pseudopulchellus*, *Manilkara mochisia*, *Mundulea sericea*, *Ptaeroxylon obliquum*, *Pterocarpus lucens*, and *Rhigozum zambesiacum*.

Grass cover is poor, with *Eragrostis rigidior* (4.8 % cover), *Digitaria eriantha* (2.2 % cover) and *Microchloa caffra* (1.2 % cover) being the dominant perennial species, and *Brachiaria deflexa* (6.7 % cover), *Aristida adscensionis* (2.5 % cover), and *Sporobolus panicoides* (2.4 % cover) being the dominant annual species. Common forbs include *Endostemon tenuiflorus* (3.0 % cover), *Pupalea lappacea* (1.3 % cover), *Agathisanthemum bojeri* (0.8 % cover), *Achyranthes aspera* (0.7 % cover), *Justicia flava* (0.7 % cover), *Crabbea velutina* (0.7 % cover), *Alternanthera pungens* (0.5 % cover), and *Boerhavia erecta* (0.4 % cover).

17. *Colophospermum mopane – Grewia flavescens* dense shrub tall woodland

This vegetation type is found between Sosigi Hill and the Chiredzi River on moderately shallow (60 cm deep on average), coarse-grained sandy soils derived from grits and conglomerates. The tree layer is dominated by tall (up to 20 m), relatively closely spaced *Colophospermum mopane*. The shrub layer is well developed with *Grewia bicolor*, *Gymnosporia putterlikioides*, *Grewia flavescens*, and *Thilachium africanum* being the dominant species.

The grass layer is sparse, with *Brachiaria deflexa* (3.0 % cover), *Aristida congesta* subsp. *congesta* (2.6 % cover) and *Aristida adscensionis* (1.6 % cover) being the dominant species. Common forb species include *Pupalia lappacea* (6.3 % cover), *Achyranthes aspera* (1 % cover), *Justicia flava* (1.0 % cover), and *Barleria prionitis* subsp. *ameliae* (0.9 % cover).

18. *Colophospermum mopane – Courbonia glauca* shrub open tall woodland

This vegetation type occurs on deep, red, sandy alluvial soil laid down by the Chiredzi, Nyamasikana and Mahande Rivers. The tree layer is almost entirely composed of tall, moderately widely spaced *Colophospermum mopane*. The shrub layer is well developed with *Grewia bicolor* and *Grewia monticola* contributing most to shrub canopy volume, and *Courbonia glauca* being a conspicuous indicator species.

The herbaceous layer is moderately well developed with *Urochloa mosambicensis* (25 % cover), and *Panicum maximum* (10.5 % cover) being the dominant grass species, and *Pupalia lappacea* (2.0 % cover), *Cyathula lanceolata* (0.7 % cover) and *Melhania acuminata* (0.6 %) being the most common forb species.

19. *Colophospermum mopane – Gardenia volkensii shrub woodland*

This vegetation type is found on moderately deep, fine, sandy soils derived from Stormberg sandstone. It invariably occurs at the ecotone between the Stormberg sandstone and other geologies such as paragneiss, basalt and alluvium. *Colophospermum mopane* is the dominant tree, with *Acacia welwitschii*, *Drypetes mossambicensis*, and *Sclerocarya birrea* also being common. Common shrub species include *Grewia flavescens*, *Gardenia volkensii*, *Grewia bicolor*, and *Euclea divinorum*.

The grass layer is poorly developed, with *Panicum maximum* (9.7 % cover), *Urochloa mosambicensis* (5.5 % cover), *Eragrostis lehmanniana* (4.5 % cover), *Sporobolus iocladus* (3.5 % cover), *Eragrostis rigidior* (2.0 % cover), and *Schmidtia pappophoroides* (0.9 % cover) contributing most to cover. Common forb species include *Pupalia lappacea* (1.2 % cover), *Barleria prionitis* subsp. *ameliae* (0.7 % cover), and *Melhania acuminata* (0.5 % cover).

20. *Colophospermum mopane – Kirkia acuminata* shrub tall woodland

This vegetation type is found between the western end of the Malilangwe Range and the Chiredzi River on shallow (35 cm deep on average) loam soils derived from dolerite. In places, the land surface is strewn with numerous small dolerite boulders (6.2 % of the surface is covered in rocks). The tree layer is characterised by relatively widely spaced *Colophospermum mopane* of medium height. Other common tree species include *Kirkia acuminata*, *Adansonia digitata*, *Commiphora mollis*, *Commiphora glandulosa*, *Sterculia rogersii*, and *Terminalia prunioides*. The shrub layer, which is moderately well developed, is dominated by *Grewia bicolor*, *Grewia monticola*, and *Phyllanthus pinnatus*.

Grass cover is low to moderate with *Urochloa mosambicensis* (7.3 % cover), *Heteropogon contortus* (3.5 % cover), *Panicum maximum* (2.1 % cover), *Bothriochloa radicans* (1.7 % cover), *Enterpogon macrostachyus* (2.6 % cover), and *Ennepogon scoparius* (1.7 % cover) being the dominant perennial grass species. *Aristida adscensionis* (3.2 % cover), *Brachiaria deflexa* (1.6 % cover), and *Tetrapogon tenellus* (0.3 % cover) are the common annual grass species. Forbs are abundant with *Pupalia lappacea* (3.3 % cover), *Barleria spinulosa* (1.9 % cover), *Melhania acuminata* (1.2 % cover), *Endostemon obtusifolius* (0.8 % cover), *Corchorus asplenifolius* (0.6 % cover), *Endostemon tenuiflorus* (0.6 % cover), *Rhynchosia minima* (0.6 % cover), *Ruellia patula* (0.4 % cover), *Seddera suffruticosa* var. *suffruticosa* (0.4 % cover), *Achyranthes aspera* (0.3 % cover), *Abutilon austro-africanum* (0.3 % cover), *Elytraria acaulis* (0.3 % cover), *Pavonia burchelli* (0.3 % cover), *Abutilon ramosum* (0.2 % cover), *Tephrosia villosa* subsp. *ehrenbergiana* var. *ehrenbergiana* (0.2 % cover), and *Solanum incanum* (0.2 % cover) being the dominant species.

21. *Colophospermum mopane – Terminalia prunioides* dense shrub open tall woodland

This vegetation type occurs in the northern parts of the reserve on shallow (31 cm deep on average), sandy soils derived from acid and basic gneisses. The tree layer is dominanted by tall *Colophospermum mopane.* Other common trees include *Terminalia prunioides*, *Combretum apiculatum*, and *Sterculia* *rogersii*. The shrub layer is well developed with *Grewia bicolor*, and *Grewia monticola* contributing most to shrub canopy volume.

Grass cover is low, with *Urochloa mosambicensis* (12.5 % cover), *Aristida adscensionis* (2.4 % cover), *Eragrostis superba* (2.1 % cover), *Brachiaria deflexa* (1.7 % cover), *Heteropogon contortus* (1.3 % cover), *Panicum maximum* (1.1 % cover), and *Eragrostis trichophora* (1.1 % cover) being the dominant grass species. Common species of forb include *Pupalia lappacea* (4.8 % cover), *Indigofera trita* subsp. *subulata* (1.5 % cover), *Ruellia patula* (1.4 % cover), *Corchorus asplenifolius* (1.2 % cover), *Endostemon obtusifolius* (1.1 % cover), *Rhynchosia minima* (0.9 % cover), *Elytraria acaulis* (0.6 % cover), *Melhania acuminata* (0.6 % cover), *Decorsea schlechteri* (0.5 % cover), and *Ipomoea plebeia* subsp. *africana* (0.4 % cover).

22. *Colophospermum mopane – Heteropogon contortus* open woodland

This vegetation type occurs in the north-east of the reserve on shallow (31 cm deep on average), loam soils derived from basalt. The tree layer is dominated by widely spaced *Colophospermum mopane* of medium height. Other common tree species include *Combretum apiculatum*, *Commiphora mollis*, *Kirkia acuminata*, *Combretum hereroense* and *Combretum imberbe*.

The grass layer is well developed with *Urochloa mosambicensis* (40.6 % cover) and *Heteropogon contortus* (22.1 % cover) contributing most to cover.

23. *Colophospermum mopane – Enneapogon scoparius* open woodland

This is the reserve's most extensive vegetation type. It is found on shallow (25 cm deep on average), calcareous, gravelly soil derived from basalt. The tree layer is characterised by relatively short (4 - 6 m high), widely spaced, multi-stemmed *Colophospermum mopane*. Common shrubs include *Gymnosporia pubescens*, *Commiphora africana*, *Commiphora pyracanthiodes*, *Dichrostachys cinerea*, *Grewia bicolor*, *Combretum imberbe*, *Grewia monticola*, *Philenoptera violacea*, and *Pterocarpus brenanii*.

The herbaceous layer is of diverse composition with *Enneapogon scoparius* (11.6 % cover), *Heteropogon contortus* (7.5 % cover), *Bothriochloa radicans* (7.3 % cover), *Urochloa mosambicensis* (5.6 % cover), *Enneapogon cenchroides* (4.7 % cover), *Sehima galpinii* (3.7 % cover), *Aristida adscensionis* (3.6 % cover), *Andropogon fastigiatus* (3.0 % cover), *Sorghum versicolor* (2.7 % cover), *Brachiaria eruciformis* (2.6 % cover), *Schmidtia pappophoroides* (1.9 % cover), *Brachiaria deflexa* (1.6 % cover), *Tricholaena monachne* (1.4 % cover), and *Cenchrus ciliaris* (0.5 % cover) being the dominant grass species. Common forbs include *Rhynchosia minima* (2.7 % cover), *Seddera suffruticosa* var. *suffruticosa* (1.7 % cover), *Indigofera daleoides* (1.4 % cover), *Dicoma tomentosa* (0.8 % cover), *Phyllanthus parvulus* var. *parvulus* (0.7 % cover), *Barleria lancifolia* (0.5 % cover), and *Pavonia procumbens* (0.5 % cover).

24. *Colophospermum mopane – Panicum maximum* dense shrub woodland

This vegetation type occurs on deep soils with a sandy surface horizon that is underlain by a reddish-brown clay subsoil. It is usually found at the contact between alluvium and basalt geologies, and is chracterised by a high density of small seasonal pans. The tree layer is dense, and is almost entirely composed of 4 to 6 m high, multi-stemmed, *Colophospermum mopane*. Common shrubs include *Dalbergia melanoxylon*, *Gymnosporia pubescens*, and *Euclea divinorum*.

The herbaceous layer is sparse with *Panicum maximum* (5.2 % cover), *Brachiaria deflexa* (3.5 % cover), *Brachiaria eruciformis* (3.4 % cover), and *Enneapogon cenchroides* (1.0 % cover) being the dominant grasses. *Pupalea lappacea* (1.1 % cover), and *Corchorus confusus* (0.4 %) are the dominant forb species.

25. *Combretum imberbe – Urochloa mosambicensis* wooded grassland

This vegetation type is associated with moderately deep (97 cm deep on average), light clay, basalt-derived soils that occur in the shallow linear drainage valleys of the Mahande River and it's tributaries. It occupies a catenal position intermediate between the *Colophospermum mopane – Enneapogon scoparius* open woodland on the interfluves and the *Setaria incrassata* grassland found on heavy vertic soil in the valley bottoms (Clegg, 1999a). The tree layer is characterised by widely spaced *Combretum imberbe*, *Acacia nigrescens, Colophospermum mopane*, *Acacia tortilis*, and *Philenoptera violacea*. The shrub layer is poorly developed, with *Dichrostachys cinerea* and *Hyphaene petersiana* contributing most to canopy volume.

The grass layer, which is well developed, is dominated by *Urochloa mosambicensis* (53.5 % cover), *Panicum maximum* (7.1 % cover) and *Cenchrus ciliaris* (3.3 % cover). Common forbs include *Abutilon austro-africanum* (1.3 % cover), *Duosperma quadrangulare* (0.7 % cover) and *Cyathula lanceolata* (0.5 % cover).

26. *Acacia tortilis - Dichrostachys cinerea* shrub open woodland

This vegetation type is associated with old agricultural lands on moderately deep (83 cm deep on average), coarse-grained, sandy soils derived from acid and basic gneisses. The tree layer is characterised by *Acacia tortilis* of medium height (8 – 10 m). Other common tree species include *Combretum imberbe*, *Acacia nigrescens*, *Acacia robusta* subsp. *clavigera*, and *Adansonia digitata*. The shrub layer, which is well developed, is dominated by *Dichrostachys cinerea*, *Grewia monticola*, *Grewia bicolor*, and *Grewia flavescens*.

The grass layer is moderately well developed with *Urochloa mosambicensis* (29.3 % cover), *Aristida adscensionis* (1.9 % cover), *Aristida congesta* subsp. *congesta* (1.5 % cover) and *Brachiaria deflexa* (1.2 % cover) being the dominant grass species. Common forbs include *Pupalia lappacea* (2.3 % cover), *Hermbstaedtia odorata* (0.7 % cover), and *Tephrosia purpurea* (0.5 % cover).

27. *Acacia nigrescens – Combretum apiculatum* shrub open woodland

This vegetation type occurs in the northern parts of the reserve on shallow (36 cm deep on average), coarse-grained, sandy soils derived from acid and basic gneisses. Common trees include *Acacia nigrescens*, *Combretum apiculatum*, *Combretum imberbe*, *Lannea schweinfurthii* var. *stuhlmannii*, *Sclerocarya birrea*, *Terminalia prunioides*, *Acacia erubescens*, and *Berchemia discolor*. The shrub layer, which is well developed, is dominated by *Grewia monticola*, *Grewia flavescens*, *Grewia bicolor*, and *Dichrostachys cinerea*.

Grass cover is high, with *Urochloa mosambicensis* (60.7 % cover), *Panicum maximum* (5.0 % cover), *Digitaria eriantha* (3.0 % cover), and *Heteropogon contortus* (1.5 % cover) being the dominant grass species. Common forbs include *Hermbstaedtia odorata* (1.5 % cover), *Pupalia lappacea* (1.2 % cover), *Tehprosia longipes* (0.8 % cover), *Melhania acuminata* (0.7 % cover), *Corchorus asplenifolius* (0.6 % cover), and *Pavonia procumbens* (0.5 % cover).

28. *Colophospermum mopane – Commelina kotschyi* shrub open woodland

This vegetation type occurs on moderately deep (75 cm deep on average), basalt-derived, heavy clay soils, with shrink-swell properties. The tree layer is characterised by widely spaced, multi-stemmed *Colophospermum mopane* of medium height (4 – 6 m). Common shrubs include *Colophospermum mopane*, *Philonoptera violacea*, *Pterocarpus brenanii*, and *Dichrostachys cinerea*.

The grass layer is well developed with *Sehima galpinii* (31.5 % cover), *Brachiaria eruciformis* (14.4 % cover), *Lintonia nutans* (2.5 % cover), *Heteropogon contortus* (0.6 % cover), *Andropogon fastigiatus* (0.5 % cover), and *Enneapogon cenchroides* (0.5 % cover) being the dominat grass species. Forbs are abundant, with *Commelina kotschyi* (6.3 % cover), *Abutilon austro-africanum* (2.9 % cover), *Ocimum obovatum* (1.2 % cover), and *Neorautanenia brachypus* (0.4 % cover) contributing most to cover.

29. *Combretum imberbe – Acacia robusta* open woodland

This vegetation type is found on moderately deep, sandy soils of shallow drainage valleys underlain by acid and basic gneisses. The tree layer is characterised by tall *Combretum imberbe*, *Acacia nigrescens*, *Acacia robusta* subsp. *clavigera*, and *Acacia galpinii*. Common shrubs include *Grewia monticola*, *Grewia bicolor*, *Combretum hereroense* and *Dichrostachys cinerea*.

The grass layer is well developed, with *Urochloa mosambicensis* (63.0 % cover), and *Panicum maximum* (11.8 % cover) being the dominant grasses. Common forbs include *Ocimum gratissimum* subsp. *gratissimum* (0.7 % cover) and *Corchorus asplenifolius* (0.7 % cover).

30. *Setaria incrassata* grassland

This vegetation type is found on deep, vertic, basalt-derived soils at the bottom of shallow, linear, drainage valleys. Woody vegetation is sparse, with *Combretum imberbe*, *Philenoptera violacea*, and *Combretum hereroense* contributing most to woody canopy volume.

The grass layer is very well developed, with *Setaria incrassata* (36.4 % cover), *Ischaemum afrum* (33 % cover), and *Dichanthium annulatum* (7.1 % cover) being the dominant species. *Rynchosia albissima* (1.8 % cover) is the dominant forb.

31. *Brachystegia glaucescens – Albizia petersiana* open woodland

Localised patches of this vegetation type are found on relatively flat topography with deep, fine-grained, sandy soils derived from Stormberg sandstone. The tree layer is characterised by large, spreading, widely spaced *Brachystegia glaucescens*. Other common tree species include *Albizia petersiana*, *Strychnos madagascariensis*, and *Pteleopsis myrtifolia*. The shrub layer is poorly developed, with *Hippocratea indica*, *Maerua parvifolia* and *Senna petersiana* being the dominant species.

Grass cover is medium to sparse, with *Digitaria eriantha* (13.5 % cover), *Aristida scurius* (11.6 % cover), *Pogonarthria squarrosa* (5.0 % cover), and *Perotis patens* (1.4 % cover) being the dominant grass species. Forbs are abundant, with *Waltheria indica* (5.2 % cover), *Dicerocaryum eriocarpum* (5.0 % cover), *Aystasia gangetica* (3.4 % cover), *Sida cordifolia* (2.8 % cover), *Hermannia glanduligera* (1.6 % cover), *Blepharis maderaspatensis* (1.2 % cover), *Celosia trigyna* (1.1 % cover), *Oxygonum* sp.

(0.6 % cover), *Pupalia lappacea* (0.8 % cover), and *Vernonia steetziana* (0.7 % cover) contributing most to cover.

32. *Acacia nigrescens – Grewia villosa* open woodland

This vegetation type occurs on the north-eastern parts of the reserve on shallow, calcareous, basalt-derived soils, with relatively high clay content (26 %). The tree layer is characterised by widely spaced *Acacia nigrescens*, with *Sclerocarya birrea*, *Combretum imberbe*, *Commiphora mollis*, *Colophospermum mopane*, *Combretum hereroense* and *Combretum apiculatum* also being common. *Grewia monticola*, *Grewia villosa*, *Flueggea virosa*, and *Dichrostachys cinerea* contribute most to shrub canopy volume.

The grass layer, which is well developed, is dominated by *Urochloa mosambicenis* (45.3 % cover). Other common grass species include *Cenchrus ciliaris* (7.4 % cover), *Panicum maximum* (7.2 % cover), *Heteropogon contortus* (3.9 % cover), and *Brachiaria eruciformis* (3.3 % cover). Common forbs include *Rhynchosia minima* (0.9 % cover), *Pupalia lappacea* (0.6 % cover), *Rhynchosia albissima* (0.6 % cover), *Abutilon austro-africanum* (0.5 % cover), *Corchorus confusus* (0.5 % cover), and *Melhania acuminata* (0.5 % cover).

33. *Acacia nigrescens – Acacia nilotica* open woodland

This vegetation type occurs on moderately deep (67 cm deep on average), vertic clay soils derived from basalt. The tree layer is characterised by tall, widely spaced *Acacia nigrescens*, with *Combretum imberbe* and *Acacia nilotica* also being common. The shrub layer is sparse with *Dichrostachys cinerea*, *Grewia villosa* and *Philenoptera violacea* being the dominant species.

The grass layer is well developed, with *Urochloa mosambicensis* (21 % cover), *Panicum maximum* (20.3 % cover), and *Sehima galpinii* (19.3 % cover) being the dominant grass species. Common forbs include *Abutilon austro-africanum* (0.8 % cover), *Pupalia lappacea* (0.7 % cover), *Commelina kotschyi* (0.5 % cover), and *Rhynchosia albissima* (0.5 % cover).

34. *Dichrostachys cinerea – Dalbergia melanoxylon* open woodland

This vegetation type occurs on lower lying topographical positions than the *Acacia nigrescens – Acacia tortilis* open woodland, in association with deep, basalt-derived, vertic clays. The tree layer is poorly developed with widely spaced *Acacia nigrescens*, and *Acacia nilotica* being the dominant species. Common shrubs include *Dichrostachys cinerea*, *Dalbergia melanoxylon*, *Colophospermum mopane, Grewia villosa*, *Euclea divinorum*, *Ehretia amoena*, and *Philenoptera violacea*.

The grass layer, which is moderately well developed, is dominated by *Brachiaria eruciformis* (18.5 % cover), *Cenchrus ciliaris* (5.8 % cover), *Sehima galipinii* (21.9 % cover), *Rottboellia cochinchinensis* (3.2 % cover), *Setaria incrassata* (3.0 % cover), *Panicum maximum* (2.3 % cover), and *Ischaemum afrum* (1.4 % cover). Common forbs include *Duosperma quadrangulare* (8.4 % cover), *Launea cornuta* (2.5 % cover), *Rhynchosia albissima* (1.9 % cover), *Abutilon austro-africanum* (1.1 % cover), *Abutilon indicum* subsp. *guineense* (0.9 % cover), and *Ipomoea coscinosperma* (0.5 % cover).

35. *Adansonia digitata – Gyrocarpus americanus* shrub open tall woodland

This vegetation type is found on steep hill slopes, with shallow, sandy soils derived from Stormberg sandstone. The woody layer is of diverse composition, with *Adansonia digitata*, *Kirkia acuminata*, *Gyrocarpus americanus*, *Commiphora mollis*, *Acacia nigrescens*, *Brachystegia glaucescens*, *Lannea schweinfurthii* var. *stuhlmannii*, *Pterocarpus lucens*, *Xylia torreana*, and *Combretum imberbe* being the common tree species. *Anisotes rogersii*, *Androstachys johnsonii*, *Grewia flavescens*, *Acacia erubescens*, and *Phylanthus pinnatus* contribute most to shrub canopy volume.

The grass layer is poorly developed, with *Panicum maximum* (14.8 % cover), *Urochloa mosambicensis* (5.4 % cover), *Enteropogon macrostachyus* (4.3 % cover), *Aristida adscensionis* (2.7 % cover), and *Brachiaria deflexa* (2.4 % cover) being the dominant grass species. Common forb species include *Commelina benghalensis* (1.9 % cover), and *Pupalea lappacea* (1.7 % cover).

36. *Colophospermum mopane – Brachiaria eruciformis* open woodland

This vegetation type is associated with relatively flat topography with deep, calcareous, vertic clay soils derived from basalt. The tree layer is almost entirely composed of widely spaced, multi-stemmed, *Colophospermum mopane*. The shrub layer, which is poorly to moderately well developed, is dominated by *Colophospermum mopane*, *Dalbergia melanoxylon*, *Grewia bicolor, Acacia nigrescens*, and *Commiphora africana*.

Grass cover is high, with *Brachiaria eruciformis* (24.8 % cover), *Sehima galpinii* (18.4 % cover), *Panicum maximum* (3.6 % cover), *Aristida adscensionis* (4.3 % cover), *Cenchrus ciliaris* (2.7 % cover) and *Lintonia nutans* (2.4 % cover) being the dominant grass species. Common forb species include *Abutilon austro-africanum* (2.7 % cover), *Commelina kotschyi* (1.3 % cover), *Indigofera schimperi* (1.3 % cover), *Neorautanenia brachypus* (0.5 % cover), and *Pupalia lappacea* (0.3 % cover).

37. *Acacia nigrescens – Combretum imberbe* open woodland

This vegetation type is associated with deep, heavy clay, basalt-derived soils found in broad, flat, low lying topographical positions. The tree layer is characterised by widely spaced *Acacia nigrescens*, with *Combretum hereroense*, and *Philenoptera violacea* also being common. The shrub layer is dominated by *Dichrostachys cinerea*, *Gymnosporia senegalensis*, *Acacia borleae*, and *Combretum imberbe*.

Grass cover is high, with *Setaria incrassata* (32.9 % cover), *Urochloa mosambicensis* (9.7 % cover), *Sehima galpinii* (9.4 % cover), *Panicum maximum* (9.2 % cover), *Rottboellia cochinchinensis* (7.3 % cover), and *Digitaria eriantha* (4.3 % cover) being the dominant grass species. Common forbs include *Rhynchosia albissima* (5.2 % cover), *Corchorus confusus* (0.5 % cover), and *Abutilon austro-africanum* (0.4 % cover).

38. *Colophospermum mopane – Endostemon tenuiflorus* open woodland

This vegetation type is found on very shallow (17 cm deep on average), rocky, loam soils derived from basalt. The tree layer is composed of relatively widely spaced *Colophospermum mopane*, with *Combretum apiculatum*, *Kirkia acuminata*, and *Commiphora glandulosa* also being common. *Colophospermum mopane* and *Grewia bicolor* dominate the shrub layer.

Grass cover is sparse, with *Aristida adscensionis* (5.9 % cover), *Urochloa mosambicensis* (5.7 % cover), *Andropogon fastigiatus* (2.0 % cover), *Brachiaria eruciformis* (1.9 % cover), *Heteropogon contortus* (1.9 % cover), *Enneapogon cenchroides* (1.6 % cover), *Brachiaria deflexa* (1.2 % cover), and *Bothriochloa radicans* (1.1 % cover) being the dominant species. Common forb species include *Endostemon tenuiflorus* (4.1 % cover), *Endostemon obtusifolius* (2.6 % cover), *Tephrosia villosa* (2.0 % cover), *Indigofera schimperi* (0.6 % cover), *Melhania acuminata* (0.6 % cover), and *Tephrosia purpurea* subsp. *leptostachya* var. *pubescens* (0.5 % cover).

3.3.5. *Recent fire history*

Approximately 29 % of the reserve was burnt in October 2001 (Figure 3.6). A total of 57 land units were distinguished by the final classification step, which subdivided vegetation units further on the basis of whether they had been recently burnt or not.

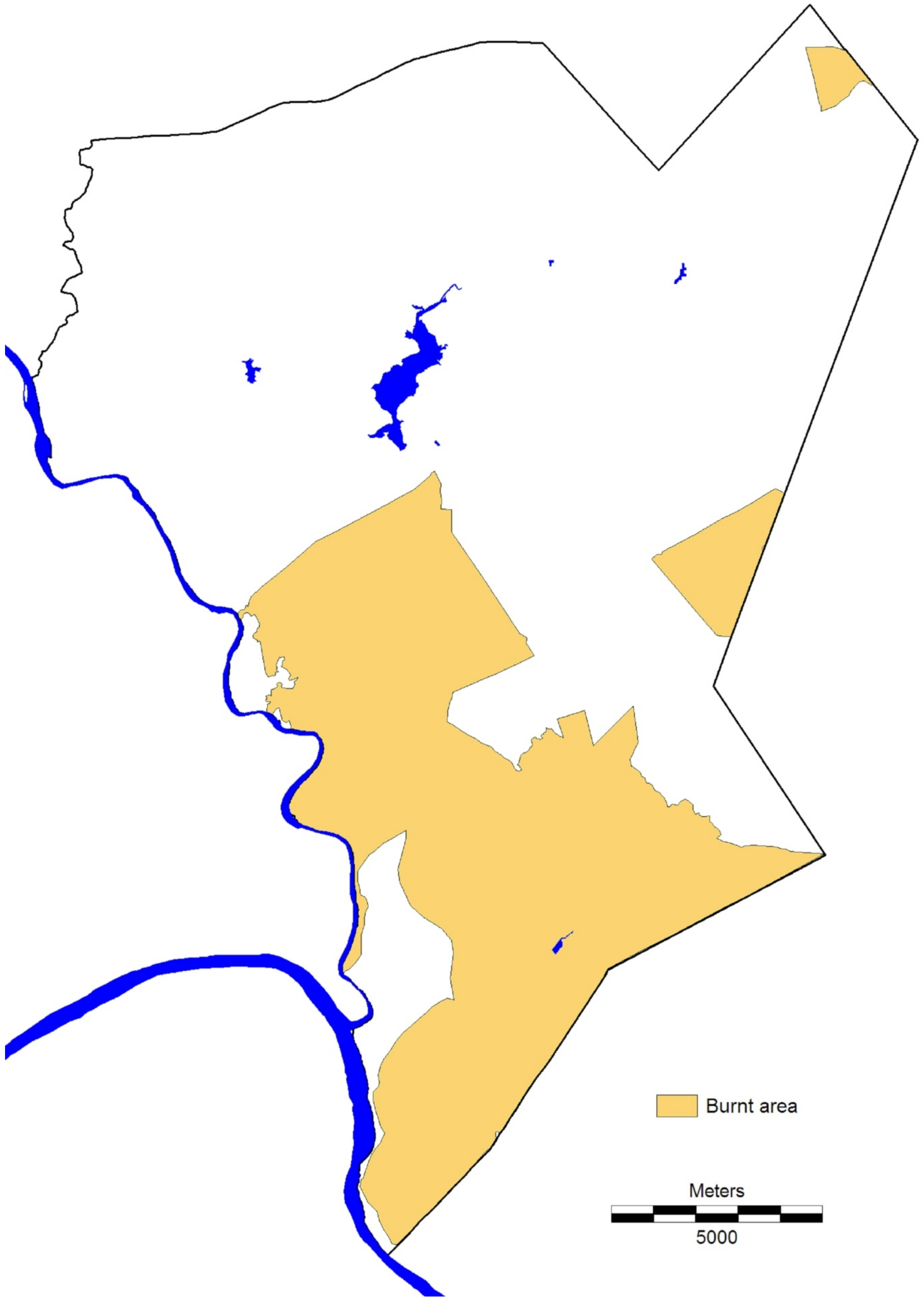


Figure 3.6 Map showing the spatial position of the area burnt in October 2001.

3.4. Discussion

3.4.1. *Ecological insights*

Ecologically meaningful land cover units

A classification of land cover units, for the assessment of the foraging ecology of elephants at the landscape level, was accomplished through an *a priori* consideration of the factors that influence elephant feeding behaviour. To derive ecologically meaningful land cover units, the classification process took into account the composition of the herbaceous and woody vegetation strata, the structure of the woody vegetation layer, the topo-edaphic variables that influence plant phenology, and recent fire history. The above can be considered the minimum set of variables required to define land cover units suitable for studying the foraging ecology of mammalian herbivores at the landscape level.

Integration of field-collected and remotely sensed data

Unlike ground-based measurements, which cannot be easily converted to estimates across entire ecosystems, remote sensing can provide simultaneous estimates across wide areas. However, although remotely sensed data have the advantage of providing synchronous measurements of broad areas, they lack the detail of field-based measurements, which provide more information at the local-scale (Kerr & Ostrovsky, 2003; Turner et al., 2003). Consequently, remotely sensed data have only limited potential for explaining the distribution of animal species. The problem of scale mismatch between traditional field measurements and remotely sensed data sources can be solved by using a combination of both remote sensing and field data collection techniques (Kerr & Ostrovsky, 2003). This integrated approach was successfully used in this study. Field-based measurements were first used to collect detailed information on vegetation at the fine scale, and then remotely sensed imagery was used to extrapolate the fine-scale information to the broad scale.

Influence of topo-edaphic variables

The identification of a strong topo-edaphic influence on vegetation structure and floristic composition accords with the findings of other vegetation studies conducted in the savanna woodlands of southern Africa (Werger, 1978; Dye & Walker, 1980; Bredenkamp, 1985; Skarpe, 1986; O'Connor & Campbell, 1986; Dunham, 1989; Scholes, 1990; O'Connor, 1992; Witkowski & O'Connor, 1996).

Sharply defined vegetation boundaries

In almost all cases, the boundaries of vegetation types were sharply defined. Sharp transitions between vegetation units were due to abrupt changes in topo-edphic conditions between vegetation types. The presence of distinct boundaries between vegetation units meant that the maximum likelihood classifier was, in most cases, able to successfully map the vegetation units from the satellite image.

3.4.2. *Limitations and future improvements*

Map accuracy

Despite the boundaries of vegetation types being easily recognisable on the ground, several of the land cover units could not be mapped accurately from the satellite imagery. Differences in spectral properties across vegetation types were largely due to variation in woody canopy cover and not variation in floristic composition. For this reason, vegetation units with different floristic composition but similar woody canopy cover had almost identical spectral properties and, therefore, could not be separated and accurately mapped by the maximum likelihood classifier. For the same reason, different grassland types could not be accurately distinguished from each other.

This problem could possibly be overcome by using satellite imagery from several different seasons (Richards, 1984; Tanser & Palmer, 2000). A "multi-temporal" approach increases the chance of identifying spectral differences between vegetation types by capitalising on seasonal variation in plant phenology between vegetation types.

Temporal change in vegetation properties

Vegetation maps are subject to change as a result of the effects of elephants and fire and, therefore, need to be periodically updated. It should be noted however, that the boundaries of the vegetation types should not be affected because these are determined by topo-edaphic factors that change over geological time. Only vegetation attributes such as species composition and structure are expected to change. Unfortunately, in order to update these attributes data must be collected using a ground–based approach, which happens to be the most time consuming and costly component of vegetation mapping.

Chapter 4. Modelling the spatio-temporal variation in the short-term rate of intake by elephants when feeding on different food types

4.1. Introduction

Given a large absolute energy requirement and a low level of cell wall digestion, it is postulated that elephants must take advantage of a high passage rate of ingesta and adopt a foraging strategy that maximizes the rate of intake of easily digestible cell solubles, if they are to meet their nutritional requirements (see chapter 1). This hypothesis can be tested by examining to what extent habitat and diet selection by elephants are explained by the rate-maximizing premise. However, before such a test can be conducted, the spatio-temporal variation in the rate of intake of cell solubles achieved by elephants when feeding on the available food types in the landscape must be quantified. Modelling the rate of food intake by elephants should, however, not be seen merely as a step towards explaining habitat and diet selection, but rather as an important process in its own right because it provides insight into the fine-scale mechanics of the foraging process.

The rate of food intake is the integrated result of multiple foraging actions that occur across a range of spatial scales. It is most often estimated using ingestion type models that functionally represent both the cross-scale linkages inherent in the foraging process and the trade-off between the factors affecting intake (Spalinger & Hobbs, 1992; Parsons et al., 1994; Farnsworth & Illius, 1996; Sauvant et al., 1996; Haschick & Kerley, 1997; Farnsworth & Illius, 1998; Illius et al., 2002; Wilson & Kerley, 2003a; Baumont et al., 2004).

Ingestion models are mechanistic models that specify intake rate as a function of constraints that limit an animal’s ability to consume food (Yearsley et al., 2001). Constraints that have been included in ingestion models are bite mass, search time and handling time (Spalinger & Hobbs, 1992; Parsons et al., 1994; Farnsworth & Illius, 1996; Sauvant et al., 1996; Haschick & Kerley, 1997; Farnsworth & Illius, 1998; Illius et al., 2002; Wilson & Kerley, 2003a; Baumont et al., 2004). Handling time is defined as the time required to crop, chew and swallow a mouthful of food. In these models, intake is determined either by the time required to search for food or by the time taken to gather and chew food (Spalinger & Hobbs, 1992).

An important development in modelling food intake by herbivores was made by Spalinger & Hobbs (1992). They recognised that searching and handling by herbivores were not mutually exclusive and competing activities because chewing, which is a component of handling, could still take place while the animal was searching for the next bite. Farnsworth & Illius (1996), building on the developments of Spalinger & Hobbs (1992), extended earlier models to include overlapping of searching and handling and showed that grazing of mammalian herbivores is consistent with it. The more general model of Farnsworth & Illius (1996) was extended further by Farnsworth & Illius (1998) to show the effect of competition between searching and the prehension and chewing components of handling on diet choice in grazing and browsing herbivores.

Despite these developments, the ingestion models mentioned above cannot be used to describe foraging by elephants at the landscape scale for two reasons. Firstly, the models assume that the prehension and chewing components of handling are mutually exclusive processes that do not overlap. Prehension and chewing have been shown to overlap for both cattle (Laca et al., 1994) and giraffe (Ginnett & Demment, 1995), and clearly these processes are also not mutually exclusive for elephants because the trunk allows prehension to take place while food is being chewed. Consequently, for an ingestion model to be applicable to elephants it must allow prehension and chewing to overlap. Secondly, the models apply to animals foraging in patches where the pattern of food availability does not change abruptly. They represent foraging at the scale of the patch and are not applicable to the study of foraging at larger spatial scales where animals travel between patches, across areas where food abundance is low. At the landscape scale, travel time between patches can vary dramatically and this, in turn, may result in large differences in the rate of food intake. Consequently, a mechanism describing travel time between patches should be part of an ingestion model applicable to the landscape scale.

The aim of this study was to examine (as hypothesised in chapter 1) whether elephants maximize their rate of intake of easily digested cell contents that contain the bulk of the energy, protein and nutrients found within plant material. Cell contents could not be used directly because of the difficulty of measurement and the wide range of food types eaten by elephants, so a proxy measure was sought, candidates for which were digestible energy, protein, and forage digestibility. Of these digestible energy is possibly the most appropriate. However, the level of digestible energy contained within a forage type is influenced by a number of factors, including plant species and part, stage of maturity, microbial activity in the fermentation chamber of the herbivore and the rate of passage through it (Owen-Smith, 1988). A complete set of parameters necessary for modelling digestion by elephants is yet to be developed, and consequently the digestible energy content of forage cannot be easily calculated for elephants. The difficulty of using digestible energy as a measure of forage quality in this study was further exacerbated by the large number of plant species, plant parts and stages of maturity involved at the landscape-scale. Use of forage digestibility was also not feasible because the well developed digestion models for other hindgut fermenters such as the horse cannot be used to predict digestion by elephants (Clauss et al., 2003b). For the above reasons, use of digestible energy as a measure of forage quality was abandoned in favour of crude protein concentration, which is more easily measured (Owen-Smith & Novellie, 1982; Owen-Smith, 1988). Digestible energy and protein contents are closely correlated in most natural forages (Westoby, 1974; Owen-Smith & Novellie, 1982), and therefore the density of crude protein was assumed to be a proxy for the level of digestible energy and other coavailable nutrients found in cell contents. It should be noted that although this correlation has been stated for digestion by ruminants in the literature, there is no reason to assume that it will not also hold for hindgut fermentors such as elephants. However, although the relationship may be true for most forage types it may be less ideal for bark and roots which are expected to be high in energy but low in protein (Greyling, 2004; Prajapati, 2008).

The first section of this chapter describes how a mechanistic ingestion model for foraging at the landscape scale was conceptualised and developed specifically for elephants. The second section describes (1) how field data were collected and used to quantify the spatio-temporal pattern of handling time, search time, trunkload mass, and protein density for the available food types in the Malilangwe landscape over one annual cycle, and (2) how the ingestion model was linked to a GIS and run to quantify the rate of protein intake for adult bulls and family units feeding in the Malilangwe landscape over one annual cycle. The third section presents the empirical data collected in the field and the outputs from the model at a monthly time step. The final section discusses the results in the light of what is already known about elephant feeding behaviour, highlights the short comings of the model, and proposes possible future improvements.

4.2. Model development

Consider a landscape composed of a number of vegetation types. Let the food in each vegetation type be patchily distributed, with high concentrations of food confined to patches and regions of low food availability between patches. Foraging by elephants under these conditions can be represented by a sequence that includes one movement between patches and one complete bout of foraging within a patch. This sequence describes the full suite of foraging processes and may be thought of as a unit that is repeated through time. Let the sequence begin when the elephant leaves a patch and starts walking to a new patch. While walking to the new patch the elephant will be chewing the last mouthful from the previous patch such that searching and chewing are overlapping processes. On arriving at the new patch, the elephant will gather a trunkload of food, that is, prehension and chewing overlap and, if it has finished chewing the previous mouthful, it will place the recently harvested food in its mouth. However, if it has not finished chewing it will wait until it has done so before placing the trunkload in its mouth. If we assume that patches are easily visible and that the distance between patches is $\frac{1}{\sqrt{D}}$, where D is the density of patches (patches/m^2) (i.e. patches are assumed to be uniformly spaced, Clark & Evans, 1954)), then the time required to walk between patches is $\frac{1}{V\sqrt{D}}$, where V is the speed of travel between patches (m/s). Therefore, the time between the last mouthful in the previous patch and the first mouthful in the new patch is given by $\frac{1}{V\sqrt{D}} + P_t$, where P_t is the time (s) required to gather a trunkload, or by C_t, the time (s) to chew a mouthful, depending on which is the largest. While the elephant is chewing the first mouthful from the new patch, it will begin to gather a second mouthful. Because food is closely spaced and easily visible within a patch we can assume that the time required to search for a trunkload is negligible. When it has finished chewing, the elephant will put the second trunkload in its mouth. The time between mouthfuls when feeding in a patch is called handling time, H_t, and it represents the time required to gather and chew a trunkload. Because of the complete overlap between prehension and chewing, H_t is equal to either P_t or C_t depending on which is the largest. The elephant will continue to feed in the patch until it decides to leave, with the total time spent in the patch given by $H_t \times N - 1$, where N is the number of bites taken in the patch. The bite rate R (bites/s) over the foraging sequence is given by:

$$R = \frac{N}{\left(\frac{1}{V\sqrt{D}} + P_t\right) + \left(H_t \times N - 1\right)} \qquad \text{for } \frac{1}{V\sqrt{D}} + P_t > C_t \text{ or} \qquad \text{eqn 1}$$

$$R = \frac{N}{C_t + \left(H_t \times N - 1\right)} \qquad \text{for } \frac{1}{V\sqrt{D}} + P_t < C_t \qquad \text{eqn 2}$$

However, when $\frac{1}{V\sqrt{D}} + P_t < C_t$, $H_t = C_t$ and, therefore, eqn 2 resolves to:

$$R = \frac{1}{C_t} \qquad \text{eqn 3}$$

Equation 3 represents the situation where the cost in time incurred by walking between patches is zero. Under these circumstances, the patchy distribution of food has no effect on bite rate and it is as if the elephant were feeding in one continuous patch. The maximum distance between patches M_{max} (m) at which this condition occurs is given by:

$$M_{\max} = (C_t - P_t) \times V \qquad \text{eqn 4}$$

Finally, the rate of protein intake I (g/s) is given by:

$$I = S \times R \qquad \text{eqn 5}$$

where S is the mass (g) of protein in a single mouthful. It should be noted that because I is measured over a period of minutes it represents the short-term protein intake rate. It differs from long-term measures of the rate of intake because it ignores processes such as satiation, digestion, excretion, and the amount of time invested in feeding. These processes tend to regulate intake rate over longer time frames (Shipley et al., 1994).

The above model was used to estimate I for adult bull elephants and members of family units when feeding on different food types. To determine the spatio-temporal pattern of I for each food type the model was linked to a GIS and run in each landscape unit, at a daily time step, for one annual cycle.

4.3. Methods

4.3.1. *Estimating prehension time and chewing time for different food types*

The time required to crop (P_t) and the time required to chew (C_t) different food types was estimated by observation of adult bull and cow elephants between April 2002 and March 2003. Observations were made in as many different vegetation types and at as many different times of day as possible. No observations were made at night. Once elephants were located, a focal individual was selected at random. Often, random selection was impossible because only those individuals at the periphery of the group were accessible. Under these circumstances, the most accessible individual was selected. The sex and age of the focal animal was recorded, and characteristics such as tusk length, shape and size, torn ears were noted to ensure recognition during sampling. The focal animal was followed on foot, or from a vehicle for the larger family units, and observed at a distance of 30 to 50 m using 8×21 binoculars. The time at the start of the feeding record was noted. The following was recorded for each trunkload gathered in a patch by talking, at the instant of each feeding action, into a head-set microphone attached to a dictophone that was running continuously: (1) when the elephant started to gather a trunkload, (2) the method of prehension used, (3) the food type being consumed, (4) the species of plant being consumed, and (5) when the trunkload was placed in the mouth.

It was difficult to determine the exact point at which the elephant finished chewing a mouthful and so this was assumed to take place the instant before the next trunkload was placed in the mouth. It was also noted when the elephant left a patch and started to feed in a new patch. The elephant was deemed to have left a woody patch if it abandoned the shrub or tree it had been feeding on or an herbaceous patch if it walked more than two paces without feeding from the herbaceous layer. If the focal elephant disappeared from view, recording was stopped. Recording continued when the elephant reappeared. If it became obvious that the elephant was walking to water as opposed to actively feeding, or if feeding was being disturbed in any other way, observation was abandoned. The route and distance travelled during the observation period was recorded by saving a track on a GPS. The dictaphone recordings were transferred to a computer where they were analysed using Winamp, a digital audio player, and Microsoft Excel. Because the dictophone was running continuously during observations, the recording preserved the intervals between feeding actions. Consequently, when the recordings were played using Winamp, the time at the start and end of each feeding action could be read to the nearest second off the digital timer. These times were transferred to an Excel spreadsheet that was used to calculate, for adult bulls and cows, the average prehension time (P_t) and handling time (H_t) for each food type. The H_t for a food type was calculated as the average of the intervals between consecutive mouthfuls of the food type that were gathered using the same method of prehension. Consecutive mouthfuls that were not from the same patch or gathered in the same way were excluded. Due to the complete overlap between prehension and chewing, if $H_t > P_t$, it was assumed that $H_t = C_t$.

4.3.2. *Estimating the spatio-temporal pattern of patch density for different food types*

During the collection of data to estimate P_t and C_t, elephants were seen to feed on many food types. In addition, some food types were gathered using several different methods of prehension, thereby increasing the number of combinations of food by prehension type. Consequently, to simplify the modelling process, only the dominant food types for which trunkload mass could be adequately estimated were selected.

Grass and Forbs

The nutritional quality of savanna grasses varies over the annual cycle as a result of changes in the amount of easily digestible soluble nutrients found in the plant cells and changes in the thickness of slowly digestible cell walls (Lyons et al., 1996; Buxton & Redfearn, 1997). Grass quality is highest at the start of the growing season because cell solubles are most abundant in young, green, actively growing tissue. Quality declines as the growing season progresses because as plant cells mature their walls become thickened with indigestible fibre. Quality declines further during the dry season because cell solubles are redistributed from the leaves to the roots thereby reducing the amount of nutrients in individual leaf cells. To account for changes in grass quality, the density of patches with (1) green grass only, and (2) a mixture of green and dry grass were estimated. When forbs senesce, their leaves do not remain on the plant but are abscised and fall to the ground. Once this happens, the stems, particularly of non-woody forbs, wither and little trace of the original plant is left. For this reason, only the density of patches with green forbs was estimated. Data were collected in the following way.

Between November 2001 and July 2003, at approximately three-month intervals, five sample points were located in each landscape unit using a stratified random strategy and Idrisi32 GIS software (Eastman, 2001). The co-ordinates of the points were uploaded onto a GPS, which was used to navigate to the sites. On arrival at a sampling point, a 50 m tape was laid out to the north. If, by adhering to this predetermined direction, a transect was forced to cross the boundary of a landscape unit or a road, the tape was laid out to the south. A 1 m^2 quadrat was placed at 2 m intervals along the tape, to give a total of 25 quadrats per site, and the aerial cover of green grass, dry grass and green forbs was estimated in each quadrat using an eight point scale (0 %; 1 %; 2-10 %; 11-25 %; 26-50 %; 51-75 %; 76-95 %; 96-100 %). In addition, the height of the tallest green grass leaf, tallest dry grass leaf, and tallest green forb was measured to the nearest centimetre (these data were used to estimate grass and forb bite mass). The density of patches (patches/m^2) with green grass, mixed green and dry grass, and green forbs was calculated for a site by counting the number of quadrats for each patch type and dividing the number by 25. Quadrats were assigned to patch types using the criteria shown in Table 4.1.

Availability of green grass and forbs is positively related to soil moisture, which is in turn related to the amount and spatial distribution of rainfall. In semi-arid environments rainfall distribution is patchy, and this causes an uneven distribution of green herbaceous forage, even at the scale of the vegetation type (Prins, 1988; Prins & Loth, 1988). It was recognised that the coarse temporal resolution of sampling would not adequately capture variability in the distribution of green herbaceous forage and, for this reason, it was decided to estimate the density of grass and forb patch types from regression models that used the average moisture (mm) in the top 30 cm of the soil for the previous 5, 10, 15, 20, 30 or 60 days as the predictor variable. Separate models were developed for each landscape unit. Data for the regression models were collected in the following way.

Table 4.1 Criteria used to assign quadrats to patch types

Patch type	Criteria
Green grass	Green grass aerial cover ≥ 1 % ≥ 90 % of total grass biomass green
Mixed green & dry grass	Total grass aerial cover ≥ 1 % < 90 % of total grass biomass green ≥ 10 % of total grass biomass green
Dry grass	Dry grass aerial cover ≥ 1 % > 90 % of total grass biomass dry
Green forb	Green forb aerial cover ≥ 2 %

Daily moisture in the top 30 cm of soil was extracted, for each sample site, from maps generated by linking a model of soil moisture balance (Hobbs et al., 1994) to Idrisi Kilimanjaro GIS software (Eastman, 2003). Daily moisture loss from the 0-30 cm profile was modelled using a negative exponential function that was dependent on available soil moisture and driven by daily rainfall and potential evaporation:

$$M_t = \left(M_{t-1} + R_t\right) \times \exp^{-k.PE}$$

where M is the soil moisture fraction, R is the rainfall fraction, PE is potential evaporation (mm) and k is an evaporative constant. M was scaled between 0 and 1, and was calculated as:

$$M = \frac{m_{soil} - m_{\min}}{m_{FC} - m_{\min}}$$

where m_{soil} is the moisture (mm) in the 0 - 30 cm profile, m_{min} is the minimum air dried moisture (mm), and m_{FC} is the field capacity of the 0 - 30 cm profile. Minimum air dried moisture was calculated, for each landscape unit, from percent silt and percent clay using the equation of Bennie et al. (1988). Field capacity was calculated using the equation of Hutson (1984). R was also scaled between 0 and 1 and was calculated by dividing the daily rainfall (mm) by $m_{FC} - m_{\min}$. Rainfall data were collected from 14 gauges within the study area and 12 gauges outside the study area (Figure 4.1).

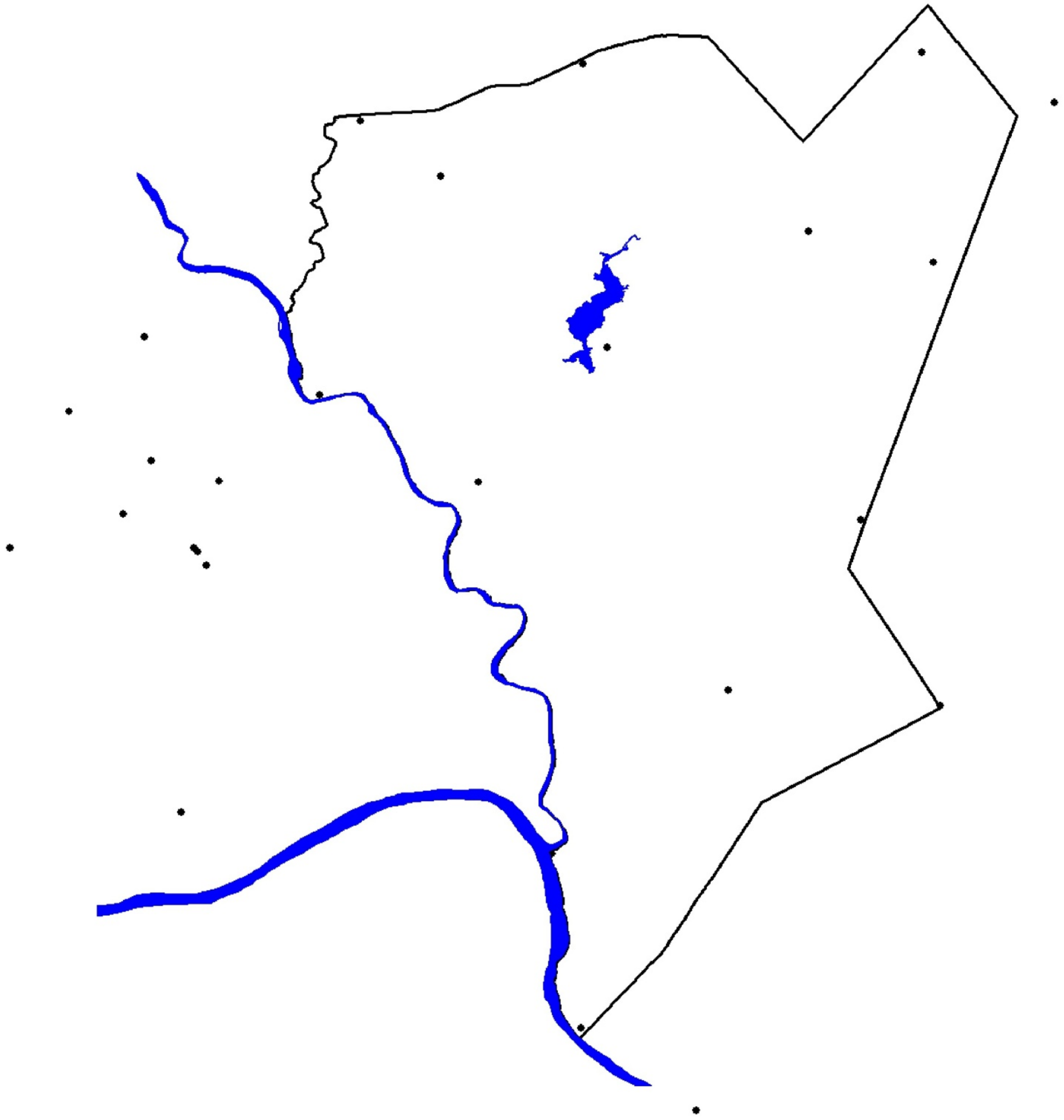


Figure 4.1 Spatial distribution of rain gauges.

A rainfall surface was generated for each rainfall event by interpolating between gauges, using the triangular irregular network module of Idrisi Kilimanjaro GIS Software (Eastman, 2003). Hobbs et al. (1994) showed that the evaporative constant k could be derived from m_{min} and, consequently, their regression equation was used to estimate k for each land unit. Daily PE data were collected from two class A evaporation pans that were located at the Zimbabwe Sugar Association, 27 km to the west of Malilangwe headquarters.

For each landscape unit, patch density at a site, D, was plotted against average soil moisture for the previous 5, 10, 15, 20, 25, 30, 45 and 60 days. From the scatter plots, it was evident that the relationship between green grass patch density and soil moisture could be described by a monotonically increasing sigmoidal curve, with lower and upper asymptotes 0 and 1 respectively. Consequently, the logistic equation:

$$D = \frac{1}{1 + \exp^{a - bM}},$$

where a and b are constants, was fitted to the data of each green grass density scatter plot using Systat 9 (SPSS, 1998). The relationship between mixed grass density and soil moisture was initially a monotonically increasing sigmoidal curve that was followed at higher levels of soil moisture by a monotonically decreasing sigmoidal curve. Consequently, the following model was fitted to the data for mixed grass density:

$$D = \left(\frac{1}{1 + \exp^{a - bM}} \right) \times \left(\frac{1}{1 + \exp^{c - dM}} \right),$$

where a, b, c and d are constants. For each landscape unit, the curve with the best fit was chosen to represent the relationship between patch density and soil moisture.

There was no relationship between density of green forb patches and soil moisture for any of the landscape units. Consequently, to estimate the density of green forb patches on a daily basis, a time series for each landscape unit was constructed by plotting the average density of patches against time and interpolating between sample points using the smoothing spline regression module of Kyplot 4.0 (KyensLab Inc., 2002). The equations of the curves for the grass patches and the interpolated data for the forb patches were linked to the land unit classification map using Idrisi Kilimanjaro GIS software (Eastman, 2003) and maps depicting the density of the different patch types were generated on a daily basis between 12th March 2002 and 10th March 2003.

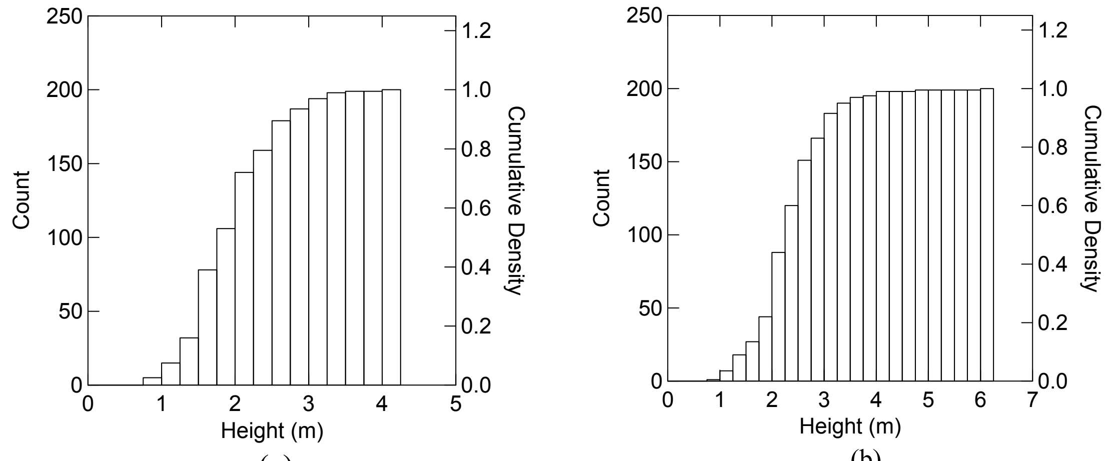
Leaves

Individual shrubs and trees were considered patches. While elephants were observed feeding, they were not seen eating senescent leaves. For this reason, shrubs and trees with only senescent leaf were excluded and only woody plants with > 25 % of their canopies with green leaf were used to estimate patch density. The 25 % cut-off was chosen because below this level it becomes difficult for elephants to harvest a trunkload that is comprised completely of green leaves. Elephants also avoided very young leaves of *Colophospermum mopane* (those with a reddish colour) possibly because at this stage mopane leaves are very unpalatable due to a high concentration of polyphenolics and the presence of strong smelling resinous exudates (Styles & Skinner, 1997). Consequently, mopane shrubs and trees with only very young leaves were excluded. Other species that were also excluded because they were avoided by elephants and other browsers, possibly due to the presence of secondary chemicals in the leaves were *Courbonia glauca*, *Euclea divinorum*, *Maerua parvifolia*, *Salvadora persica*, and *Thilachium africanum*. While it was recognised that many other plant species in the study area possibly contain secondary chemicals that potentially reduce their attractiveness to herbivores (Freeland & Janzen, 1974; Cooper & Owen-Smith, 1985), the influence of plant chemical defence on the diet of elephants was limited in this study to the exclusion of foliage from the plant species listed above. Due to the vast array of different defensive chemicals, and the fact that their concentration is subject to fluctuations in response to season (Styles & Skinner, 1997) and browsing pressure (du Toit et al., 1990; Wessels et al., 2007), a more comprehensive representation of their effects was not considered practicable given the scale of the study.

Data used to estimate the density of woody plants with green leaf were collected in the following way. Between November 2001 and July 2003, at approximately three-month intervals, five sample points were located in each landscape unit using a stratified random strategy and Idrisi32 GIS software (Eastman, 2001). In October 2002, spatial variability in rainfall caused the leaves of woody plants in parts of several landscape units to flush earlier than other parts. To capture this variation an additional 6 landscape units were added to the landscape classification. The additional landscape units were mapped from an October 2002 landsat 7 ETM+ image by using a Normalized Vegetation Index (NDVI) to isolate areas with an early flush of leaf. The co-ordinates of the sample points were uploaded onto a GPS, which was used to navigate to the sites. At each site, the nearest woody plant was assessed, using an eight-point scale (0 %; 1 %; 2-10 %; 11-25 %; 26-50 %; 51-75 %; 76-95 %; 96-100 %), and the following recorded: (1) species, (2) whether the plant was a shrub (≤ 3 m) or a tree (> 3 m), (3) percent of the canopy volume with new leaves and (4) percent of the canopy volume with mature green leaves. Once the first woody individual had been assessed, the next nearest individual was assessed in the same way. This process was repeated until 5 trees and 5 shrubs of each species had been sampled. To reduce sampling to manageable proportions, only species with a canopy volume > 25 and > 15 m^3/ha were sampled for trees and shrubs respectively. For each species of tree and shrub, the data from the 25 individuals sampled were averaged to give a single estimate for each date. To improve the temporal resolution of the time series data for each shrub and tree species, data were pooled across landscape units with similar topo-edaphic conditions. The percent canopy volume with new green leaf, V_{new}, and mature green leaf, V_{mature}, was estimated, on a daily basis, for each species of shrub and tree in a landscape unit, by interpolating between data points using the smoothing spline regression module of Kyplot 4.0 (KyensLab Inc., 2002). The total canopy volume with green leaf was calculated, for each shrub and tree species in a landscape unit, as:

$$V_{total} = V_{new} + V_{mature}$$

Bull elephants are taller than cows and are, therefore, capable of stripping leaves from a greater height. To determine the maximum reach for bulls and cows, a sample point was randomly located in woodland utilised by bulls only and in woodland often frequented by family units. In both woodlands, trees had leaf up to 8 m. The nearest tree to each sample point was selected and the height above the ground of each break point, on branches broken by elephant, was measured to the nearest centimetre. Once this was done, the next nearest tree was assessed in the same way. This process was repeated until the heights of 200 break points had been measured at each site. A frequency histogram showing the cumulative number of breaks at 0.25 m height intervals was plotted for each site. The histograms showed a maximum height of just over 6 m and 4 m for the bull and cow areas respectively (Figure 4.2) Consequently, 6 m and 4 m were taken as the maximum reach height for bulls and cows respectively.



(a) (b)

Figure 4.2 Histogram showing the cumulative frequency of height above the ground of break points in (a) woodland frequented by family units and (b) woodland utilised by bulls only.

The density of woody plants with green leaf available to bulls, D_{bull}, was calculated on a daily basis, for each landscape unit, as:

$$D_{bull} = \sum_{i=1}^{n} d_{i,tree,bull}\, p_{i,tree} + \sum_{i=1}^{n} d_{i,shrub}\, p_{i,shrub} \ ,$$

where $d_{i,tree,bull}$ is the density of the i^{th} tree species with canopy volume below 6 m, $p_{i,tree}$ is the Boolean probability (0 or 1) that $V_{total,i,tree} > 25$ %, $d_{i,shrub}$ is the density of the i^{th} shrub species and $p_{i,shrub}$ is the Boolean probability (0 or 1) that $V_{total,i,shrub} > 25$ %. The total density of woody plants with green leaf available to cows, D_{cow}, was calculated in the same way except that $d_{i,tree,cow}$ was based on individuals with canopy volume below 4 m. By linking the estimates of D_{bull} and D_{cow} for each landscape unit to the land unit classification map using Idrisi Kilimanjaro GIS software (Eastman, 2003) maps depicting the density of woody plants with green leaf available to bulls and cows were generated, on a daily basis, between 12th March 2002 and 10th March 2003.

Bark from canopy branches

Individual shrubs and trees of species from which elephants were commonly known to eat bark from canopy branches, were considered patches. The density of patches with bark available to bulls, in each landscape unit, was calculated as:

$$D_{bull} = \sum_{i=1}^{n} d_{i,shrub} + \sum_{i=1}^{n} d_{i,tree,bull} \ ,$$

where $d_{i,shrub}$ is the density of the i^{th} shrub species utilised for bark and $d_{i,tree,bull}$ is the density of the i^{th} tree species, that was utilised for bark, with canopy below 6 m. The density of woody plants in each landscape unit that was available for bark utilisation by cows was calculated in the same way, except $d_{i,tree}$ was based on the density of trees with canopy below 4 m. Note that although elephants can harvest bark from the branches of trees whose canopies are out of reach by first felling the tree, it was decided to simplify the modelling process and restrict harvesting of canopy bark to those trees that did not have to be felled first.

4.3.3. *Estimating the spatio-temporal pattern of protein bite mass for different food types*

Grass

Generally, when feeding on grass elephants up-root and consume a whole tuft at each bite. However, for robust perennials only the upper parts of a tuft are eaten, the roots and bases of the tillers being discarded (Note that when elephants are specifically targeting the rhizomes of robust perennials the opposite is observed.) Consequently, for robust perennials the mass of a bite was represented by the average mass of the upper portions of the tuft and for other species by the average mass of the whole plant.

The mass of plants in green grass patches and, therefore, bite mass of protein when feeding on green grass, $S_{grass,green,protein}$, varies both spatially and temporally because of differences between species, soil types and stages of growth. To capture this variation, $S_{grass,green,protein}$ was estimated daily for each landscape unit as:

$$S_{grass,green,protein} = \left(aH_{green}B\right) \times P_{green} \ ,$$

where H_{green} is the average height (cm) of the tallest green leaf, B is the average basal area (cm^2) of a tuft, P_{green} is the average protein density (g/g dm) of a green grass tuft and a is a constant. The bite mass of protein when feeding from mixed grass patches was estimated in the same way except values for H_{green} and P_{green} were substituted by values for mixed grass patches.

An estimate of a was derived for each landscape unit using the following method. A list of grass species was compiled by recording the dominant perennial grass species in each vegetation type. Twenty-five tufts, covering a range of leaf heights, basal areas and vegetation types, were selected for each species on the list. For each tuft, the height above the ground of the tallest leaf and the circumference of the base was measured to the nearest centimetre. The tuft was then uprooted, dried to constant mass, and weighed to the nearest gram. The data for individual grass species were then used to construct data sets for each vegetation type by pooling the data for each of the dominant grass species. Estimates of a were derived for each vegetation type by fitting the above equation to the data sets using the linear regression module of Systat 9 (SPSS, 1998).

To estimate H_{green}, and H_{mixed} on a daily basis, a time series for each landscape unit was constructed by plotting the average height data, that were collected during estimation of grass patch density, against time and interpolating between sample points using the smoothing spline regression module of Kyplot 4.0 (KyensLab Inc., 2002). Data for H_{mixed} were calculated as the average of H_{green} and H_{dry} for each sample point.

The average basal area of tufts in each landscape unit was estimated in the following way. In each landscape unit, between 50 and 100 tufts of each of the dominant perennial grass species were randomly selected. The circumference of each tuft was measured to the nearest centimetre. The point at which the coefficient of variation stabilised determined the number of tufts sampled for each species. It was recognised that there is a limit to the size of tufts elephants will uproot in a single trunkload. To estimate the preferred maximum circumference of tufts for bulls and members of family units 100 tufts of *Setaria incrassata* that had been uprooted, fed on and discarded were collected from beds of *Setaria incrassata* where bulls only and members of cow herds only had been feeding. *Setaria incrassata* was chosen as the target species because, of all the grass species at Malilangwe, it has individuals with the largest tuft circumference and therefore provides an opportunity to estimate the upper limit of tuft size selection. The average tuft circumferences selected by adult bulls and members of family units were calculated. These values were used to adjust the tuft circumference data sets for each grass species by setting a ceiling on the size of tufts selected by adult bulls and members of family units. The adjusted tuft circumference data were used to calculate the average basal area for each species. The average basal area of a tuft selected by adult bulls, B_{bull}, was estimated for each landscape unit as:

$$B_{bull} = \sum_{i=1}^{n} B_{i,bull} C_i ,$$

where $B_{i,bull}$ is the average basal area of a tuft of the i^{th} species selected by adult bulls and C_i is the proportional aerial cover of the i^{th} species. The average basal area of a tuft selected by members of cow herds, B_{cow}, was calculated in a similar way except that $B_{i,bull}$ was replaced by $B_{i,cow}$.

P_{green}, P_{dry} and P_{mixed} were estimated for each landscape unit in the following way. A list of grass species was compiled by recording the dominant perennial and annual grass species in each vegetation type. The following traits were recorded for each species: (1) maximum width (mm) of the leaf blade, (2) maximum length (mm) of the leaf blade, (3) maximum plant height (mm), (4) specific area of the leaf blade (cm^2/g) and (5) whether the species was an annual or a perennial. Data on the maximum width and length of the leaf blade, maximum plant height and whether the species was an annual or a perennial were obtained from Gibbs Russell et al. (1991) and van Oudtshoorn (2004). The specific area of the leaf blade was measured in the following way. Pressed samples of leaf blade were scanned at 300 dpi and the resulting image was imported into Idrisi Kilimanjaro GIS software (Eastman, 2003) where the total area (cm^2) of the samples was calculated. The samples were then dried to constant mass and weighed to nearest hundredth of a gram. The leaf specific area was then calculated by dividing the total area of the sample by its mass. To divide the grass species into groups based on similarity of the above traits a standardized grass species by traits matrix was subjected to hierarchical clustering using an Euclidian distance metric and complete linkage (furthest neighbour) method using Systat 9 (SPSS, 1998). Two species were then selected from each group produced by the classification. Randomly selected green and dry plants of each of the chosen species were collected at the end of the growing season and during the cool dry season respectively. The plants were pooled to create composite green and dry samples for each species and the composite samples were then analysed for crude protein by Feed Lab Services, Harare. On drying, annual grass species generally wither to such an extent that little trace of the plant is left. For this reason P_{dry} was not estimated for annual grass species. Using the crude protein estimates and measured traits of the selected species as a calibration dataset, regression tree models with a least squares loss function were developed to predict P_{green} and P_{dry} from the measured traits using Systat 9 (SPSS, 1998). These models were then used to estimate P_{green} and P_{dry} for the remaining species. P_{mixed} was calculated as the average of P_{green} and P_{dry}. The average protein density of green grass plants was then calculated for each landscape unit as:

$$P_{green} = \sum_{i=1}^{n} P_{i,green} C_i ,$$

where $P_{i,green}$ is the protein density (g/g dm) of the i^{th} grass species and C_i is the relative aerial cover of the i^{th} grass species. P_{mixed} was calculated for each landscape unit by substituting $P_{i,green}$ for $P_{i,mixed.}$

Annual grass species dominated the herbaceous layer of some vegetation types and because elephants also utilise annual grasses the most important annual grass species were selected for measurement. However, the seasonal variation in mass of annual grass plants was considered less significant than the variation in the mass of perennial grass plants and therefore, only the dry mass of 25 randomly selected plants was measured for each species. From this the average dry mass of a plant was calculated for each species. For these vegetation types $S_{grass,green,protein}$ was estimated as:

$$S_{grass,green,protein} = \sum_{i=1}^{n} W_i P_{i,green} C_i \,,$$

where W_i is the average dry mass of the i^{th} annual grass species, $P_{i,green}$ is the protein density (g/g dm) of the i^{th} green annual grass species and C_i is the relative percent aerial cover of the i^{th} annual grass species.

Forbs

When feeding on forbs, elephants up root and consume a whole plant at each bite. It was assumed that the mass of individual forb plants was at a maximum at the end of the growing season and that the mass declined from maximum as the dry season progressed due to browsing and senescence. It was assumed that the decline in mass was proportional to the change in average forb height and, consequently, the bite mass of protein when feeding on forbs, $S_{forb,protein}$, was calculated, for each vegetation type, as:

$$S_{forb,protein} = \sum_{i=1}^{n} W_i H_{forb} P_i C_i \,,$$

where W_i is the average dry mass of the i^{th} forb species at the end of the growing season, H_{forb} is the average height of green forbs relative to the maximum average height measured for the vegetation type, P_i is the protein density (g/g dm) of the i^{th} forb species and C_i is the proportional aerial cover of the i^{th} forb species.

In contrast to the pattern of abundance of grasses, the forb component of the herbaceous layer at Malilangwe is seldom dominated by a few species. Instead, many forb species occur in low abundance. Consequently, to reduce data collection to manageable proportions, the researcher must decide either to sample a portion of the species intensively or decrease sampling intensity and cover more species. It was decided to take the latter approach and the average dry mass of each species of forb, W_i, was estimated, at the end of the growing season, from the dry mass of 5 randomly selected individuals.

The protein density for each forb species, P_i, was estimated in the following way. A list of forb species was compiled by recording the dominant forb species in each vegetation type. The following traits were then measured for each species: (1) leaf specific area (cm^2/g), (2) leaf-to-stem ratio, and (3) force required to crush the stem (Nm). Leaf specific area was measured using the same method used to calculate the specific area of the leaf blade of grasses. The leaf-to-stem ratio was calculated for each species by separately weighing the dry leaves and stems of 5 randomly chosen plants. The leaf-to-stem ratio was calculated for each plant and then the average of the 5 values was calculated to arrive at a final estimate. The force required to crush the stem was measured in the following way. The stem of an entire, randomly chosen forb plant was cut up into approximately 2 cm sections. Twenty sections were randomly chosen and, in turn, each section was closed in a miniature vice. The vice was closed by turning a threaded bolt with a miniature torque wrench. The vice was closed until the section of stem began to deform and split. The force required to reach this point was recorded. The average force was calculated from the 20 measurements. To divide the forb species into groups based on similarity of the above traits, a standardized forb species by traits matrix was subjected to hierarchical clustering using a Euclidian distance metric and complete linkage (furthest neighbour) method using Systat 9 (SPSS, 1998). Two species were then selected from each group produced by the classification. Randomly selected green plants of each of the chosen species were collected at the end of the growing season. The plants were pooled to create a composite sample for each species and the samples were then analysed for crude protein by Feed Lab Services, Harare. Using the crude protein estimates and measured traits of the selected species as a calibration dataset, a regression tree model with a least squares loss function was developed using Systat 9 (SPSS, 1998) to predict protein density from the measured traits. This model was then used to estimate P_i for the remaining species.

Leaves

The mass of an individual leaf or leaflet influences the mass of leaves gathered with each trunkload from woody plants. When feeding from plants with small leaves, elephants extract small trunkloads because the mass of individual leaves is low and, because small leaves are difficult to handle, many leaves fall from the trunk's grasp. The converse is true for woody plants with large leaves. To account for variation between species of woody plants, the mass of a trunkload of leaves, S_{leaf}, was estimated for each woody species using a linear regression model with the mass of a leaf unit as the predictor variable:

$$S_{leaf,i} = aM_{leaf,i}$$

where $S_{leaf,i}$ is the dry mass of a trunkload of the i^{th} woody species, $M_{leaf,i}$ is the dry mass of a leaf unit of the i^{th} woody species and a is a constant. Separate models were created for bulls and cows. A leaf unit was defined as the smallest unit held by the trunk and was most often represented by a leaflet. The data used to create the regression models were collected by observing adult and subadult bull and cow elephants stripping or plucking leaves from a range of woody plant species. When an elephant moved off, five samples were gathered from the plant it had been feeding on by simulating the amount of leaf it had extracted at each trunkload. The average dry weight of the 5 samples provided an estimate of S_{leaf}. In this way, estimates of S_{leaf} were obtained for a range of species, across a number of different bulls and cows. The average dry mass of a leaf unit was calculated for each species by randomly selecting 5 individual plants of each species and collecting between 10 and 100 leaf units, depending on the size of a unit, from each individual. The leaf units were often too small to be weighed individually and, consequently, the weight of a leaf unit was calculated indirectly from the specific leaf area.

The protein density (g/g dm) of mature green leaves was estimated for each woody species in the following way. The leaf specific area (cm^2/g) of mature green leaves was measured for each woody plant species used in estimation of leaf patch density. A subset of 19 woody species covering a wide range of leaf specific area values was selected and samples of mature green leaves were collected from randomly selected individuals of each chosen species. The samples were pooled to create composite samples for each species, which were then analysed for crude protein content (Feed Lab Services, Harare). The estimates of crude protein content and the values for leaf specific area were then used to calibrate a linear regression model in Systat 9 (SPSS, 1998) that predicted the crude protein density of mature green leaves from leaf specific area. The regression model was then used to predict the crude protein density of mature green leaves for the remaining woody plant species.

The average mass of protein from a bite of green leaf for bulls was then estimated for each landscape unit as:

$$S_{leaf,protein,bull} = \sum_{i=1}^{n} S_{leaf,i,bull} P_{leaf,i} D_{i,bull} \ ,$$

where $S_{leaf,i,bull}$ is the dry mass of a trunkload of green leaf gathered by an adult bull from the i^{th} woody species, $P_{leaf,i}$ is the protein density of green leaf of the i^{th} woody species and $D_{i,bull}$ is the density (no. individuals/ha) of the i^{th} woody species with canopy volume below 6 m and > 25 % canopy volume with green leaf. $S_{leaf,protein,cow}$ was calculated in the same way except $S_{leaf,i,bull}$ was substituted by the value for cows and $D_{i,bull}$ was replaced by $D_{i,cow}$ which was the density (no. individuals/ha) of the i^{th} woody species with canopy volume below 4 m and > 25 % canopy volume with green leaf.

Bark from canopy branches

Elephants remove bark from the canopy branches of shrubs and trees by breaking off a branch, placing it in the mouth and then chewing off the bark along the length of the branch. The average mass of bark, W, extracted from a branch was estimated for the most commonly used species in the following way.

For each species, 10 to 13 branches, across a range of diameters and lengths, were collected. Each branch was gathered from a separate, randomly chosen plant. For each branch, the bark was removed, dried to constant mass and weighed to the nearest gram. Once the bark had been removed, the length (cm) and diameter (mm) at 10 cm intervals was measured for each branch. The diameter measurements at 10 cm intervals were used to calculate an average diameter for each branch. Equations predicting the mass of bark from a branch were developed using Systat 9 (SPSS, 1998), for each species, by estimating the parametres of the following model using non-linear regression:

$$W = aLD + b(LD)^2 ,$$

where W is the dry mass of bark, L is the length of the branch, D is the average diameter of the branch and a and b are constants. One hundred branches that had been fed on by adult bulls and 100 branches that had been fed on by members of family units were collected for each plant species. For each branch, the length and average diameter was measured for the part from which bark had been removed. When a forked branch was debarked, each fork was measured separately. The mass of bark removed from each branch was then estimated using the regression equations. The average mass of bark removed from branches of each species was calculated for adult bulls and members of family groups by calculating the average of the respective samples.

The protein density of bark was estimated by cutting branches from randomly selected individuals of the most commonly utilised woody species during the cool dry season and stripping off the bark from the branches. The bark from the separate branches was pooled to create composite samples for each species, which were then analysed for crude protein content by Feed Lab Services, Harare. The average protein bite mass of bark for bulls, $S_{bark,bull}$, was then calculated for each vegetation type as follows:

$$S_{bark,protein,bull} = \sum_{i=1}^{n} W_{i,bull} P_i D_{i,bull} \ ,$$

where $W_{i,bull}$ is the average dry mass of bark removed by bulls for the i^{th} species, P_i is the protein density (g/g/dm) of bark of the i^{th} species, and $D_{i,bull}$ is the relative density of the i^{th} species with canopy below 6 m. $S_{bark,cow}$ was calculated in a similar way except $W_{i,bull}$ was replaced by $W_{i,cow}$ and $D_{i,bull}$ by $D_{i,cow}$ which was the relative density of individuals of the i^{th} species with canopy below 4 m.

4.3.4. *Estimating the speed of travel between patches*

The speed of travel between patches *(V)* was estimated for adult bulls, adult cows and subadults by observing an elephant feeding and recording the distance (m) travelled between two feeding stations, and the time (s) taken to travel the distance. Twenty arbitrarily chosen individuals were sampled for each sex and age class. Where more than one estimate was obtained per individual, the estimates were averaged to calculate a single estimate for the individual. Differences in travel speed between adult bulls, adult cows and subadults were tested using the analysis of variance module of Systat 9 (SPSS, 1998). No obvious seasonal difference in the speed of travel between patches was noticed during the period of elephant observation and, consequently, no attempt to uncover seasonal differences was made.

4.3.5. *Estimating the number of trunkloads per patch for each food type*

For grass and forbs elephants were assumed to harvest a single trunkload per patch. For the other food types the number of trunkloads per patch (*N*) was estimated separately for adult bulls and cows as the average across all observations.

4.3.6. *Running the ingestion model for each food type*

To estimate the spatio-temporal pattern of the short-term rate of intake of protein (*I*) for adult bulls and cows when feeding on different food types the ingestion model was linked to Idrisi Kilimanjaro GIS software (Eastman, 2003) and run for each food type, at a daily time step, for one annual cycle.

4.4. Results

4.4.1. *Estimates of prehension time and chewing time for different food types*

Adult bulls, adult cows and subadult bulls were observed 105, 25 and 10 times respectively, with a total of 66 hours of feeding recorded across 32 vegetation types. The spatial distribution of the observations is shown in Figure 4.3. Adult cows and subadult bulls were observed less frequently than adult bulls because they tended to associate in large groups (up to 80 individuals) and were therefore more difficult to approach on foot. A total of 109 plant species were fed on but this is an underestimate because the contents of many trunkloads could not be identified to species level.

Elephants fed on the following food types: whole grass plants, grass inflorescences (only observed for cows), grass roots, whole forb plants, leaves of woody plants, twigs of woody plants, bark from canopy branches of trees and shrubs, bark from the main stems of trees, bark from roots of trees and shrubs, roots of trees and shrubs, tubers, flowers and fruits. Often a trunkload was composed of more than one food type e.g. leaves and twigs or leaves, twigs and fruits.

Harvesting methods differed within and across food types. Grass plants were plucked by wrapping the trunk around the above ground portions of a tuft and pulling to uproot the plant. If soil was attached to the roots or a significant amount of senescent leaf material was present, this was removed by thrashing the tuft against the chest or front leg. Most often the entire grass plant was consumed, but when the base of the tillers were particularly robust, only the upper portion of the tuft was eaten, the roots and bases of the tillers being discarded. Grass roots were harvested in the same way except the above ground portions of the plant were discarded and only the roots eaten. Grass inflorescences were gathered by wrapping the trunk around a number of culms and pulling. Forbs with an erect growth form were plucked in a similar way to grass tufts, with the entire plant being consumed. Forbs with a creeping or climbing growth habit were gathered by extracting a long length, bundling it in the trunk, and then inserting the bundle into the mouth. Leaves of woody plants were either stripped or plucked. Stripping was most commonly done by wrapping the trunk around a leafy branch and then pulling the trunk along the length of the branch. Leaves were also stripped by loosely grasping a leafy branch in the mouth and then allowing the branch to run through the mouth while moving away from the plant. Stripping often resulted in a significant amount of twigs being included in the trunkload. Leaves were plucked using the projections at the end of the trunk. Plucking resulted in fewer twigs being included in the trunkload compared to stripping, but the mass of the trunkload was reduced. Leaves and twigs were harvested by wrapping the trunk around a slender branch and then bending the branch until it snapped. The entire branch was then consumed. For woody species with bark of a high tensile strength e.g. *Acacia tortilis*, leaves and twigs were harvested by grasping the end of a branch in the mouth and then drawing the branch taught across the end of a tusk until it snapped. Preference for this harvesting technique is indicated by the development of a marked groove a few centimetres back from the tip of the working tusk. Often an additional action such as breaking down a branch or felling the tree was required before a trunkload of leaves or leaves and twigs could be harvested. Bark was harvested from the canopy branches of shrubs and trees by snapping off a branch (approximately 2 cm in diameter) with the trunk, placing it in the mouth and then chewing off the bark along the length of the branch. Bull elephants harvested bark from the main stems of trees by gouging and prising out sections using their tusks. Once gouging had created a piece of bark that could be grasped by the trunk with sufficient purchase, the bark was stripped away from the trunk by pulling upwards. This was only possible for tree species with bark of an adequate tensile strength. Bulls most frequently employed this technique, presumably because they have the strength to gouge and pull the bark. Cows preferred to either snap the main stem or locate a tree whose main stem had been snapped and then strip off small pieces of bark by pulling on the torn, jagged edges of bark that were created when the stem was snapped. Cows frequently employed this technique when harvesting bark from the main stems of small (main stems of approximately < 15 cm diameter) *Colophospermum mopane* trees. Roots were harvested by digging with the feet, uprooting shrubs by plucking with the trunk, pushing over trees or by grasping exposed roots with the trunk and pulling to lift long sections out of the soil. Tubers (e.g. those of *Jatropha* spp.) were particularly sought after by cows after rain in areas with sandy soil. A unique method was used to harvest tubers. First the tuber would be partially excavated by ploughing backwards and forwards through the soil with a foot. The moist soil after rain facilitated digging because the soil did not slide back into the hole. Once part of the tuber was exposed the elephant would kneel down and impale the tuber with a tusk. On rising it would remove the tuber from the tusk with the trunk and place it in the mouth. Fruits where either plucked from the plant or picked up from the ground after the tree had been shaken to dislodge the fruits. When gathering small fruits from the ground e.g. pods from *Acacia tortilis*, the fruits were swept into a pile, which was then ladelled into the mouth using the trunk.

Estimates of prehension and handling times for food types harvested using different modes of prehension are shown for each sex and age class in Table 4.2 and Table 4.3 respectively. Estimates with low sample sizes were retained to illustrate that food types could be harvested in different ways. The low sample sizes for estimates of prehension time reflect the difficulty experienced, particularly for the food types from the herbaceous layer, in determining the point at which prehension began. Often the trunk would be directed to the herbaceous layer where, largely hidden from view, it would move around apparently without any particular purpose and then suddenly a trunkload would be plucked and taken to the mouth. The suddenness of the action and lack of warning made estimation of the time taken to gather the trunkload difficult. Prehension times were relatively short for trunkloads of green grass, leaves and forbs; intermediate for trunkloads of leaves and twigs and mixed grass; and relatively long for trunkloads of bark and roots. Additional harvesting actions, such as shaking a tuft of grass to remove senescent material, breaking a canopy branch or felling a tree substantially increased the prehension time relative to instances when additional actions were not required. Adult cows and subadults appeared to forage with greater urgency than adult bulls. This observation is supported by the shorter prehension times of adult cows and subadults relative to adult bulls across most food types.

Handling times were relatively short for trunkloads of green grass, forbs, leaves and fruits, intermediate for trunkloads composed of leaves and twigs, long for trunkloads of canopy bark and roots and very long for trunkloads of main stem bark. Handling times for most food types were longer for adult bulls than for adult cows and subadults. Handling time was mostly constrained by chewing, but prehension did appear to limit handling when an additional action such as breaking a branch or felling a tree was necessary before a trunkload could be harvested. Handling of a trunkload of leaves and stems by adult cows and subadult bulls appeared to be prehension limited.

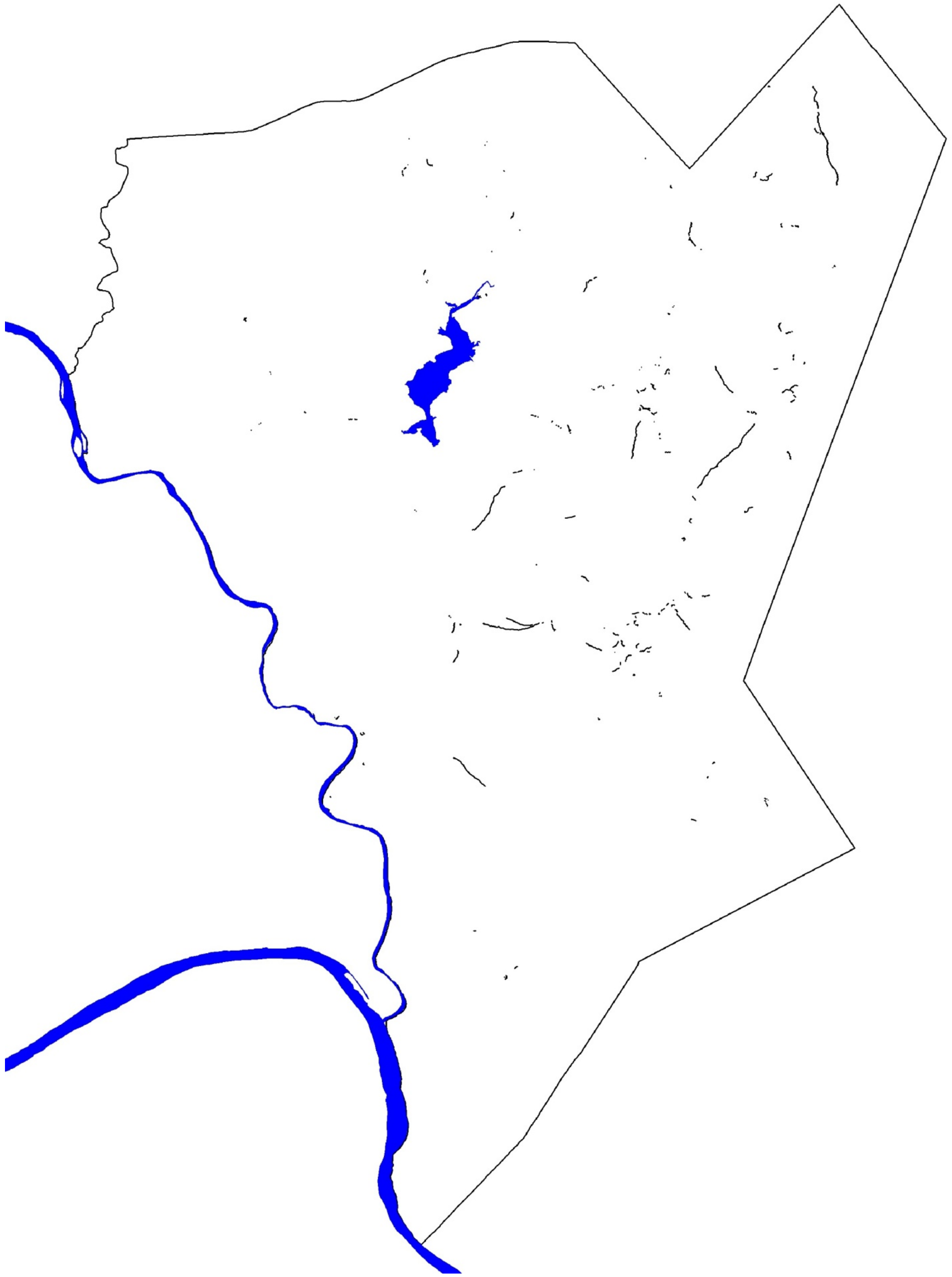


Figure 4.3 The spatial distribution of the tracks saved on a GPS while following elephants.

Table 4.2 Average prehension time for food types harvested using different modes of prehension. The estimates represent the time (s) taken to gather a single trunkload and place it in the mouth. Sample size and the 95 % confidence interval are given in curved and square parentheses respectively. The symbol – denotes no data

		Prehension time (s)		
Food type	**Mode of prehension**	**Adult bull**	**Subadult bull**	**Adult cow**
Grass - green	Pluck tuft	7 (26) [± 2.3]	4 (9) [± 2.0]	5 (5) [± 3.5]
	Pluck & shake tuft to remove soil from roots	10 (1)	-	-
Grass - mixed green & dry	Pluck & shake tuft to remove dry material	12 (129) [± 1.2]	9 (10) [± 3.1]	10 (14) [± 2.1]
Forb	Pluck whole plant	6 (16) [± 2.0]	-	-
	Pluck & shake plant to remove soil from roots	7 (3) [± 6.8]	-	-
Leaves	Strip	10 (169) [± 1.1]	7 (5) [± 2.6]	7 (57) [± 1.0]
	Break off canopy branch & strip	16 (2) [± 1.6]	-	-
	Snap-bend canopy branch & strip	26 (20) [± 5.3]	-	14 (1)
	Fell tree & strip	50 (10) [± 27.3]	-	-
Leaves & twigs	Pluck	19 (248) [± 1.9]	14 (5) [± 9.6]	12 (50) [± 2.8]
Leaves & fruits	Strip	-	-	9 (6) [± 4.0]
Leaves, twigs & fruits	Pluck	-	-	11 (2) [± 4.2]
Twigs	Pluck	10 (6) [± 8.8]	-	4 (1)
Bark from canopy branches	Break off canopy branch & chew off bark	23 (90) [± 3.1]	48 (2) [± 67.9]	16 (37) [± 2.9]
	Strip bark from canopy branch using trunk	20 (18) [± 6.5]	-	29 (1)
	Break off canopy branch & strip bark using trunk	35 (1)	-	-
	Fell tree, break canopy branch & strip bark using trunk	38 (1)	-	-
Bark from main stem	Snap main stem & remove bark using trunk	-	-	15 (15) [± 5.1]
	Remove bark from main stem using tusks	75 (20) [± 42.1]	-	-
Bark from root	Strip bark from root using trunk	27 (12) [± 11.9]	-	-
	Dig root using feet & strip bark using trunk	114 (2) [± 98.4]	-	-
Root	Break off root using trunk	8 (2) [± 5.5]	-	21 (3) [± 4.5]
	Dig using feet & break off root using trunk	64 (8) [± 46.4]	-	-
	Dig root using feet	48 (3) [± 23.8]	-	-
	Pluck shrub & break off root using trunk	36 (5) [± 7.0]	-	38 (1)
Fruit	Shake tree & pick up fallen fruit from ground	44 (2) [± 18.0]	-	-

Table 4.3 Average handling time for food types harvested using different modes of prehension. The estimates represent the time (s) taken to gather and chew a single trunkload. Sample size and the 95 % confidence interval are given in curved and square parentheses respectively. The superscripts * and $^{\psi}$ indicate whether the handling time represents chewing time or prehension time respectively. It could not be determined if handling was constrained by prehension or chewing for estimates with no superscript. The symbol – denotes no data

		Handling time (s)		
Food type	**Mode of prehension**	**Adult bull**	**Subadult bull**	**Adult cow**
Grass - green	Pluck tuft	12 (1524) [± 0.3] *	9 (346) [± 0.6] *	9 (150) [± 0.6] *
Grass – mixed green & dry	Pluck & shake tuft to remove dry material	27 (99) [± 2.4] *	38 (10) [± 8.1] *	27 (10) [± 5.0] *
Grass inflorescence	Pluck inflorescence	-	-	6 (31) [± 0.7]
Forb	Pluck whole plant	12 (1097) [± 0.4] *	10 (98) [± 1.0] *	11 (168) [± 1.1] *
	Pluck & shake plant to remove soil from roots	22 (3) [± 2.3] *	-	-
Leaves	Strip	13 (829) [± 0.6] *	17 (9) [± 15.0] *	9 (126) [± 0.9] *
	Snap-bend canopy branch & strip	32 (16) [± 6.9] $^{\psi}$	-	-
	Fell tree & strip	43 (4) [± 30.4] $^{\psi}$	-	-
Leaves & twigs	Pluck	25 (747) [± 1.7] *	13 (45) [± 2.6] $^{\psi}$	12 (194) [± 1.4] $^{\psi}$
Leaves & fruits	Strip	-	-	13 (4) [± 4.9]
Twigs	Pluck	27 (12) [± 7.9] *	-	19 (5) [± 9.6] *
Bark from canopy branches	Break off canopy branch & chew off bark	45 (99) [± 5.9] *	29 (1) $^{\psi}$	32 (32) [± 6.2] *
	Strip bark from canopy branches using trunk	51 (21) [± 13.3] *	-	36 (1) *
Bark from main stem	Snap main stem & remove bark using trunk	-	-	27 (18) [± 9.2] *
	Remove bark from main stem using tusks	101 (26) [± 40.0] *	-	-
Bark from root	Strip bark from root using trunk	64 (24) [± 21.6] *	-	30 (1)
	Dig root using feet & strip bark using trunk	139 (3) [± 58.8] *	-	-
Root	Break off root using trunk	36 (73) [± 8.3] *	-	24 (7) [± 14.8] *
	Pluck shrub & break off root using trunk	36 (1) $^{\psi}$	-	-
	Dig using feet & break off root using trunk	72 (8) [± 56.8] *	-	-
Roots from grass	Pluck tuft	26 (14) [± 6.8] *	-	-
	Pluck & shake tuft to remove soil from roots	36 (20) [± 6.1] *	-	-
Fruit	Pick up fruit from ground	12 (16) [± 3.4]	-	-
	Pluck	-	48 (10) [± 33.5]	
	Shake tree & pick up fallen fruit from ground	58 (2) [± 19.4] $^{\psi}$	-	-

4.4.2. *Spatio-temporal pattern of patch density for different food types*

Grass

The average daily rainfall (mm) over the study period, and the amount (mm) and spatial distribution of rain for each month are shown in Figure 4.4 and Figure 4.5 respectively. Rain fell on 77 of the 364 days, giving an average total across the study area of 645 mm. In terms of rainfall, the study period was unusual because (1) it was preceded by a below average 2001/2002 rainy season, and (2) unseasonably heavy falls occurred in April, July, September and October. For most months, the distribution of rainfall was patchy (Figure 4.5).

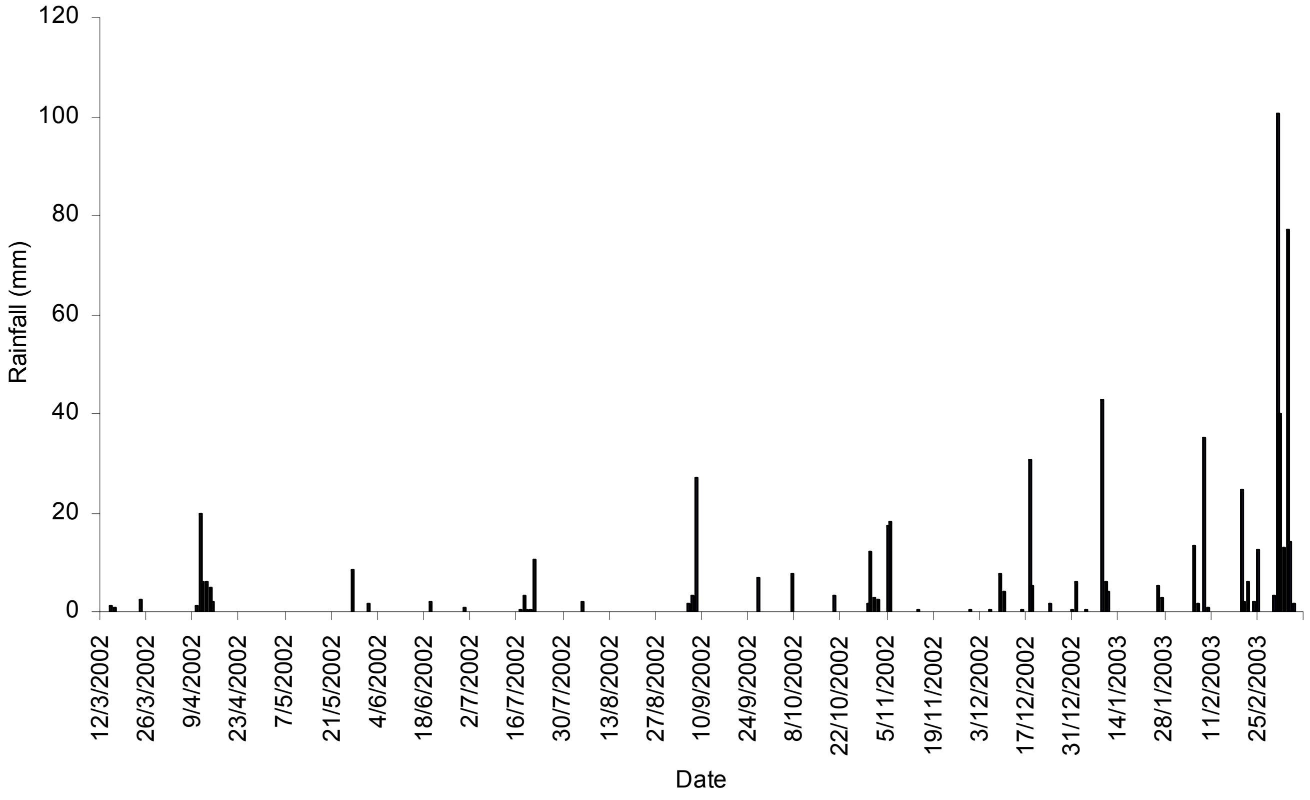
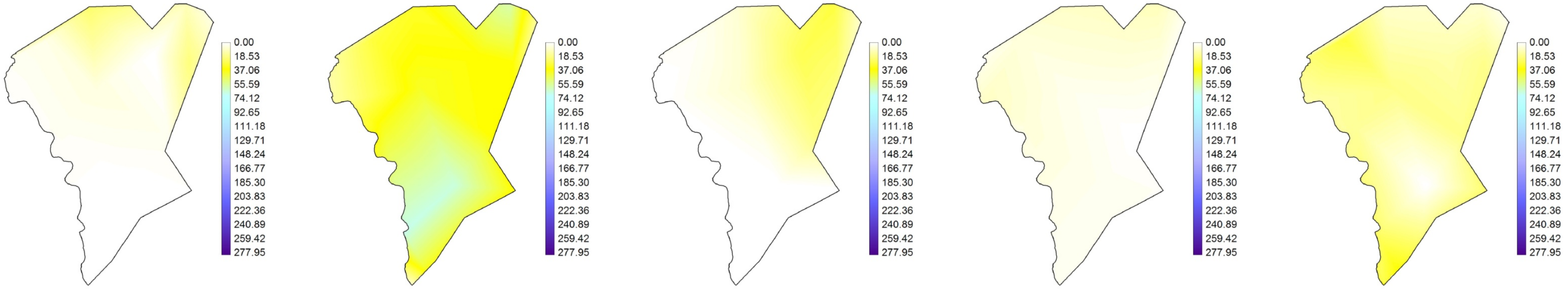


Figure 4.4 Average rainfall (mm) across the study are for each day of the study period. For the spatial positions of the 26 rain gauges used to collect the data see Figure 4.1.

Daily potential evaporation (PE) over the study period is shown in Figure 4.6. There was large daily variation in PE but, in general, PE was high in the hot months (average = 6.2 mm/day) and low in the cool months (average = 3.8 mm/day). The maximum PE recorded was 11.4 mm/day.



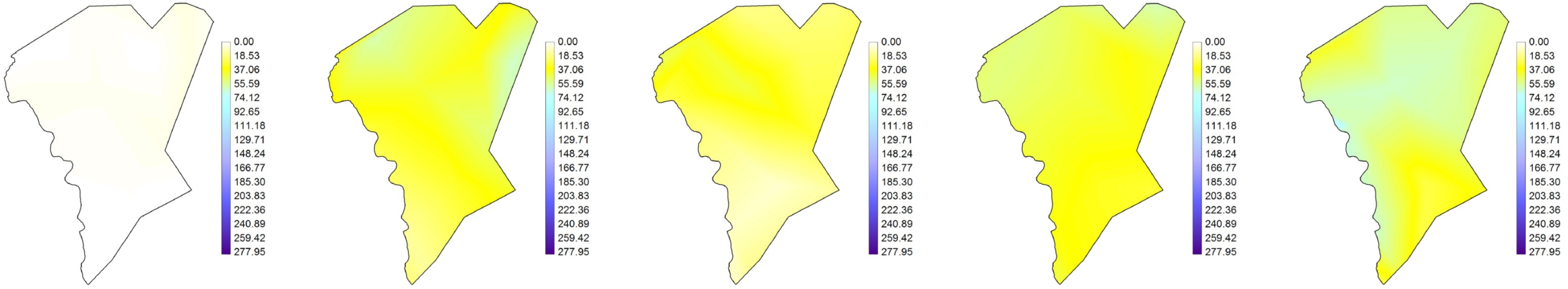
12th – 31st March 2002

April 2002

May 2002

June 2002

July 2002



August 2002

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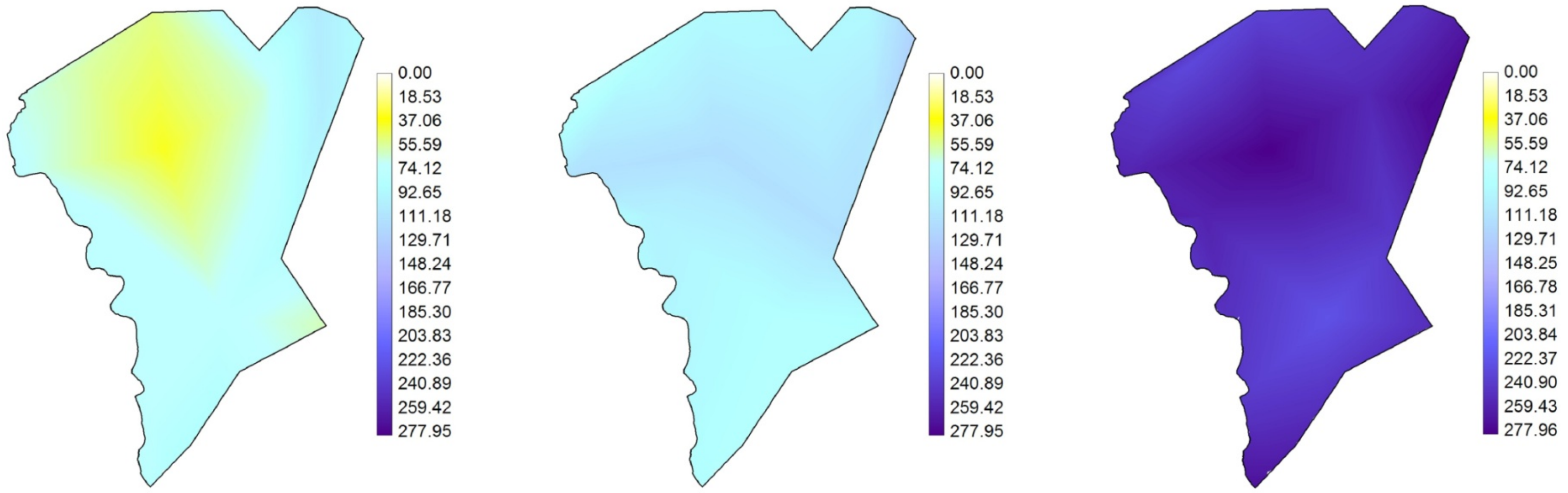


January 2003

February 2003

1st - 10th March 2003

Figure 4.5 Amount (mm) and distribution of rain across the study area for each month of the study period. Maps were created by interpolating between rainfall data collected at 26 rain gauges using a triangular irregular network (TIN).

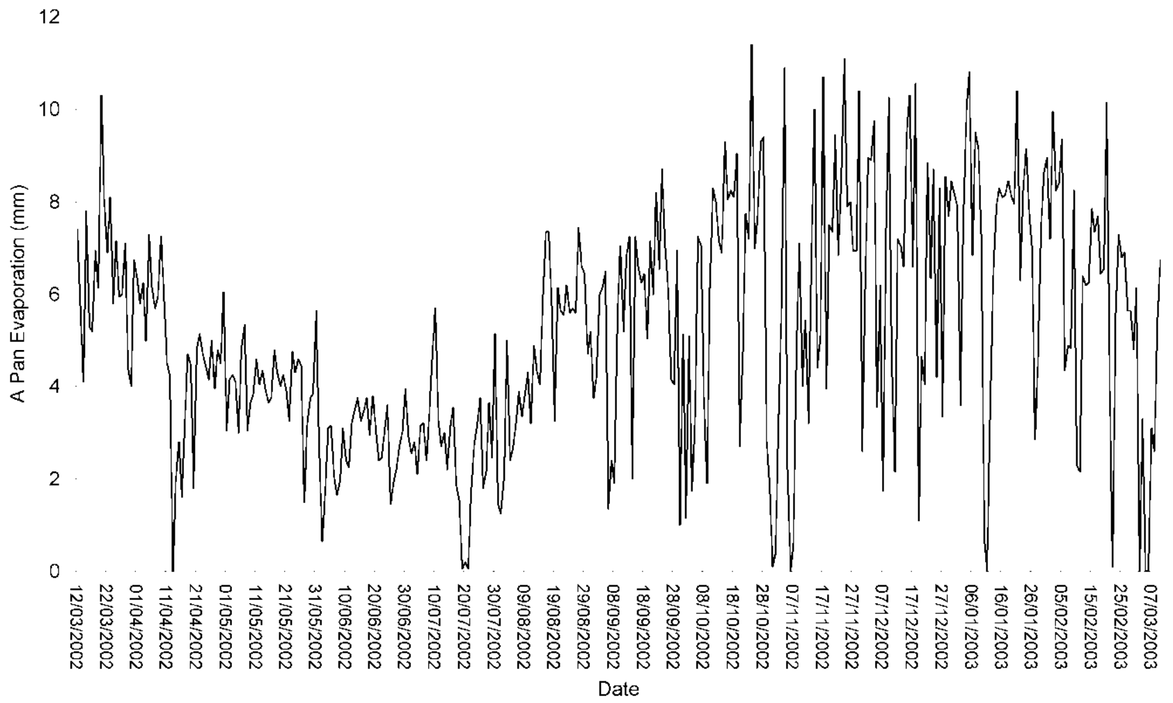


Figure 4.6 Daily A Pan evaporation (mm) over the study period. Data were collected at the Experimental Station of the Zimbabwe Sugar Association, 27 km west of Malilangwe Headquarters.

Average field capacity, average minimum air-dried soil moisture and estimates of the evaporative constant for the soil of each vegetation type are shown in Table 4.4. Estimated field capacity varied between 42 mm per 0-300 mm profile for the *Lannea schweinfurthii – Pteleopsis myrtifolia* shrub woodland and 101 mm per 0-300 mm profile for the *Acacia nigrescens – Combretum hereroense* open woodland. Minimum air-dried soil moisture ranged from 5 mm per 0-300 mm profile for the soil of vegetation types with < 7 % clay to 20 mm per 0-300 mm profile for the soil of the *Acacia nigrescens – Combretum hereroense* open woodland that had a clay content of 44 %. Estimates of the evaporative constant varied across vegetation types implying different rates of soil moisture loss.

The average daily soil moisture in the top 30 cm of soil across the study area is shown in Figure 4.7. The soil moisture time series shows a number of pulses each characterised by a steep rise in soil moisture in response to rainfall, and a less steep decline as soil moisture is lost through evapo-transpiration. Heavy rains caused an increase in soil moisture in April and September 2002, but otherwise soil moisture levels were relatively low until November 2002 when the 2002/2003 rainy season began. Inter-season droughts caused soil moisture levels to drop between mid-November and mid-December 2002 and during January 2003, but in response to heavy rains, levels rose again in February and March 2003.

Table 4.4 Average field capacity (m_{FC}), average minimum air-dried soil moisture (m_{min}) and estimates of the evaporative constant (k) for the soil of each vegetation type. For a key to vegetation type numbers see Figure 3.1

Vegetation type	Sample size	Average clay (%)	Average sand (%)	Average silt (%)	Average field capacity of top 30 cm of soil profile (mm)	Average moisture of air-dried soil in top 30 cm of profile (mm)	Average evaporative constant (k)
1	4	9.5	80.5	10.0	58	8	0.0115
2	11	13.1	82.7	4.2	52	7	0.0118
3	15	7.5	87.9	4.7	48	6	0.0124
4	12	5.3	91.8	2.8	42	5	0.0128
5	5	8.0	88.8	3.2	45	6	0.0125
6	3	8.0	88.7	3.3	46	6	0.0125
7	10	5.2	90.4	4.4	45	5	0.0127
8	6	12.3	78.3	9.3	60	9	0.0113
9	9	13.8	80.0	6.2	56	8	0.0115
10	7	11.1	82.3	6.6	54	8	0.0117
11	9	9.6	83.1	7.3	54	7	0.0118
12	5	35.2	49.6	15.2	93	17	0.0080
13	4	19.0	72.0	9.0	66	11	0.0106
14	1	26.0	66.0	8.0	71	12	0.0099
15	4	12.5	81.5	6.0	55	8	0.0116
16	6	12.0	81.7	6.3	55	8	0.0117
17	22	14.5	79.2	6.4	57	9	0.0114
18	11	12.0	83.3	4.7	52	7	0.0118
19	3	6.7	89.3	4.0	46	5	0.0125
20	9	17.8	72.9	9.3	66	10	0.0107
21	14	14.6	78.1	7.3	59	9	0.0113
22	6	18.7	69.7	11.7	70	11	0.0103
23	18	19.6	68.4	12.0	72	12	0.0101
24	7	29.7	59.1	11.1	80	15	0.0091
25	6	30.0	54.0	16.0	89	16	0.0085
26	3	10.0	84.0	6.0	52	7	0.0119
27	17	14.6	78.5	6.9	58	9	0.0113
28	2	21.0	69.0	10.0	70	12	0.0102
29	3	13.3	80.7	6.0	56	8	0.0115
30	5	34.0	47.2	18.8	97	18	0.0077
31	3	6.7	90.7	2.7	43	5	0.0127
32	6	27.3	59.0	13.7	82	15	0.0091
33	12	38.0	47.5	14.5	95	18	0.0077
34	5	41.2	42.8	16.0	100	19	0.0072
35	3	20.7	68.0	11.3	72	12	0.0101
36	23	31.4	54.1	14.5	88	16	0.0085
37	4	44.0	41.5	14.5	101	20	0.0070
38	6	21.0	63.3	15.7	79	13	0.0096

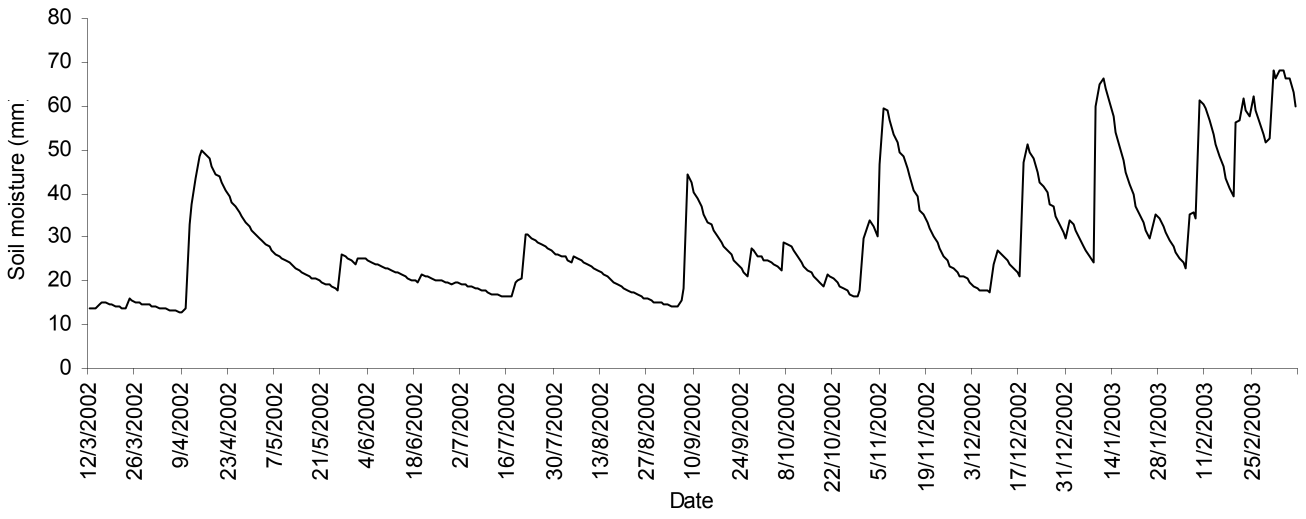


Figure 4.7 Average soil moisture (mm) in the top 30 cm of soil across the study area for each day of the study period.

Figure 4.8 shows the spatial distribution of soil moisture stored in the top 30 cm of soil for each month of the study period. In general, more water was stored in the basalt-derived soils that occur in the southern and eastern parts of the study area than in the sandier soils of the western and northern parts that are derived from alluvium, sandstone and paragneiss. The highest levels of soil water were stored in the heavy clay soils of the *Setaria incrassata* grassland, the *Acacia nigrescens – Acacia nilotica* open woodland, the *Dichrostachys cinerea – Dalbergia melanoxylon* open woodland and the *Acacia nigrescens – Combretum hereroense* open woodland. The lowest levels were stored in the very sandy soils derived from sandstone.

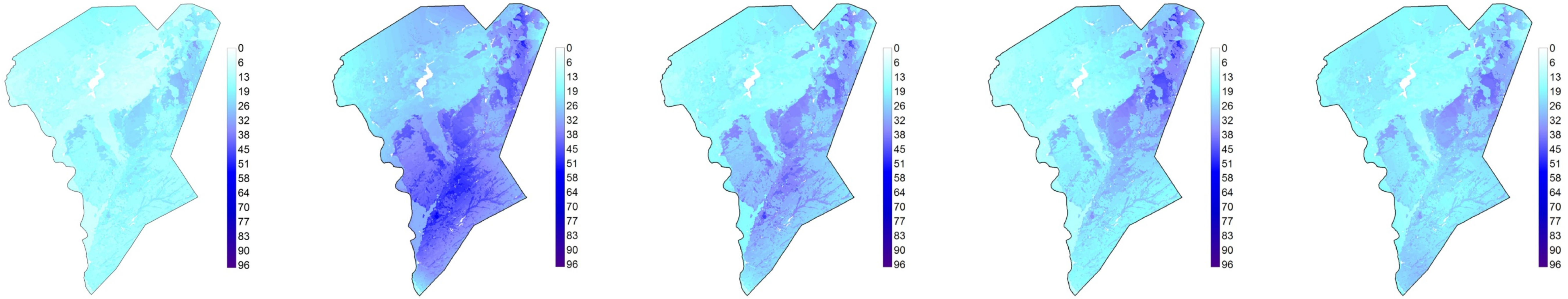
The relationship between the density of green and mixed grass patches and soil moisture in the 0-300 mm profile is shown for each landscape unit in Figure 4.9 and Figure 4.10, and Figure 4.11 and Figure 4.12 respectively. The fits were good for most landscape units (Table 4.5 & Table 4.6) considering that (1) soil moisture was not measured directly but modelled from rainfall and potential evaporation, and (2) site specific factors, such as soil surface conditions, that influence moisture balance at small spatial scales, were not included in the model. The lag period that produced the best fit varied across landscape units and, in general, burnt sections of vegetation types required longer lag periods than unburnt parts.

The density of mixed grass patches increased as soil moisture levels rose from low to intermediate levels because dry grass plants began to green up. In most landscape units, the density of mixed patches declined as soil moisture increased to high levels because grass plants greened up fully, converting mixed patches into green patches. As expected, the density of green grass patches increased with increasing soil moisture, but for most landscape units the upper asymptote of the sigmoid curve was not reached.

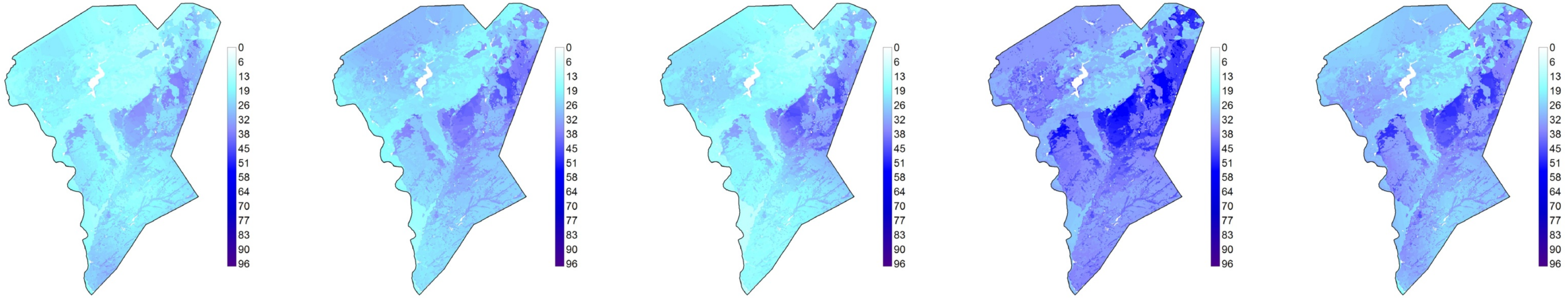
Apart from slight increases in April 2002, November 2002, and January 2003, the density of green grass patches was low across the study area up to February 2003, after which density increased sharply. In contrast, the amount and timing of rainfall was sufficient to maintain a relatively high density of mixed grass patches throughout the study period (Figure 4.13).

The spatial distribution of green and mixed grass patches is shown for each month of the study period in Figure 4.14 and Figure 4.15 respectively. The *Colophospermum mopane – Panicum maximum* dense shrub woodland was notable in that it supported a relatively high density of green grass patches for all months except September. By supporting high densities of green grass patches relative to the other vegetation types, the *Albizia petersiana – Strychnos potatorum* shrub open woodland was also conspicuous. In November, a prominent flush of green grass occurred in the north-western part of the study area between Malilangwe Dam and the Chiredzi River. The density of green grass patches was consistently low in the *Brachystegia glaucescens – Androstachys johnsonii* dense shrub open tall woodland, the *Colophospermum mopane – Terminalia pruinoides* dense shrub open tall woodland, and the *Colophospermum mopane – Endostemon tenuiflorus* open woodland.

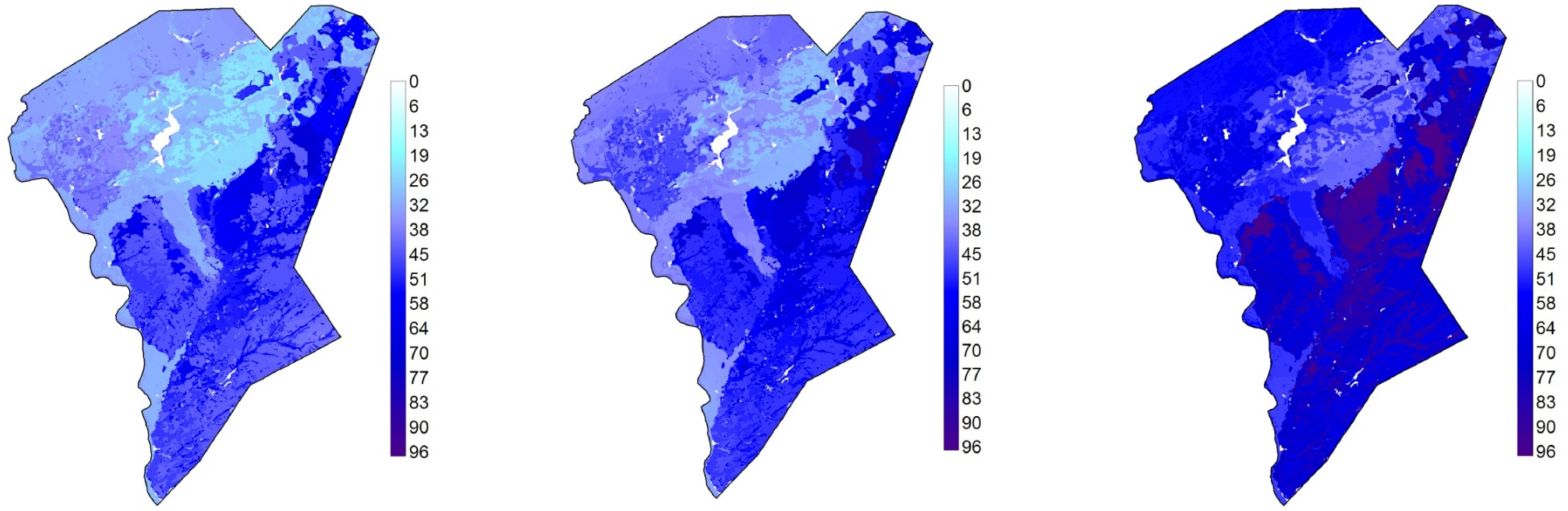
A distinctive feature of the spatio-temporal pattern of density of mixed grass patches was the consistently low density in the north-western part of the study area between Malilangwe Dam and the Chiredzi River. Low densities of mixed grass patches were also observed in the *Acacia nigrescens – Acacia nilotica* open woodland to the west of Banyini from March to October. High densities of mixed grass patches occurred on the paragneiss in the northern parts of the study area between November 2002 and March 2003 and around Nyamsaan and Manyoka in the north-east in June, September, October and November.



12th – 31st March 2002 **April 2002** **May 2002** **June 2002** **July 2002**



August 2002 **September 2002** **October 2002** **November 2002** **December 2002**



January 2003 **February 2003** **1st - 10th March 2003**

Figure 4.8 Average moisture (mm) in the top 30 cm of soil for each month of the study period.

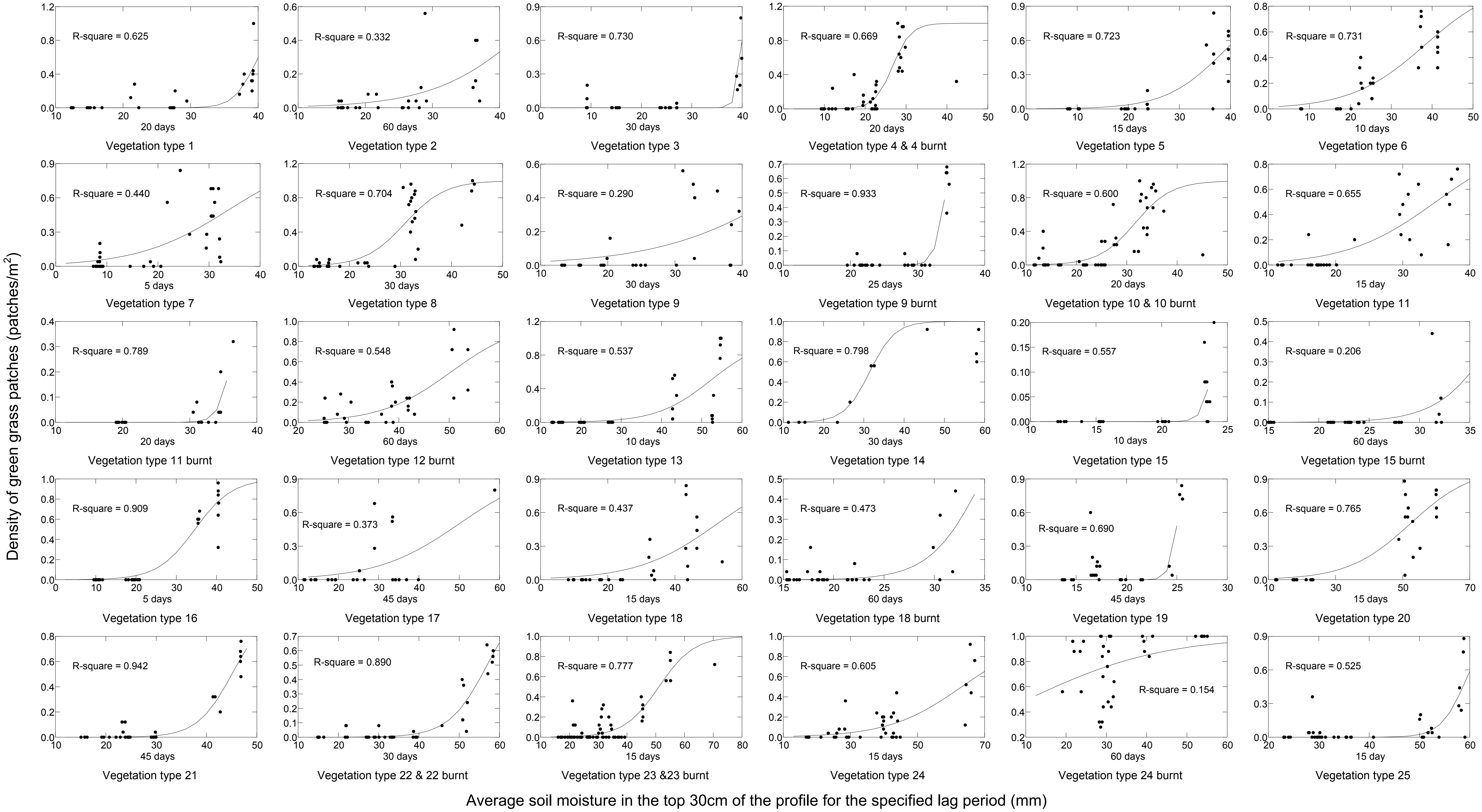


Figure 4.9 Relationship (Y = 1/(1+EXP(a-bX)) between the density of green grass patches (patches/m^2) and average soil moisture (mm) in the top 30 cm of the profile for vegetation types 1 - 25. For a key to vegetation types see Figure 3.1.

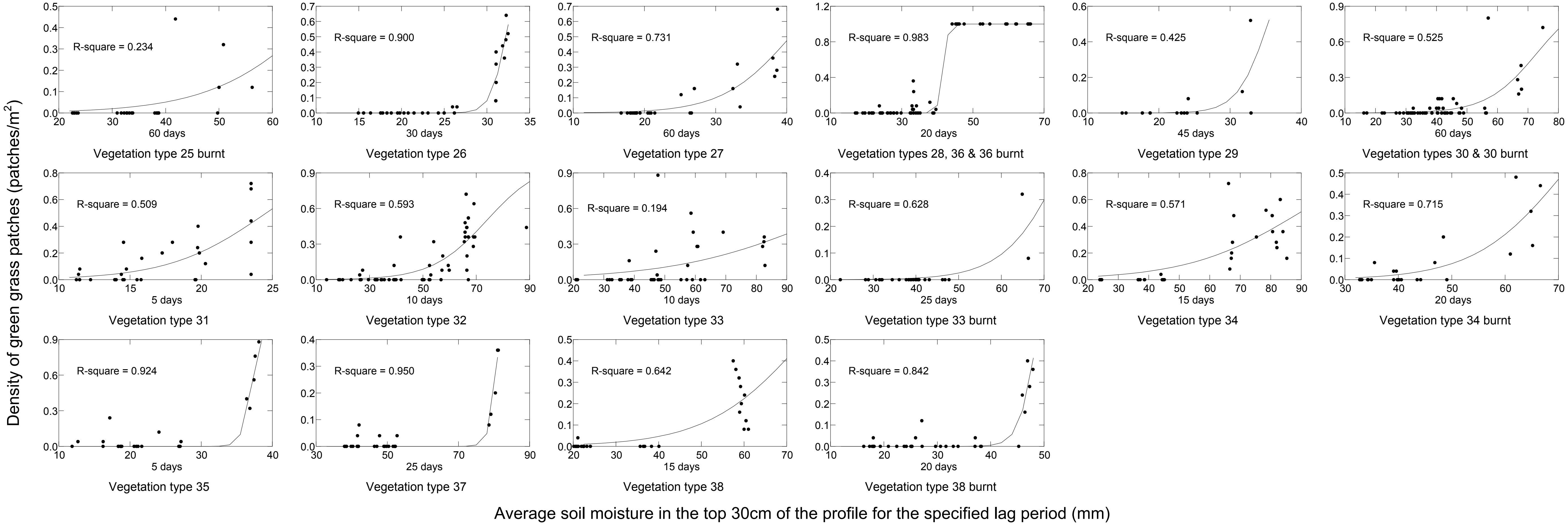


Figure 4.10 Relationship (Y = 1/(1+EXP(a-bX)) between the density of green grass patches (patches/m^2) and average soil moisture (mm) in the top 30 cm of the profile for vegetation types 25 - 38. For a key to vegetation types see Figure 3.1.

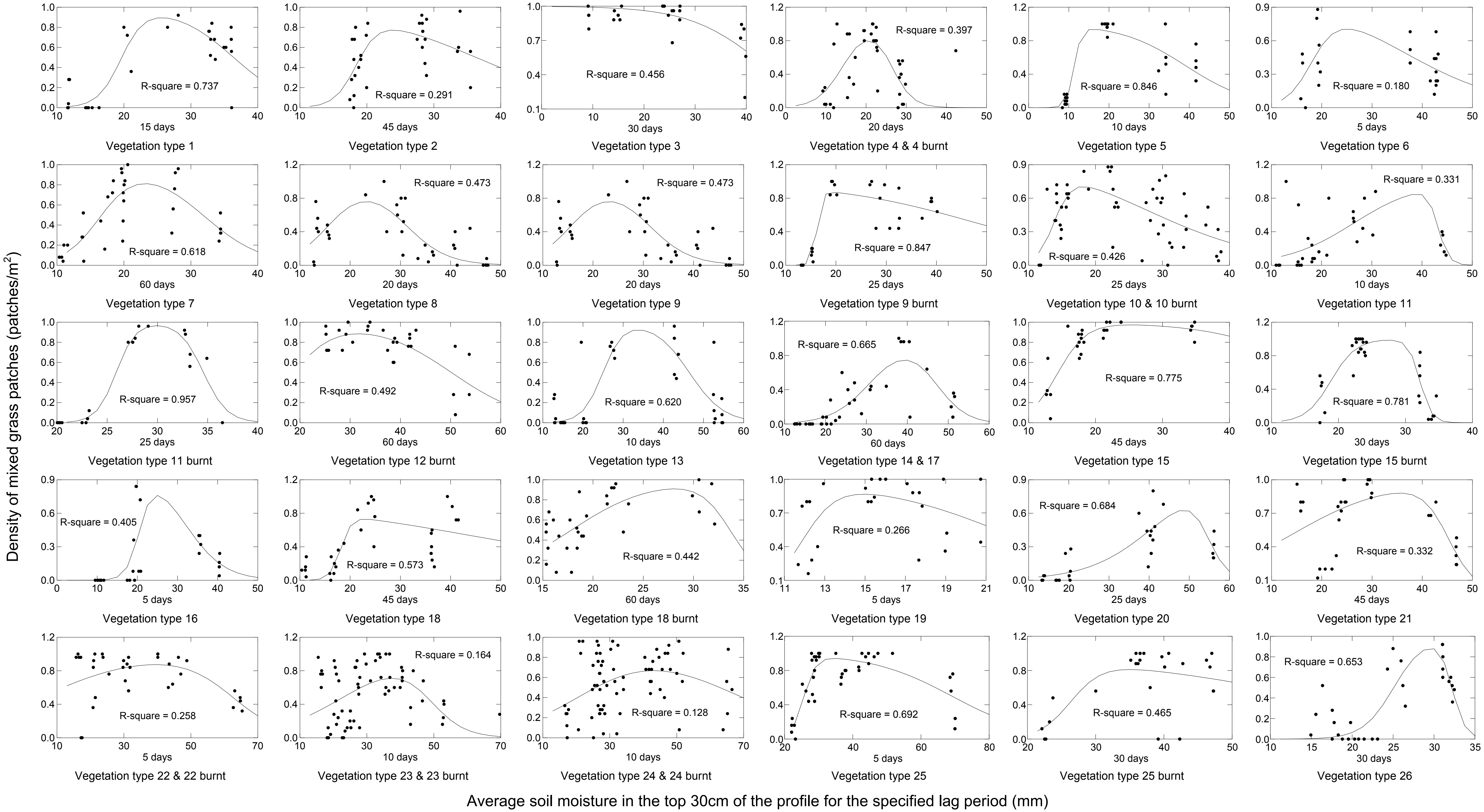


Figure 4.11 Relationship (Y = (1/(1+EXP(a-bX)) × (1/(1+EXP(c-dX))) between the density of mixed grass patches (patches/m^2) and average soil moisture (mm) in the top 30 cm of the profile for vegetation types 1 - 26. For a key to vegetation types see Figure 3.1.

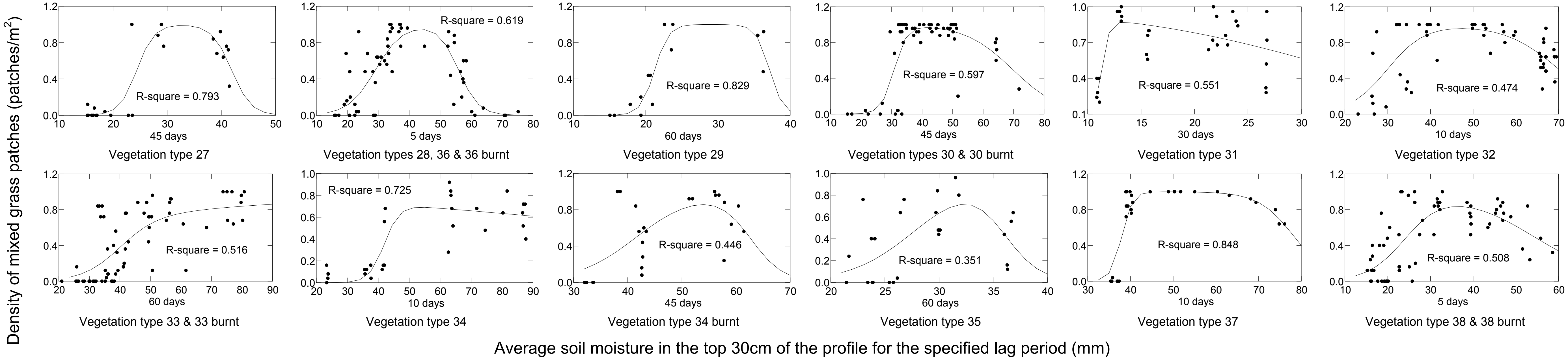


Figure 4.12 Relationship ($Y = (1/(1+EXP(a-bX)) \times (1/(1+EXP(c-dX)))$ between the density of mixed grass patches (patches per m^2) and average soil moisture (mm) in the top 30 cm of the profile for vegetation types 25 - 38. For a key to vegetation types see Figure 3.1.

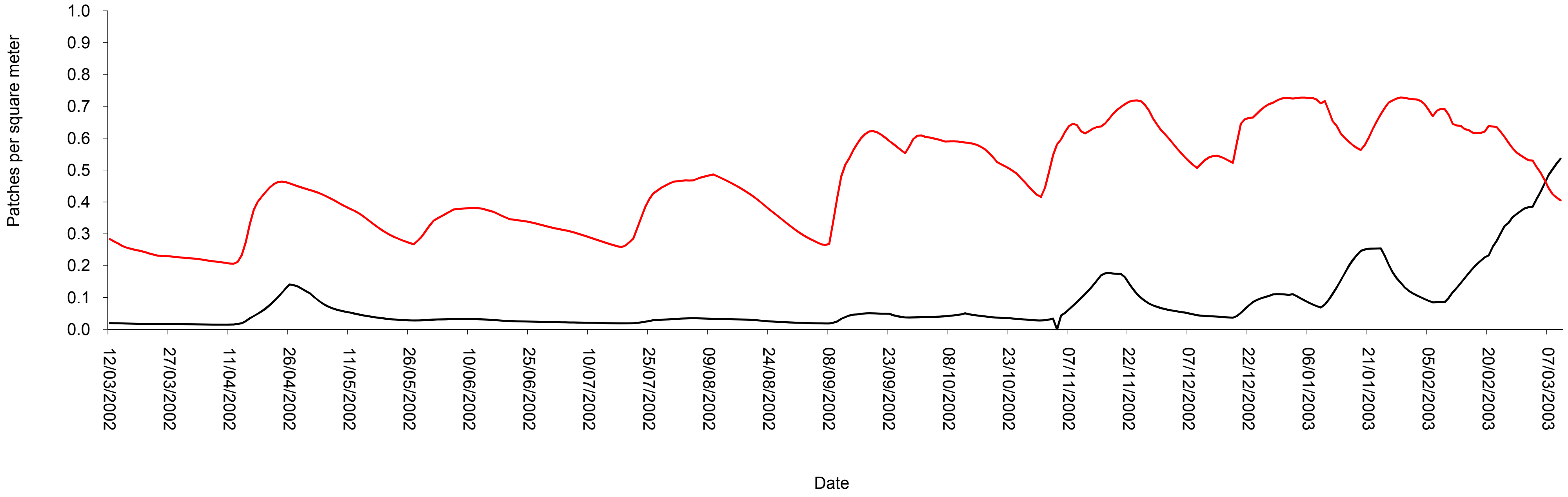
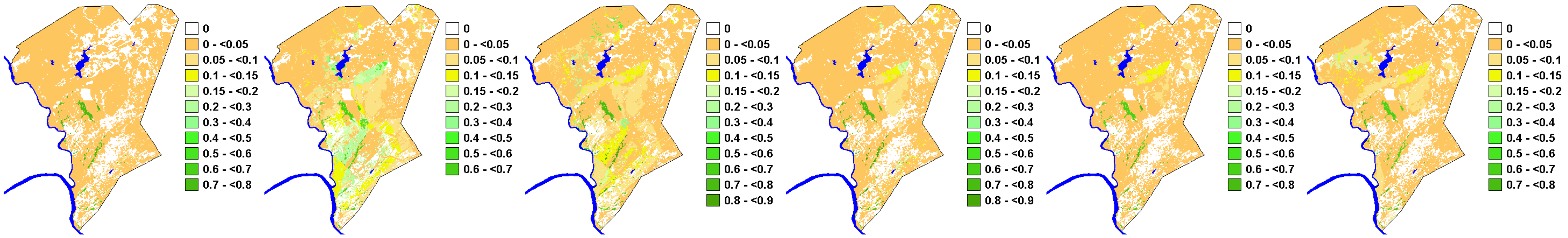


Figure 4.13 Daily average density of green (—), and mixed (—) grass patches (patches/m^2) during the study period.



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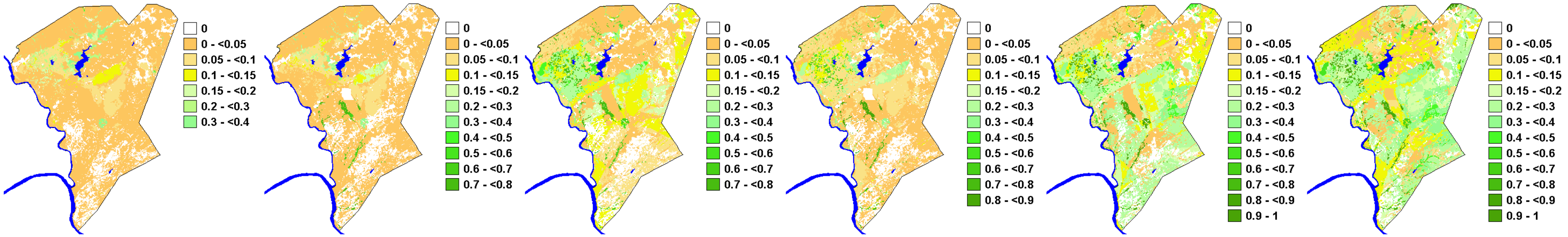

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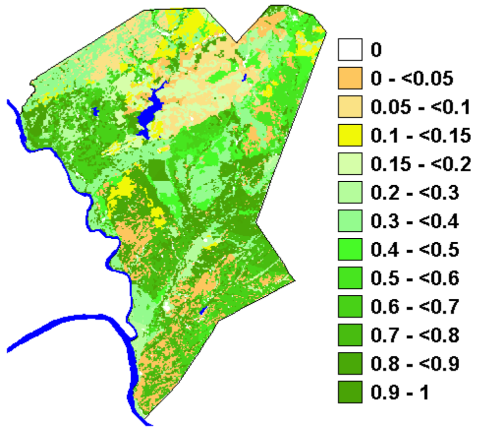
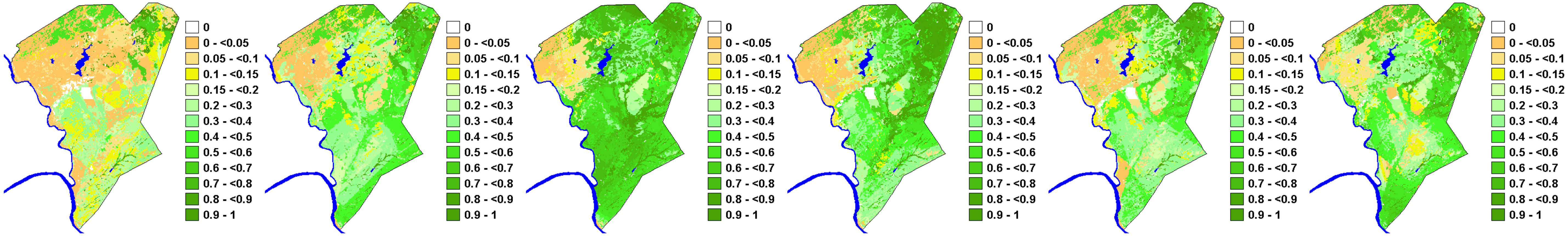


1st – 10th March 2003

Figure 4.14 Average density of green grass patches (patches/m^2) for each month of the study period.



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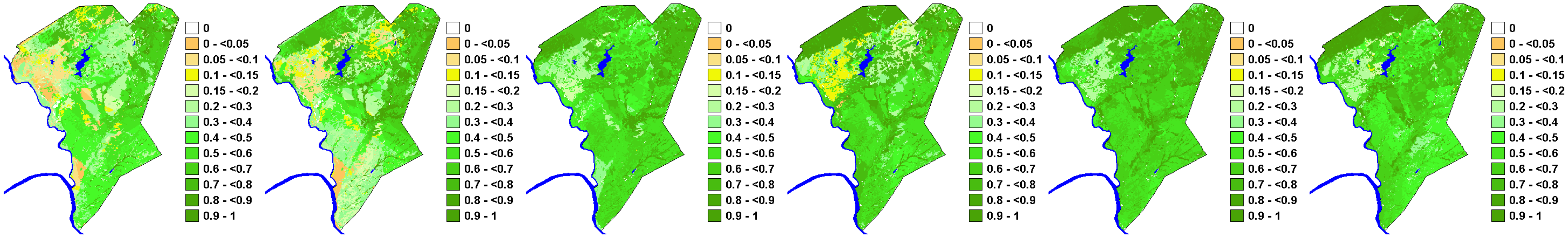

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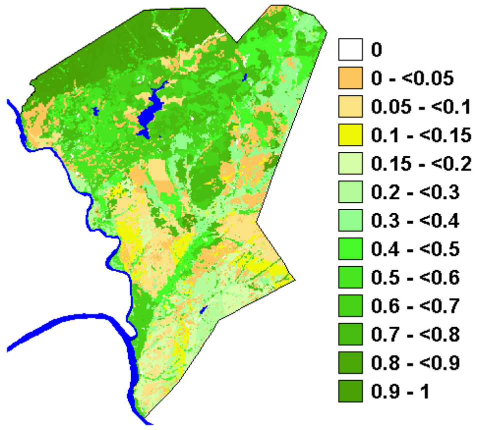


1st – 10th March 2003

Figure 4.15 Average density of patches with a mixture of green and dry grass (patches/m^2) for each month of the study period.

Table 4.5 Parameter estimates for the sigmoid curve (Y = 1/(1+EXP(a-bX)) fitted to the density of green grass patches (patches/m^2) and soil moisture (mm) data for each landscape unit. For a key to land unit numbers see Figure 3.1

Landscape unit	Lag period (days)	Estimate of parameter a	Estimate of parameter b	Corrected R^2	Number of outliers removed
1	20	25.021708	0.634788	0.625	0
2	60	6.297283	0.139927	0.332	0
3	30	67.41153	1.694953	0.730	0
4 & 4 burnt	20	12.056486	0.450791	0.669	0
5	15	6.824855	0.176697	0.723	0
6	10	4.24668	0.110756	0.731	0
7	5	3.814731	0.112025	0.440	0
8	30	7.890511	0.25568	0.704	0
9	30	4.861977	0.099356	0.290	0
9 burnt	25	41.973747	1.228888	0.933	0
10 & 10 burnt	20	8.801631	0.277669	0.600	0
11	15	5.2983	0.151736	0.655	0
11 burnt	20	33.907858	0.909516	0.789	0
12 burnt	60	7.234465	0.143547	0.548	0
13	10	7.863002	0.150526	0.537	0
14	30	10.098803	0.32102	0.798	0
15	10	53.592045	2.166783	0.557	5
15 burnt	60	13.092682	0.341582	0.206	0
16	5	7.483464	0.21624	0.909	0
17	45	4.902026	0.097985	0.373	0
18	15	4.446372	0.084453	0.437	0
18 burnt	60	13.352158	0.38368	0.473	0
19	45	59.99997	2.396972	0.690	0
20	15	5.672468	0.108526	0.765	0
21	45	13.140784	0.291772	0.942	0
22 & 22 burnt	30	12.033531	0.211407	0.890	0
23 &23 burnt	15	8.453855	0.165383	0.777	0
24	15	5.823046	0.092172	0.605	0
24 burnt	60	0.619214	0.059016	0.154	0
25	15	24.037034	0.406535	0.525	0
25 burnt	60	6.7599	0.095889	0.234	0
26	30	35.689978	1.107989	0.900	0
27	60	8.496844	0.20982	0.731	0
28, 36 & 36 burnt	20	60.000000	1.441003	0.983	0
29	45	16.571924	0.469401	0.425	0
30 & 30 burnt	60	8.950586	0.122977	0.525	0
31	5	7.203572	0.293153	0.509	0
32	10	7.210995	0.097499	0.593	0
33	10	4.223658	0.041753	0.194	0
33 burnt	25	10.656375	0.139998	0.628	0
34	15	4.890572	0.054717	0.571	0
34 burnt	20	8.495386	0.119656	0.715	0
35	5	53.348337	1.441037	0.924	0
37	25	62.671361	0.765168	0.950	0
38	15	6.574818	0.088786	0.642	0
38 burnt	20	30.004155	0.617819	0.842	0

Table 4.6 Parameter estimates for the symmetric sigmoid curve (Y = (1/(1+EXP(a-bX)) × (1/(1+EXP(c-dX))) fitted to the density of mixed grass patches (patches/m^2) and soil moisture (mm) data for each landscape unit. For a key to land unit numbers see Figure 3.1

Landscape unit	Lag period (days)	Estimate of parameter a	Estimate of parameter b	Estimate of parameter c	Estimate of parameter d	Corrected R^2	No. outliers removed
1	15	11.350866	0.578925	-8.437521	-0.231953	0.736660	0
2	45	-4.076182	-0.112271	11.437840	0.616632	0.290806	0
3	30	-60.000000	0.102000	-5.993272	-0.139039	0.455942	0
4 & 4 burnt	20	-10.438331	-0.395011	4.535590	0.318535	0.397034	0
5	10	-4.772075	-0.121954	12.308410	1.089576	0.846492	0
6	5	-3.563487	-0.098458	7.402496	0.405698	0.179533	5
7	60	-7.236928	-0.227536	6.239610	0.377976	0.618185	0
8	20	-7.440077	-0.241008	4.343176	0.273196	0.472578	0
9	25	-3.256981	-0.067454	29.134404	1.795635	0.847135	0
9 burnt	30	-12.352190	-0.366048	44.383700	1.928027	0.399839	0
10 & 10 burnt	25	-2.974165	-0.108588	10.815492	0.774913	0.425784	1
11	10	-40.606535	-0.940771	3.929329	0.149125	0.331310	0
11 burnt	25	26.756600	1.033331	-29.272092	-0.846399	0.956693	0
12 burnt	60	-6.785118	-0.135262	4.405027	0.237001	0.491757	0
13	10	-10.874459	-0.234082	10.006555	0.401090	0.620115	0
14 & 17	60	-12.503685	-0.267005	6.573493	0.210945	0.664945	0
15	45	-7.224738	-0.134955	6.769965	0.470436	0.775305	0
15 burnt	30	-37.762755	-1.173903	10.140652	0.537315	0.780600	0
16	5	-6.573428	-0.205585	12.970913	0.629460	0.404806	2
18	45	-2.013363	-0.042678	17.302980	0.950876	0.573481	0
18 burnt	60	-21.901028	-0.650025	4.613445	0.258464	0.441852	0
19	5	-6.381866	-0.287174	14.572108	1.217385	0.265773	0
20	25	-22.450090	-0.413138	4.968848	0.118516	0.684407	0
21	45	-17.128611	-0.379398	1.397899	0.102256	0.332062	0
22 & 22 burnt	5	-8.332798	-0.133751	0.423241	0.070656	0.257660	0
23 & 23 burnt	10	-9.592394	-0.197344	2.223699	0.094705	0.164534	0
24 & 24 burnt	10	-4.027163	-0.063101	2.116908	0.089114	0.127818	0
25	5	-5.789616	-0.083766	14.291023	0.557034	0.691671	0
25 burnt	30	-3.703291	-0.060364	11.554790	0.436718	0.465377	0
26	30	-40.109911	-1.244648	13.335208	0.531904	0.652877	0
27	45	-23.333269	-0.557159	15.262473	0.625449	0.793468	0
28, 36 & 36 burnt	5	-17.316453	-0.309555	6.655922	0.228632	0.619429	0
29	60	-39.573438	-1.065451	22.144181	1.042432	0.829159	0
30 & 30 burnt	45	-8.985760	-0.129027	14.825600	0.480843	0.596685	0
31	30	-3.268970	-0.099740	28.694832	2.555773	0.550830	0
32	10	-11.167090	-0.159312	6.861395	0.229493	0.474438	0
33 & 33 burnt	60	-0.232531	0.017694	6.498794	0.165022	0.516243	0
34	10	-1.399349	-0.010593	17.251042	0.410343	0.724752	0
34 burnt	45	7.543544	0.181158	-21.024772	-0.335768	0.446442	0
35	60	9.190051	0.327596	-21.489750	-0.599358	0.350953	0
37	10	-18.779493	-0.239806	29.999998	0.790738	0.848052	0
38 & 38 burnt	5	5.633223	0.232224	-6.238966	-0.115170	0.507598	0

Forbs

The average density of green forb patches declined gradually from 0.2 patches/m^2 on the 12th of March 2002 to a minimum of 0.046 patches/m^2 on the 7th of September 2002. This was followed by a rise in density up to a maximum of 0.366 patches/m^2 on the 10th of March 2003 (Figure 4.16).

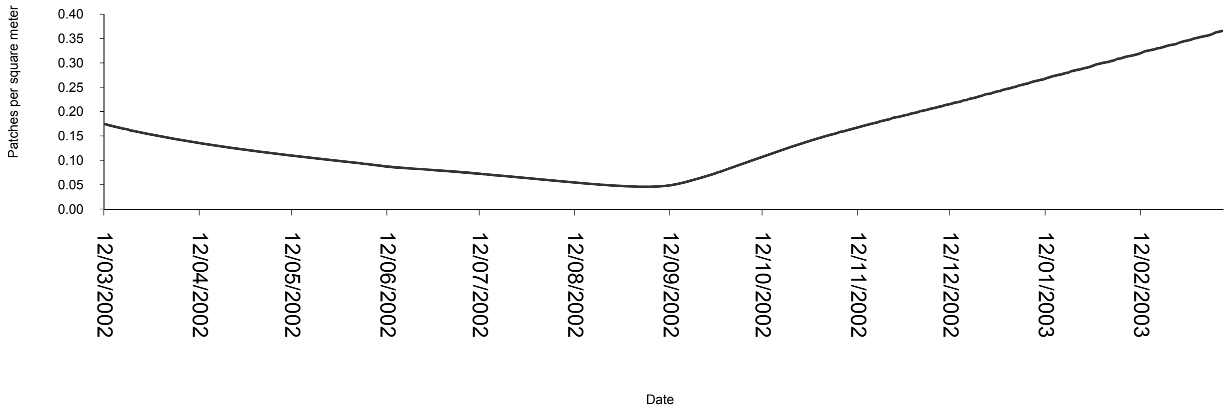


Figure 4.16 Daily average density of green forb patches (patches/m^2) during the study period.

The temporal pattern of patch density varied among landscape units but in most cases, density began to decline from February 2002, with low levels being reached by May 2002. Thereafter, density generally remained low until rain in September 2002 triggered new growth (Figure 4.17, Figure 4.18). Notable exceptions to this general trend were the *Colophospermum mopane – Leucas glabrata* shrub woodland, the *Albizia petersiana – Strychnos potatorum* shrub open woodland and the *Colophospermum mopane – Terminalia pruinoides* dense shrub open tall woodland, which supported high densities of green forb patches when density had declined to low levels in the other vegetation types.

In general, the spatial pattern of forb patch density was opposite to that shown by the density of grass patches, with higher densities occurring in the north and north-west of the study area than in the southern, eastern and north-eastern parts (Figure 4.19).

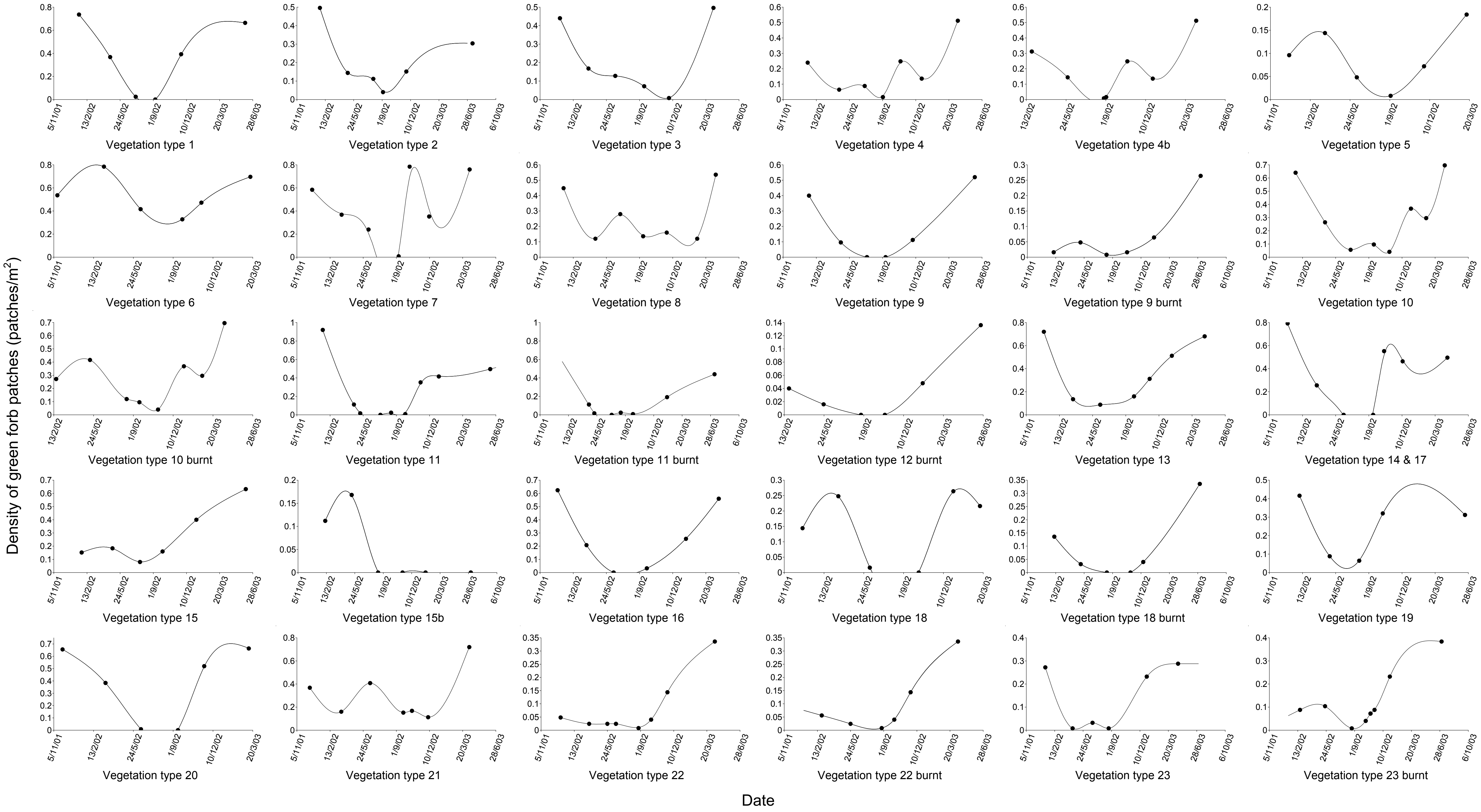


Figure 4.17. Change over time of the density of green forb patches (patches/m^2) for vegetation types 1-23 derived from interpolation between estimates using smoothing spline regression. For a key to vegetation type numbers see Figure 3.1.

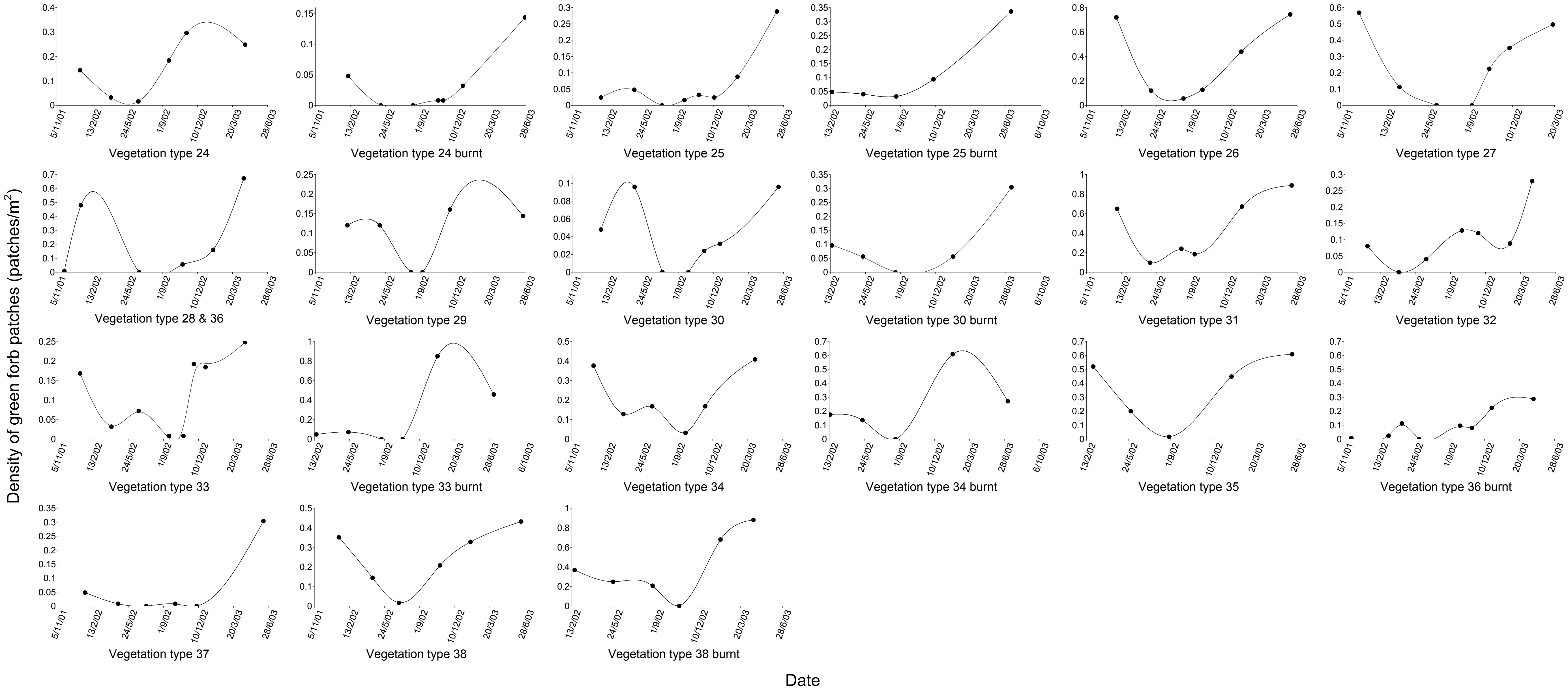
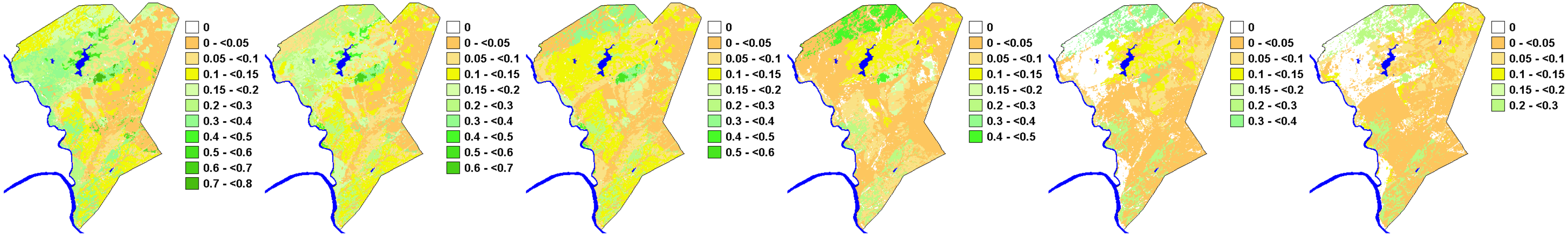
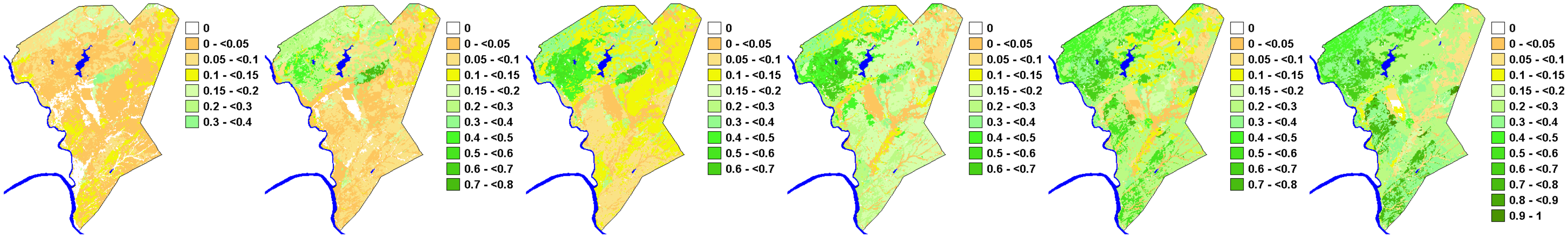


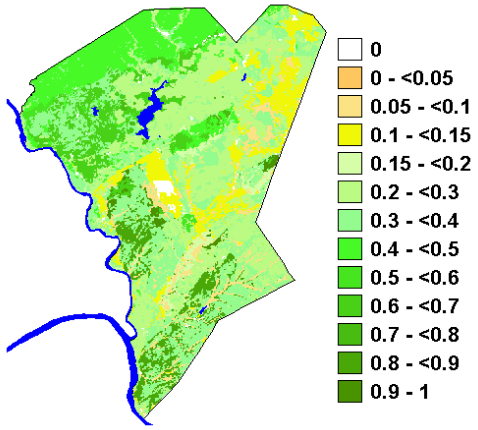
Figure 4.18 Change over time of the density of green forb patches (patches/m^2) for vegetation types 24-38 derived from interpolation between estimates using smoothing spline regression. For a key to vegetation type numbers see Figure 3.1.



12th – 31th March 2002 **April 2002** **May 2002** **June 2002** **July 2002** **August 2002**



September 2002 **October 2002** **November 2002** **December 2002** **January 2003** **February 2003**



1st – 10th March 2003

Figure 4.19 Average density of green forb patches (patches/m^2) for each month of the study period.

Leaves

The average density of patches of green leaf accessible to adult bulls declined gradually from 0.116 patches/m^2 on the 12th of March to 0.110 patches/m^2 on the 10th of May, and then declined more rapidly, reaching a minimum of 0.021 patches/m^2 on the 9th of September (Figure 4.20). Rain fell on the 9th of September triggering a flush of new leaf that caused the density of patches to increase steadily until a maximum of 0.109 patches/m^2 was reached on the 26th of December. Thereafter patch density remained constant. The average density of patches accessible to adult cows was slightly lower than for bulls but otherwise followed the same temporal pattern.

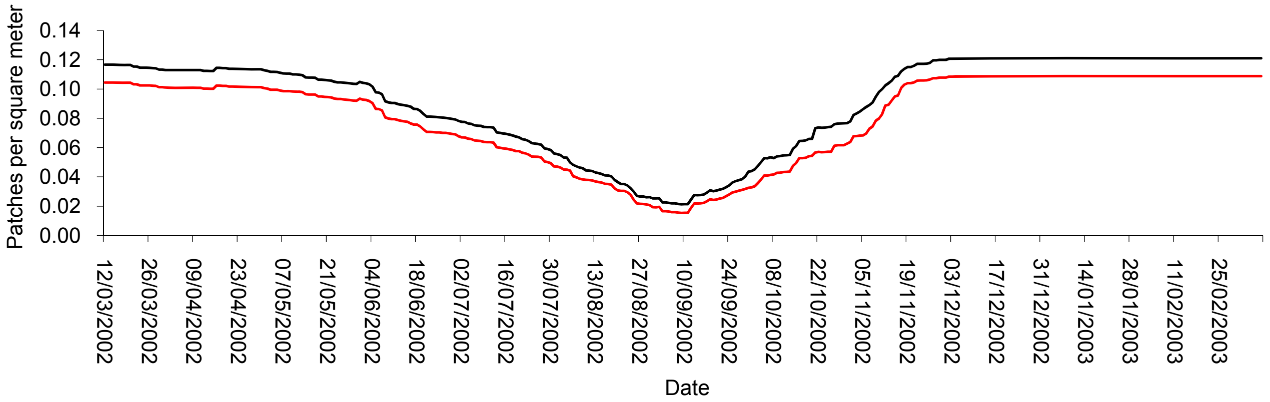


Figure 4.20 Daily average density of woody plants (individuals/m^2) with canopy accessible to adult bulls (—) and adult cows (—) and > 25 % canopy with green leaf.

The temporal pattern of patch density varied among landscape units because of differences in (1) the date at which patch density began to decline, (2) the rate of decline, (3) the minimum level reached, (4) the date of leaf flush, (5) the rate of increase, and (6) the date at which maximum patch density was attained (Figure 4.21 - Figure 4.24).

During the wet months, noticeably high densities of woody plants with green leaf accessible to adult bulls and cows occurred (1) in the mopane woodlands between the Malilangwe Dam and the Chiredzi River, (2) in the *Colophospermum mopane – Terminalia pruinoides* dense shrub open tall woodland in the north of the study area, (3) in the *Colophospermum mopane – Leucas glabrata* shrub woodland, (4) in the *Albizia petersiana – Strychnos potatorum* shrub open woodland immediately to the south of the Malilangwe Range, and (5) in the *Colophospermum mopane – Panicum maximum* dense shrub woodland (Figure 4.25 and Figure 4.26). With the onset of the cool dry season, trees began to loose their leaves and by June high densities of woody plants with green leaf were confined to the *Albizia petersiana – Strychnos potatorum* shrub open woodland and *Colophospermum mopane – Panicum maximum* dense shrub woodland. By September, density of woody plants with green leaf was low over the entire study area, but the *Albizia petersiana – Strychnos potatorum* shrub open woodland had a noticeably higher density than the other vegetation types.

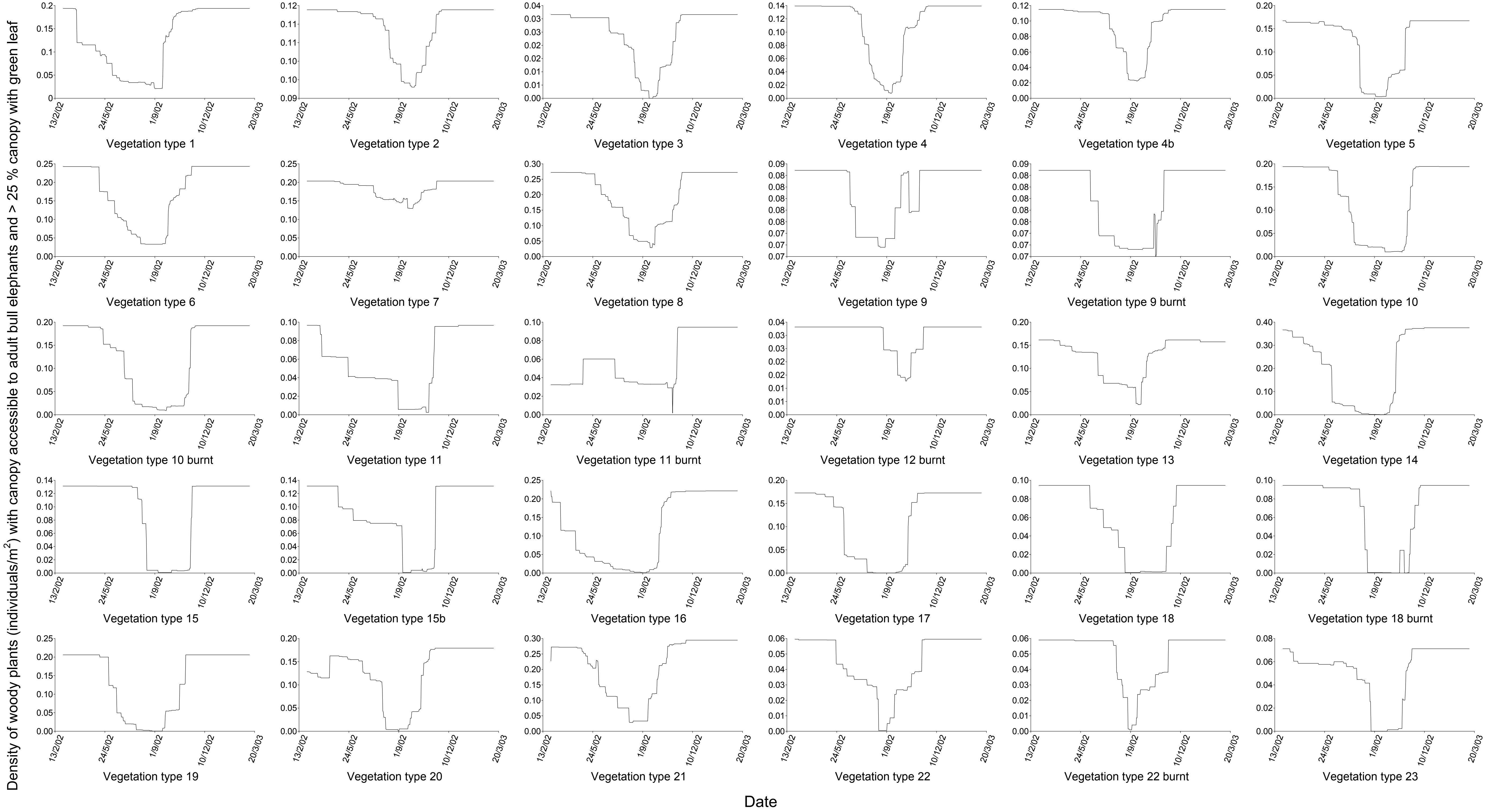


Figure 4.21 The density of woody plants (individuals/m^2) with canopy accessible to adult bull elephants and > 25 % canopy with green leaf during the study period for vegetation types 1-23. For a key to vegetation type numbers see Figure 3.1.

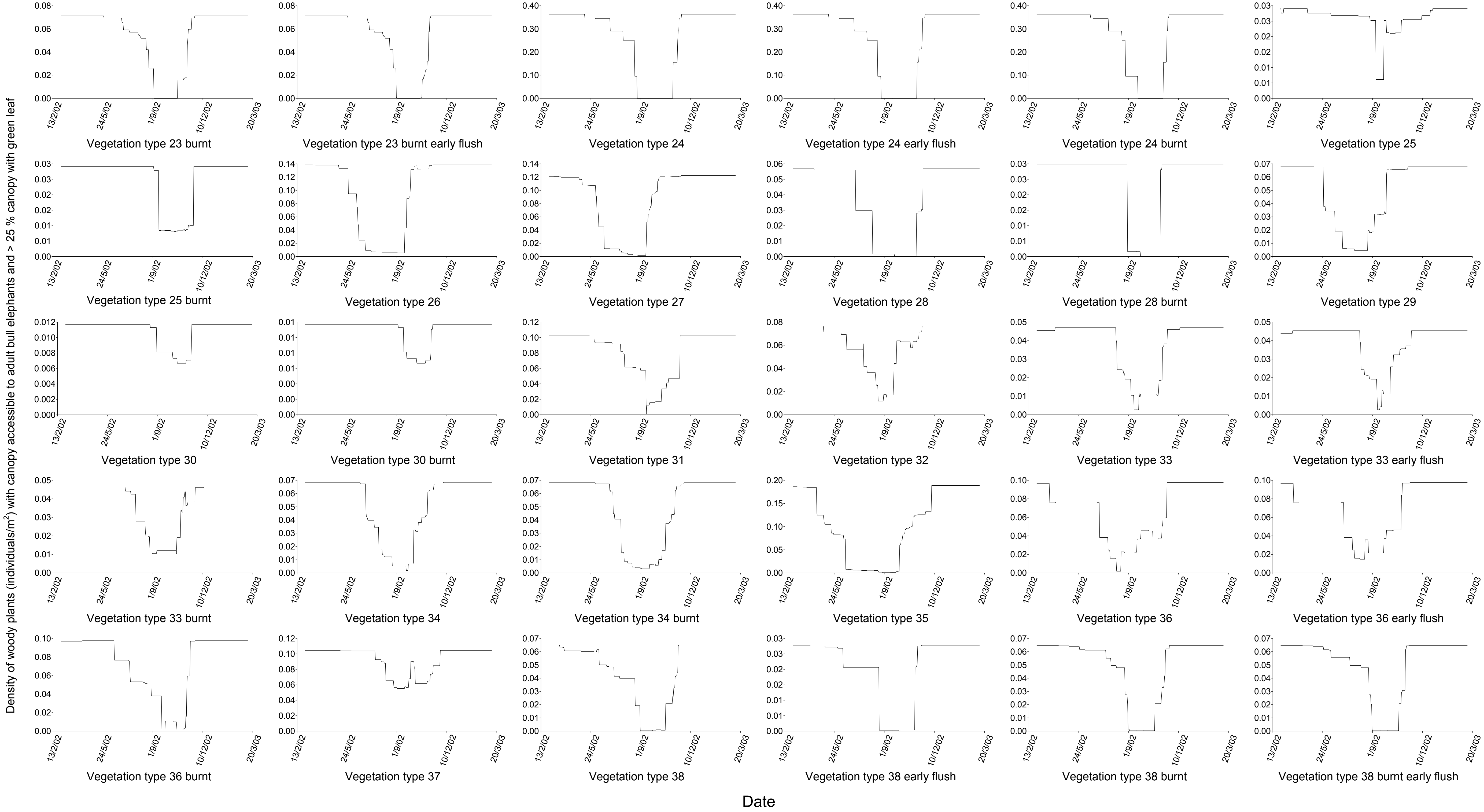


Figure 4.22 The density of woody plants (individuals/m^2) with canopy accessible to adult bull elephants and > 25 % canopy with green leaf during the study period for vegetation types 23-38. For a key to vegetation type numbers see Figure 3.1.

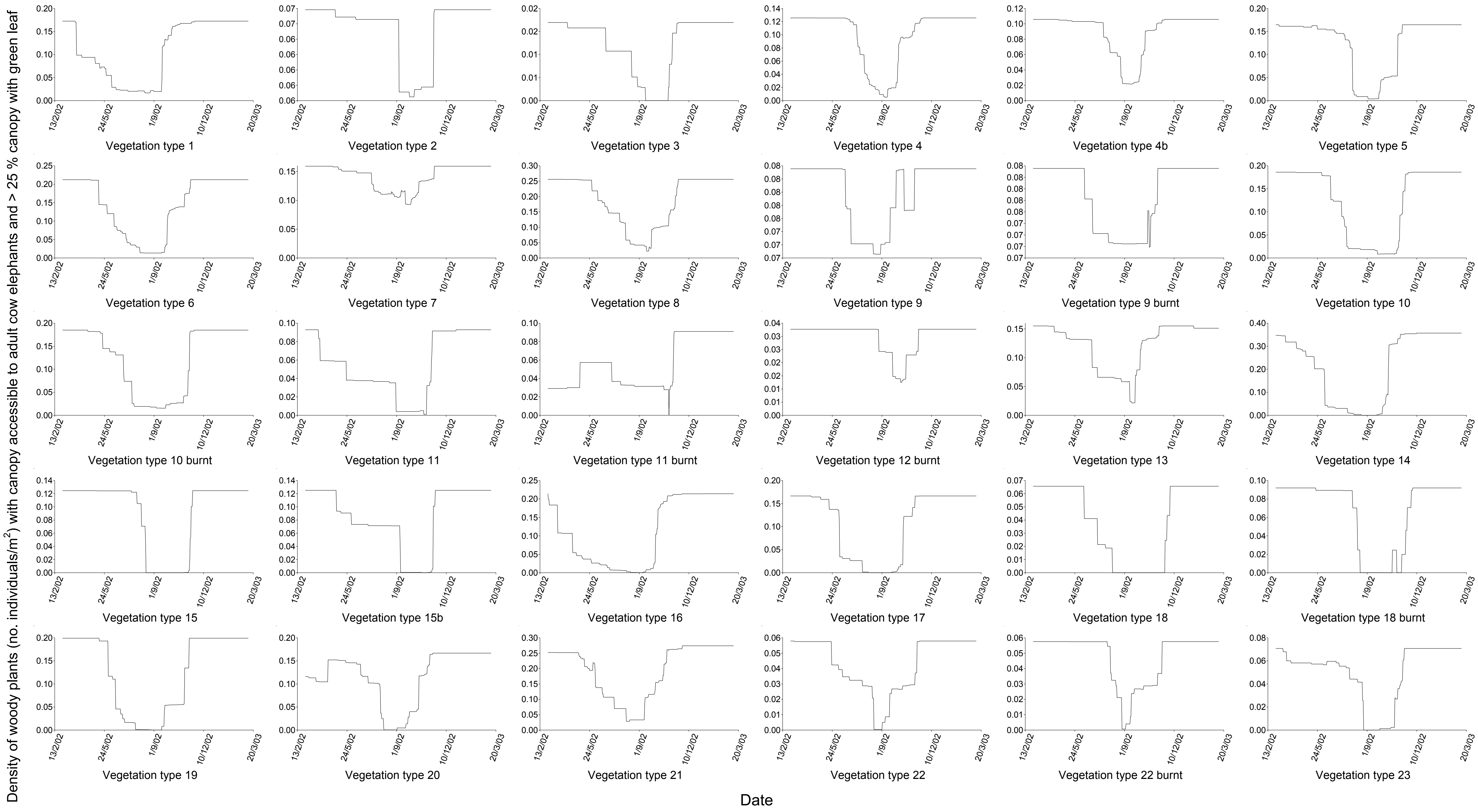
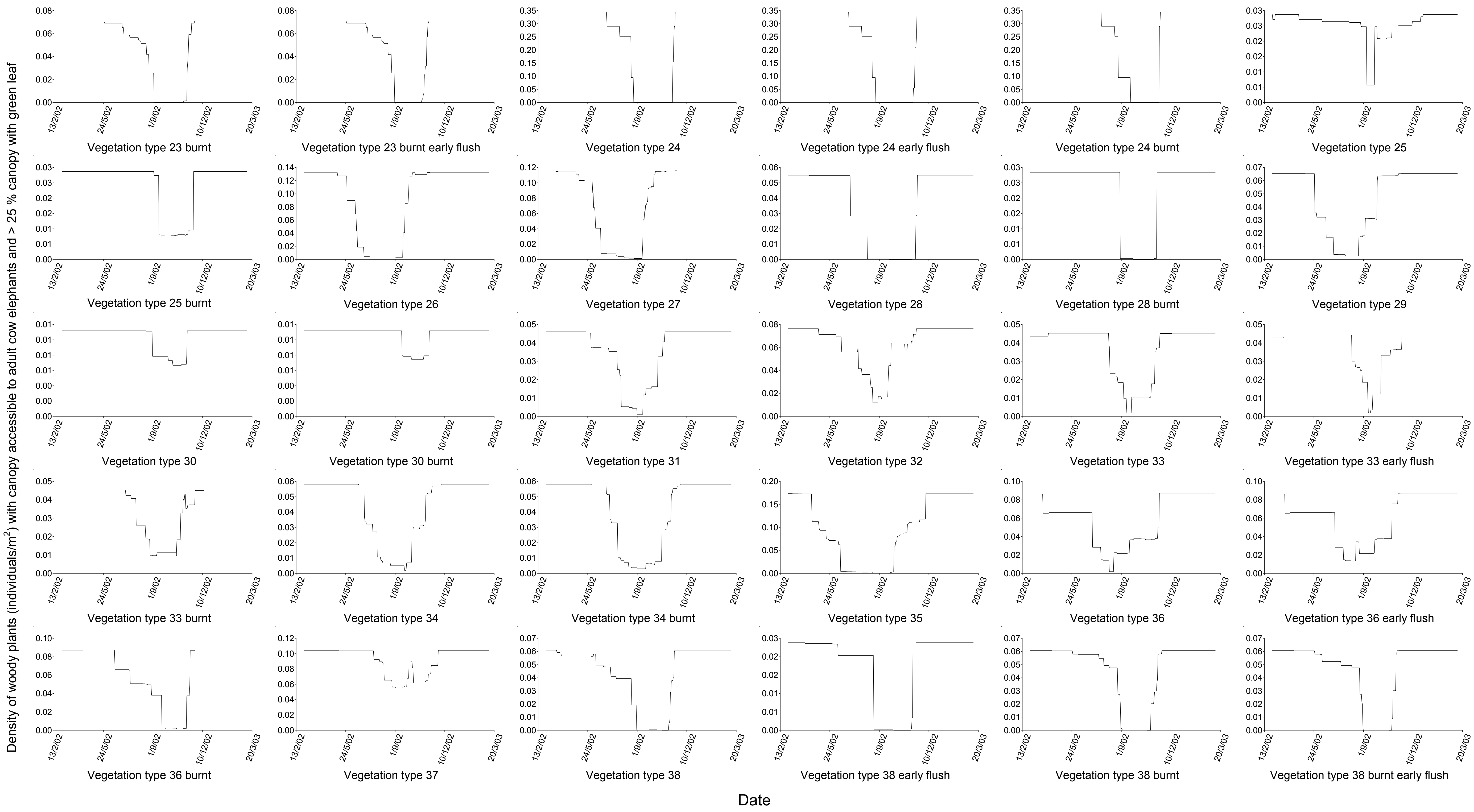
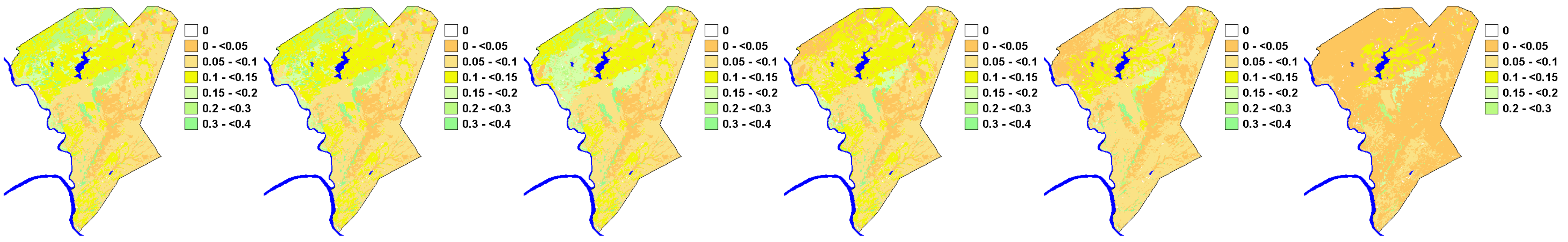


Figure 4.23 The density of woody plants (individuals/m^2) with canopy accessible to adult cow elephants and > 25 % canopy with green leaf during the study period for vegetation types 1-23. For a key to vegetation type numbers see Figure 3.1.

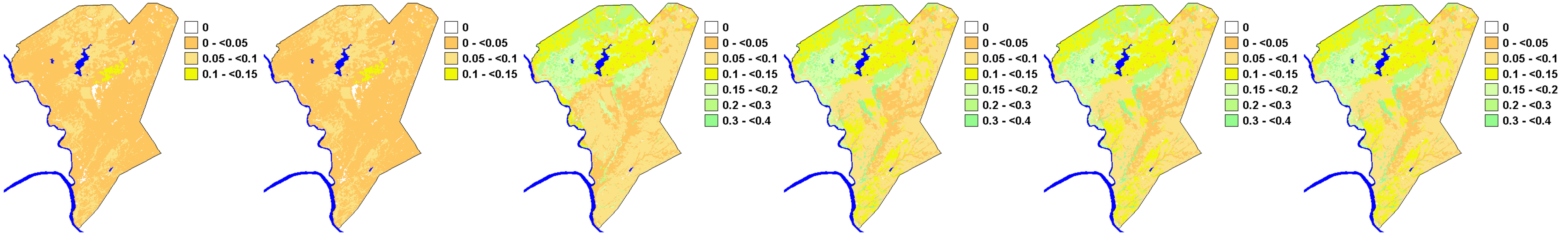


Vegetation type 23 burnt
Vegetation type 23 burnt early flush
Vegetation type 24
Vegetation type 24 early flush
Vegetation type 24 burnt
Vegetation type 25
Vegetation type 25 burnt
Vegetation type 26
Vegetation type 27
Vegetation type 28
Vegetation type 28 burnt
Vegetation type 29
Vegetation type 30
Vegetation type 30 burnt
Vegetation type 31
Vegetation type 32
Vegetation type 33
Vegetation type 33 early flush
Vegetation type 33 burnt
Vegetation type 34
Vegetation type 34 burnt
Vegetation type 35
Vegetation type 36
Vegetation type 36 early flush
Vegetation type 36 burnt
Vegetation type 37
Vegetation type 38
Vegetation type 38 early flush
Vegetation type 38 burnt
Vegetation type 38 burnt early flush

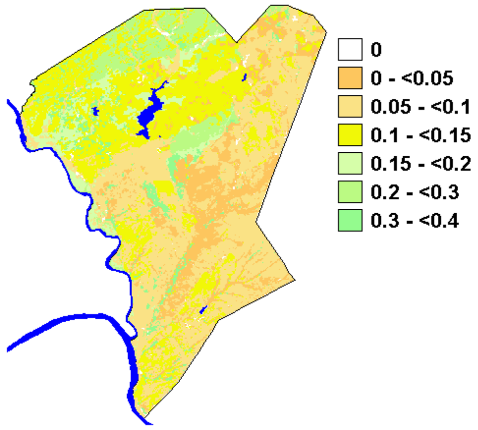
Figure 4.24 The density of woody plants (individuals/m^2) with canopy accessible to adult cow elephants and > 25 % canopy with green leaf during the study period for vegetation types 23-38. For a key to vegetation type numbers see Figure 3.1.



12th – 31th March 2002 **April 2002** **May 2002** **June 2002** **July 2002** **August 2002**

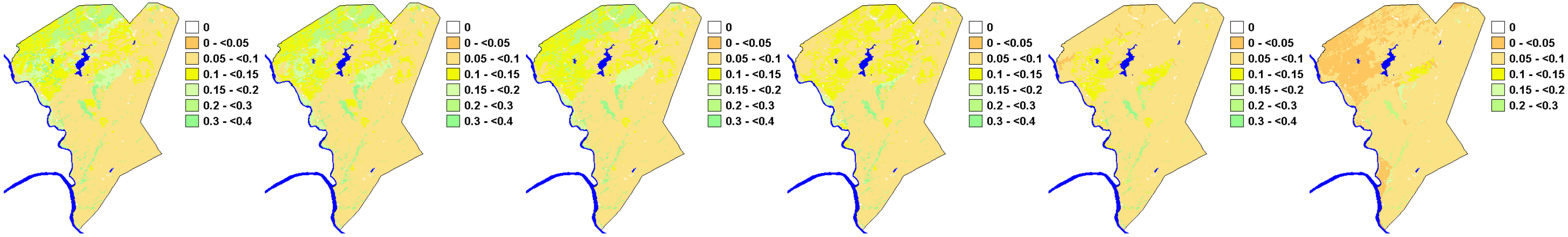


September 2002 **October 2002** **November 2002** **December 2002** **January 2003** **February 2003**

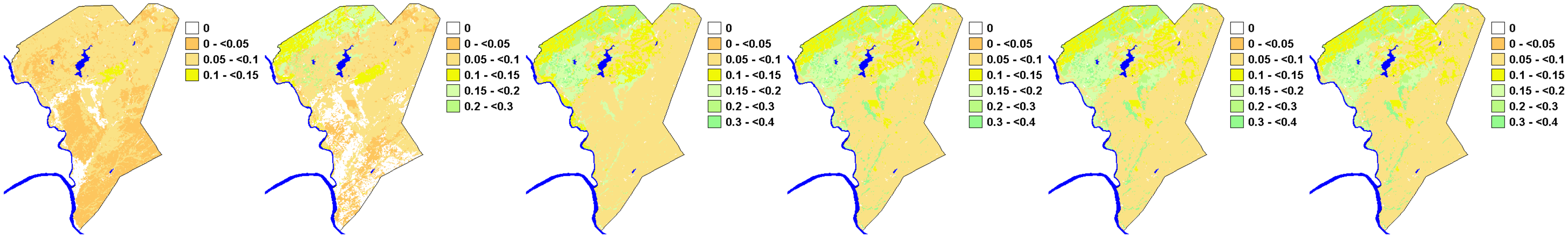


1st – 10th March 2003

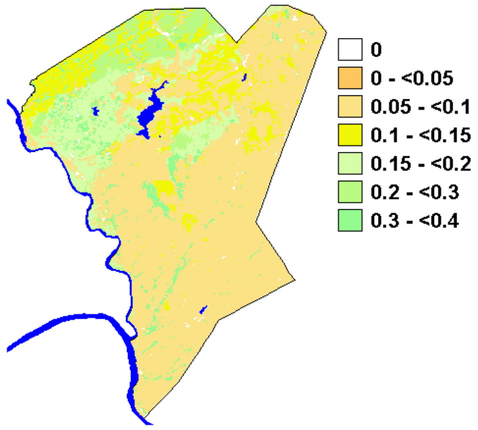
Figure 4.25 Average density of woody plants (individuals/m^2) with canopy accessible to adult bull elephants and > 25 % canopy with green leaf for each month of the study period.



12th – 31st March 2002 **April 2002** **May 2002** **June 2002** **July 2002** **August 2002**



September 2002 **October 2002** **November 2002** **December 2002** **January 2003** **February 2003**

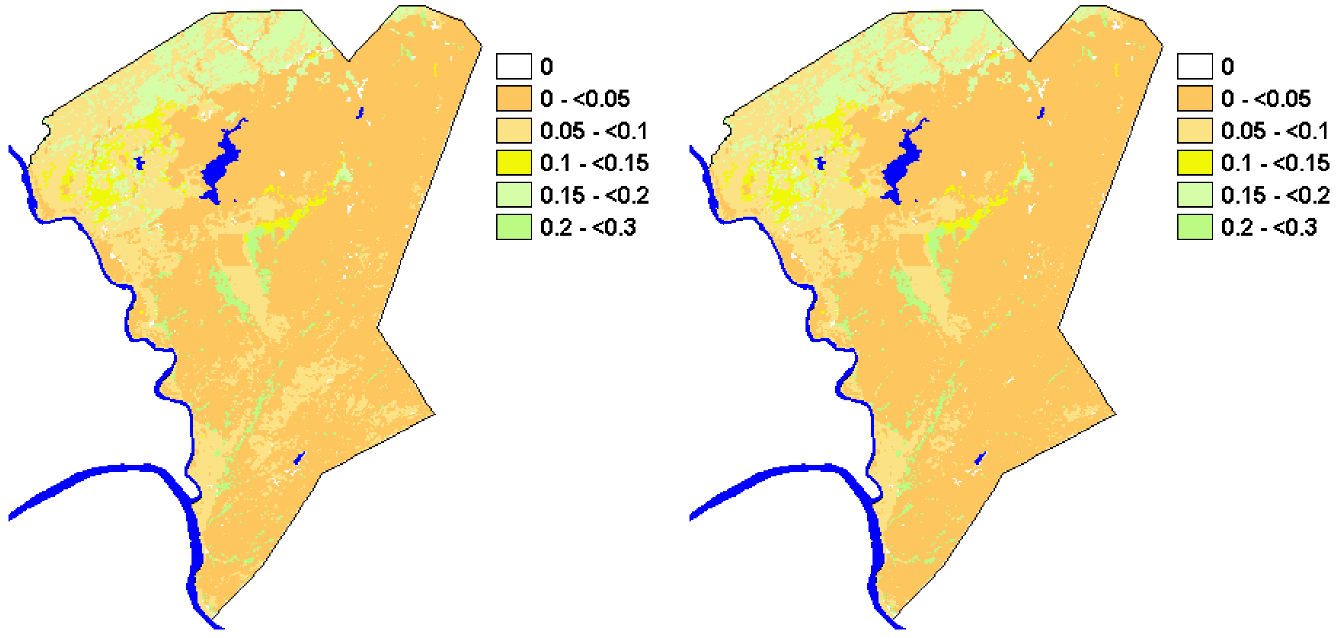


1st – 10th March 2003

Figure 4.26 Average density of woody plants (individuals/m^2) with canopy accessible to adult cow elephants and > 25 % canopy with green leaf for each month of the study period.

Bark from canopy branches

The density of woody plants commonly utilised for canopy bark that were accessible to adult bulls and cows is given for each vegetation type in Table 4.7. The *Colophospermum mopane – Panicum maximum* dense shrub woodland and the *Colophospermum mopane – Terminalia pruinoides* dense shrub open tall woodland in the extreme north had the highest densities of plants commonly utilised for canopy bark (Figure 4.27).



(a) (b)

Figure 4.27 Density of woody plants commonly utilised for canopy bark that were accessible to (a) adult bulls and (b) adult cows.

Table 4.7 Density of woody plants (plants/m^2) commonly utilised for canopy bark that were accessible to adult bulls and cows for each vegetation type. For a key to vegetation type numbers see Figure 3.1

	Density of woody plants potentially utilised for canopy bark (plants/m^2)	
Vegetation type	**Adult bulls (canopy below 6 m)**	**Adult cows (canopy below 4 m)**
1	0.0316	0.0313
2	0.0002	0.0002
3	0.0003	0.0003
4	0.0099	0.0099
5	0.1126	0.1125
6	0.0667	0.0645
7	0.0359	0.0324
8	0.0560	0.0560
9	0.0057	0.0057
10	0.0482	0.0479
11	0.0217	0.0217
12	0.0099	0.0099
13	0.0651	0.0650
14	0.1824	0.1794
15	0.0899	0.0899
16	0.0838	0.0837
17	0.1351	0.1311
18	0.0901	0.0890
19	0.1611	0.1577
20	0.0790	0.0771
21	0.1545	0.1505
22	0.0367	0.0364
23	0.0454	0.0453
24	0.2533	0.2533
25	0.0005	0.0004
26	0.0514	0.0512
27	0.0528	0.0522
28	0.0546	0.0546
29	0.0294	0.0293
30	0.0039	0.0036
31	0.0001	0.0001
32	0.0170	0.0167
33	0.0014	0.0012
34	0.0090	0.0039
35	0.0056	0.0056
36	0.0511	0.0497
37	0.0011	0.0009
38	0.0476	0.0474

4.4.3. *Estimates of the spatio-temporal pattern of protein bite mass for different food types*

Grass

The linear relationship between the dry mass of a grass tuft and the product of height of the tallest leaf and tuft basal area is shown for each vegetation type in Figure 4.28. The aerial cover of the dominant perennial grass species used to calibrate the relationship, the percent of the total grass cover afforded by the dominant perennial grass species, and estimates of the slope of the linear equation (parameter a) are given for each vegetation type in Table 4.8. Vegetation types that were dominated by the same grass species shared a common relationship. The herbaceous layers of the *Colophospermum mopane – Leucas glabrata* shrub woodland, *Colophospermum mopane – Pappea capensis* dense shrub tall woodland, *Colophospermum mopane – Acacia erubescens* dense shrub open woodland, and *Colophospermum mopane – Grewia flavescens* dense shrub tall woodland were dominated by annual grass species and, consequently, the mass of grass tufts in these vegetation types was not calibrated from leaf height and tuft basal area. Grass cover in the *Brachystegia glaucescens – Androstachys johnsonii* dense shrub open tall woodland was insignificant and, therefore, this vegetation type was excluded.

In most cases, tuft mass was well explained by the product of leaf height and tuft basal area. However, because of a marked difference in the linear relationship between tufts of *Sporobolus iocladus* and *Sporobolus consimilis*, the mass of grass tufts in the *Combretum imberbe – Sporobolus consimilis* open woodland (vegetation type 12) was predicted better using a curvilinear relationship. However, to simplify the modelling process the linear relationship was retained for this vegetation type.

Daily average height of the tallest leaf in green and mixed grass patches is shown for each landscape unit in Figure 4.29 to Figure 4.32. In green grass patches, although there was considerable variation among landscape units, the general trend was for the height of the tallest leaf to decline as the dry season progressed and then increase with the onset of the rainy season. The general trend was similar for mixed grass patches except, in many instances, the height of the tallest leaf did not decline to the same extent as in green grass patches. This was possibly due to a grazing preference for green grass.

When feeding, bulls selected grass tufts with a larger basal circumference (mean = 35.5 cm) than members of family units (mean = 22.3 cm) (Figure 4.33). The average tuft basal area for the dominant perennial grasses and an overall weighted average tuft basal area adjusted for the selection preferences of bulls and family units is shown for each vegetation type in Table 4.10. The average tuft basal area available for selection by bulls ranged from 9 cm^2 in the *Acacia tortilis – Grewia bicolor* shrub open tall woodland to 86 cm^2 in the *Setaria incrassata* grassland, while that available to family units ranged from 9 cm^2 in the *Acacia tortilis – Grewia bicolor* shrub open tall woodland to 38 cm^2 in the *Setaria incrassata* grassland.

The percent aerial cover, average dry mass of the dominant grass species, and the weighted average dry mass of a grass plant for the vegetation types with an herbaceous layer dominated by annual grass species is shown in Table 4.9.

Daily estimates of the dry mass of a trunkload of green grass for adult bulls and members of family units are shown for each landscape unit in Figure 4.34 and Figure 4.35. Although there was considerable variation between landscape units, the general trend was one of a decline in the dry mass of a trunkload of green grass as the dry season progressed followed by an increase from the onset of the rainy season. The mass of a trunkload of annual grasses was assumed to be constant over time. Estimates of the mass of trunkloads harvested by family units were always lower or equal to that harvested by bulls because the maximum basal circumference selected by members of family units was set at lower value (22.3 cm for family units as opposed to 35.5 cm for bulls). In some landscape units there was a large difference between the mass of a trunkload harvested by bulls and that harvested family units, while in other units the difference was small.

Estimates of the dry mass of a trunkload of mixed grass for adult bulls and members of family units followed a similar trend to the estimates for green grass except that, for most landscape units, the decline during the dry season was not as marked (Figure 4.36 and Figure 4.37).

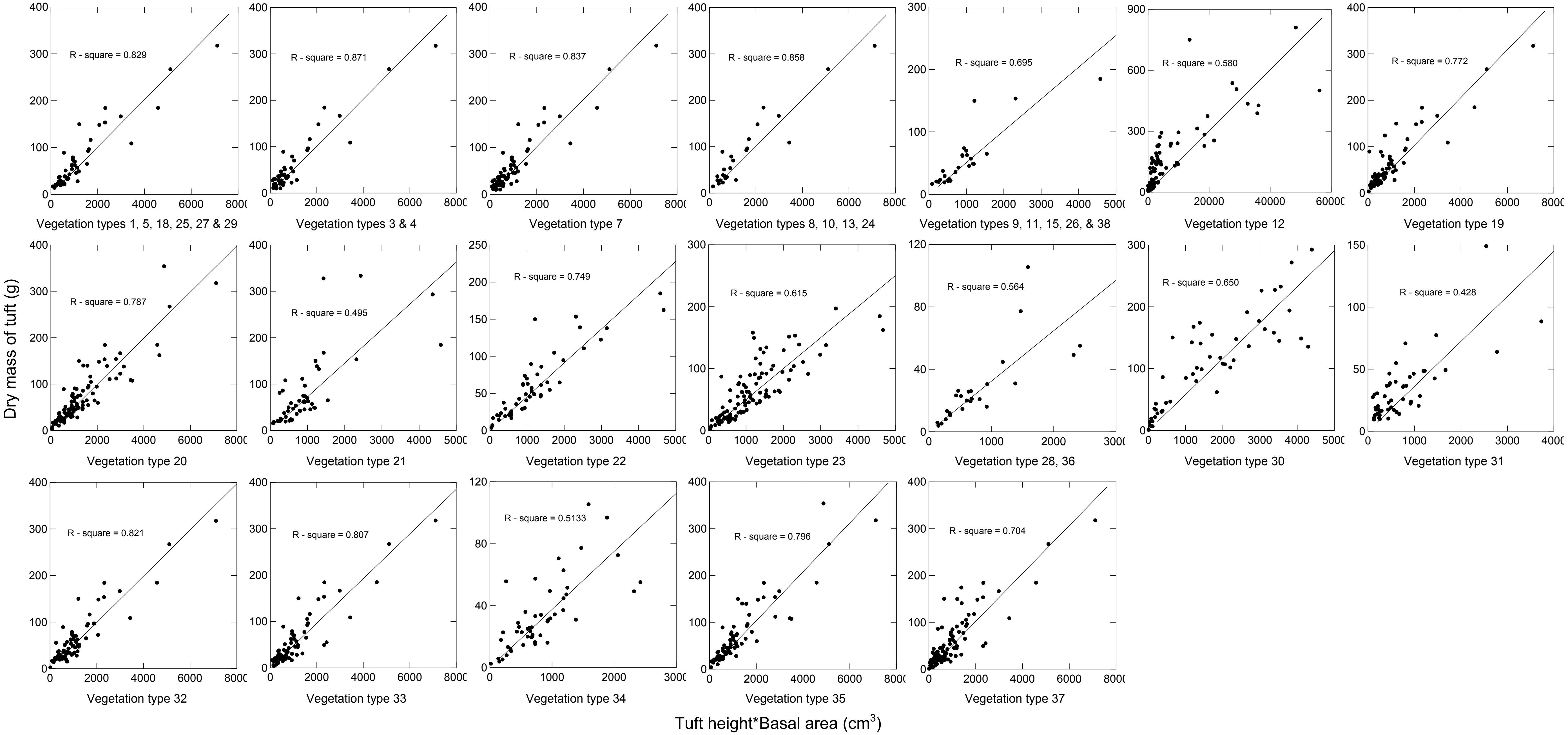


Figure 4.28 Relationship between the dry mass (g) of a grass tuft and the product of height (cm) of the tallest leaf and tuft basal area (cm^2) (Mass = a×Height×Basal area) for each vegetation type. The corrected R^2 value is given. The data set for each vegetation type was composed of measurements from 25 tufts, covering a range of heights and basal areas, of each dominant perennial grass species. Vegetation types dominated by the same grass species have a common relationship. The sward of vegetation types 6, 14, 16 and 17 were dominated by annual grass species and, therefore, these types were not included. Grass cover in vegetation type 2 was insignificant and, consequently, it was excluded. For a key to vegetation type numbers see Figure 3.1.

Table 4.8 Aerial cover (%) of the dominant perennial grass species used to calibrate the relationship between tuft mass and tuft height × basal area, the percent of the total grass cover afforded by the dominant perennial grass species and estimates of parameter a (mass = a×height×basal area) for each vegetation type. Vegetation types 6, 14, 16 and 17 were dominated by annual grass species. Grass cover in vegetation type 2 was insignificant. For a key to vegetation type numbers see Figure 3.1

Vegetation type	% aerial cover of the dominant perennial grass species used to calibrate the relationship between tuft mass and tuft height*basal area																	% of total grass cover	Estimate of parameter a
	Aristida scurius	*Bothriochloa radicans*	*Cenchrus ciliaris*	*Digitaria eriantha*	*Enneapogon scoparius*	*Enteropogon macrostachyus*	*Eragrostis lehmanniana*	*Eragrostis superba*	*Heteropogon contortus*	*Ischaemum afrum*	*Panicum maximum*	*Panicum coloratum*	*Sehima galpinii*	*Setaria incrassata*	*Sporobolus consimilis*	*Sporobolus ioclados*	*Urochloa mosambicensis*		
1											9.8						7.5	78.2	0.050541
3				21.6							10.3							83.7	0.050594
4				40.1							7.9							86.1	0.050594
5											7.2						36.4	85.3	0.050541
7				17.0							6.5						15.5	87.8	0.050670
8											28.7							80.1	0.050417
9																	76.0	93.6	0.050897
10											47.2							78.4	0.050417
11																	19.6	61.1	0.050897
12										14.1		10.0			22.2	10.7		85.1	0.015045
13											11.9							40.5	0.050417
15																	46.5	97.5	0.050897
18											10.5						25.0	84.0	0.050541
19							4.5				9.7						5.4	75.1	0.051522
20						2.6			3.5		2.1						7.3	62.8	0.049762
21						2.1											12.5	60.0	0.072608
22									22.1								40.6	96.3	0.045580
23		7.3			11.6				7.5								5.6	63.7	0.050016
24											5.2							36.7	0.050417
25											7.1						53.5	92.9	0.050541
26																	29.3	80.9	0.050897
27											5.0						60.7	90.3	0.050541
28													31.5					62.1	0.032346
29											11.8						63.2	95.2	0.050541
30										33.0				36.4				88.7	0.058139
31	11.6			13.5														89.4	0.036208
32			7.5								7.2						45.3	72.0	0.049607
33											20.3		19.3				21.0	72.8	0.048133
34			5.8										20.9					66.9	0.037493
35						4.3					14.8						5.4	82.1	0.052114
36													18.4					29.47	0.032346
37											9.2		9.5	32.9				68.9	0.051070
38																	5.7	26.9	0.050897

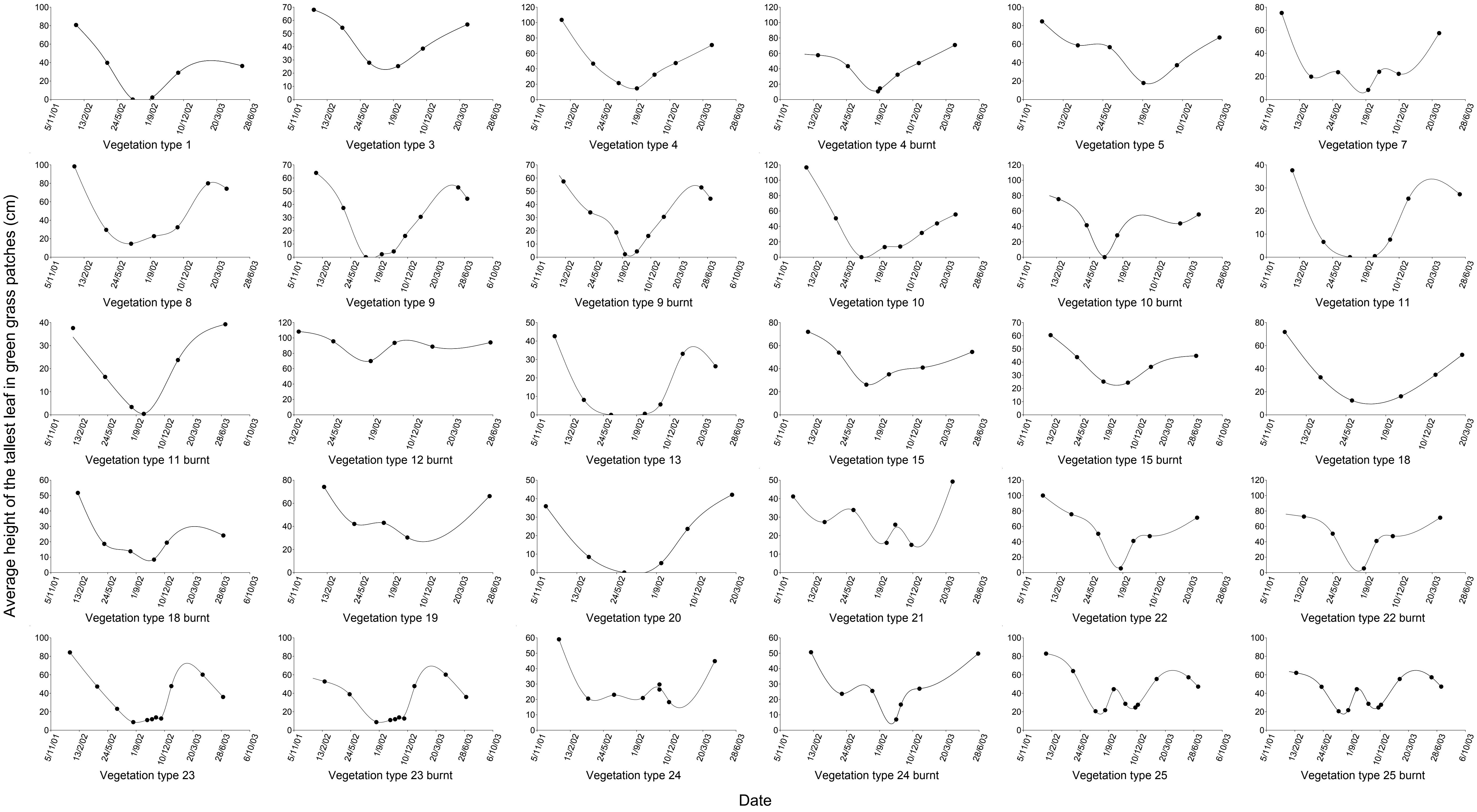


Figure 4.29 Interpolation between estimates of the average height (cm) of the tallest leaf in green grass patches using smoothing spline regression for vegetation types 1-25. For a key to vegetation type numbers see Figure 3.1.

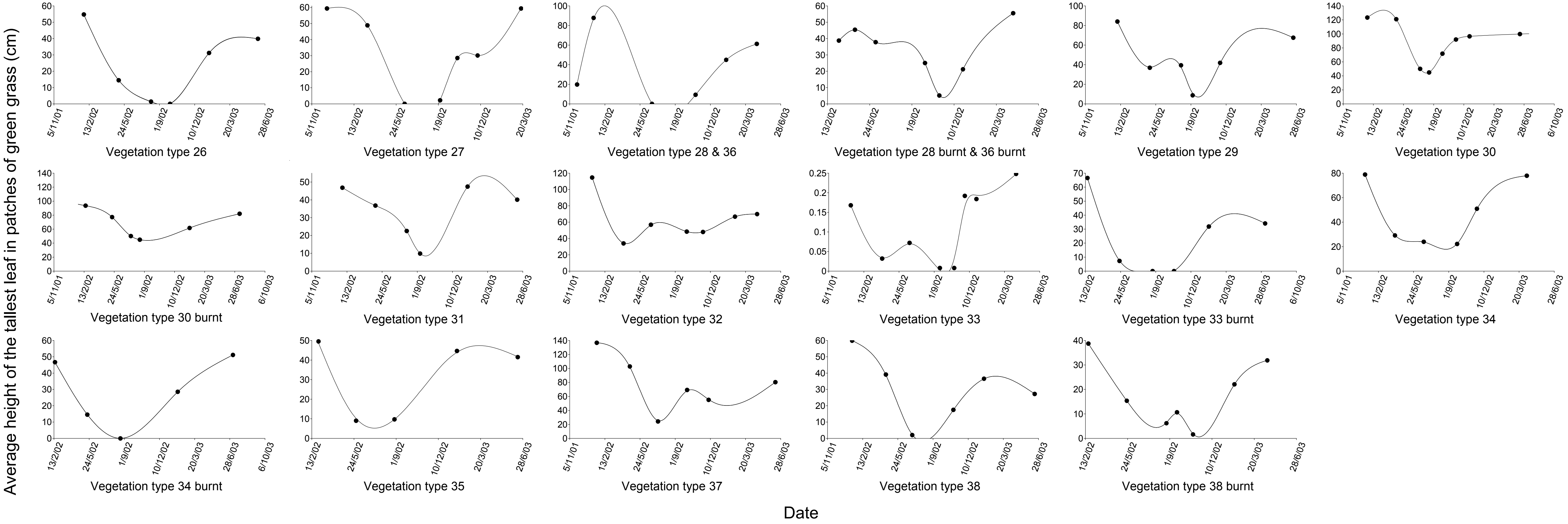


Figure 4.30 Interpolation between estimates of the average height (cm) of the tallest leaf in green grass patches using smoothing spline regression for vegetation types 26-38. For a key to vegetation type numbers see Figure 3.1.

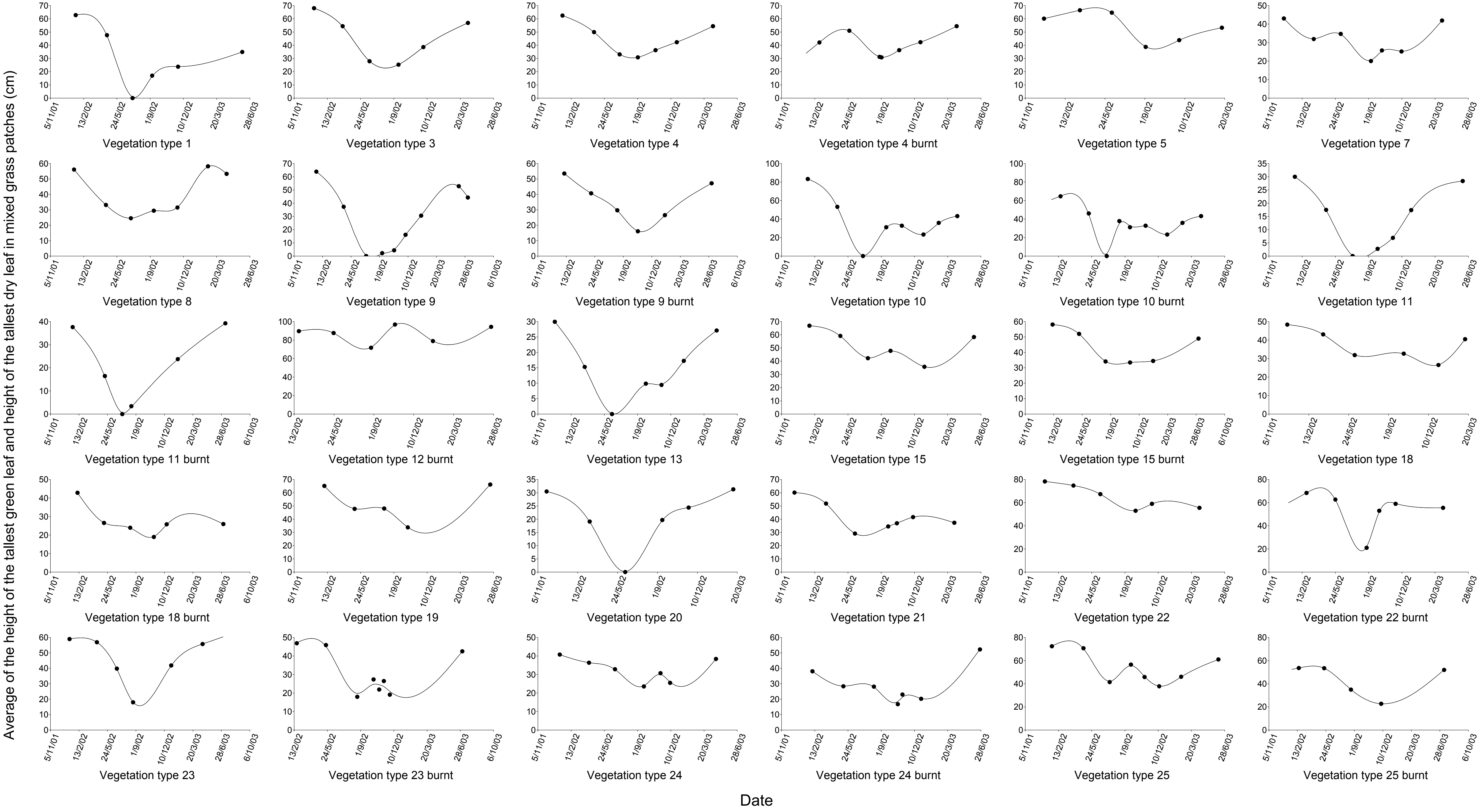


Figure 4.31 Interpolation between estimates of the average of the height of the tallest green leaf and the height of the tallest dry leaf in mixed grass patches using smoothing spline regression for vegetation types 1-25. For a key to vegetation type numbers see Figure 3.1.

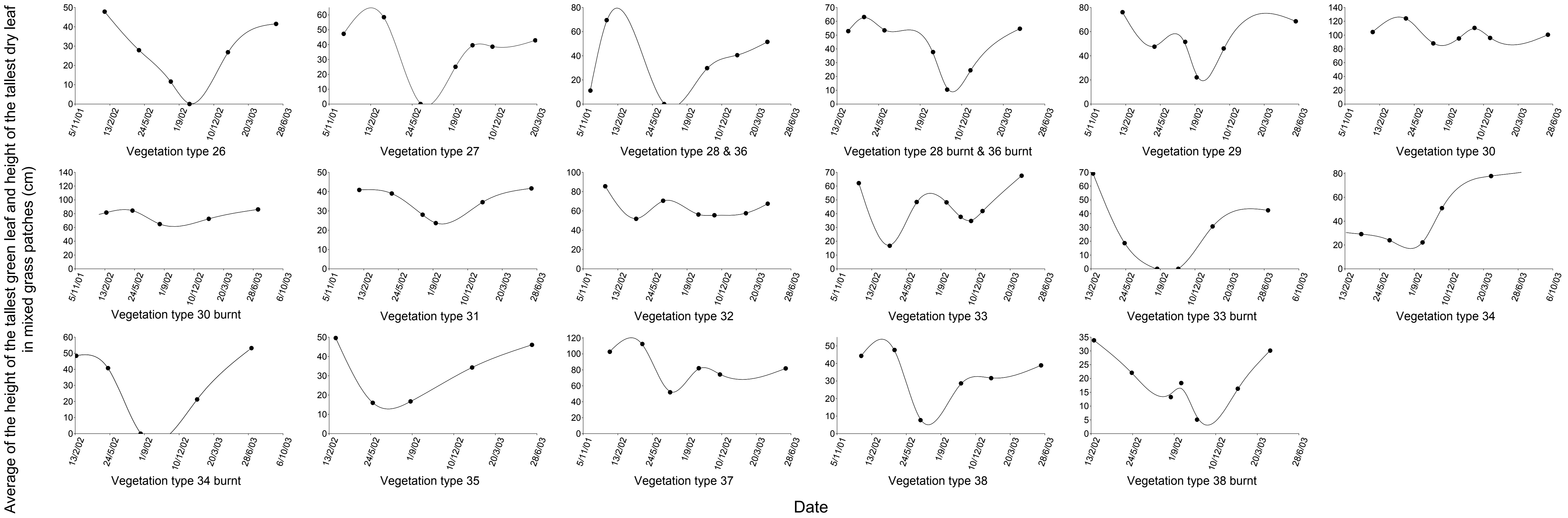
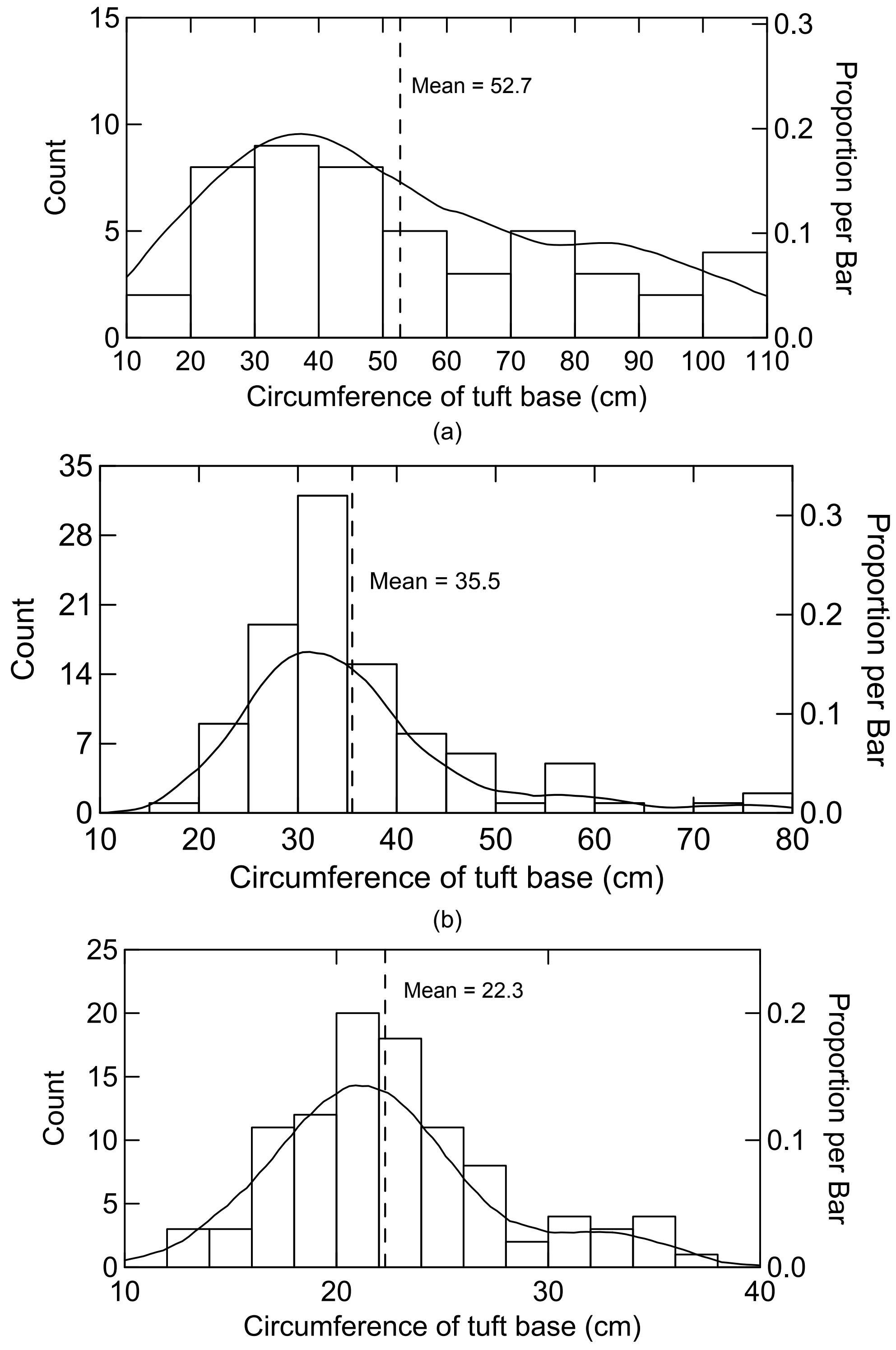


Figure 4.32 Interpolation between estimates of the average of the height of the tallest green leaf and the height of the tallest dry leaf in mixed grass patches using smoothing spline regression for vegetation types 26-38. For a key to vegetation type numbers see Figure 3.1.

Table 4.9 Percent aerial cover, average (n = 25) dry mass (g) of the dominant annual grass species, and the weighted average dry mass (g) of an annual grass plant for vegetation types 6, 14, 16 and 17. For a key to vegetation types see Figure 3.1

Vegetation type	Dominant annual grass species										Weighted average dry mass (g) of an annual grass plant
	Aristida adscensionis		*Aristida congesta*		*Brachiaria deflexa*		*Setaria sagittifolia*		*Sporobolus paniciodes*		
	% Cover	Dry mass (g)	% Cover	Dry mass (g)	% Cover	Dry mass (g)	% Cover	Dry mass (g)	% Cover	Dry mass (g)	
6	1.3	4.3		16.9	4.3	10.1		3.6		1.2	8.8
14	1.5				3.6		1.4				7.4
16	2.5				6.7				2.4		7.0
17	1.6		2.6		3.0						11.4



(a)

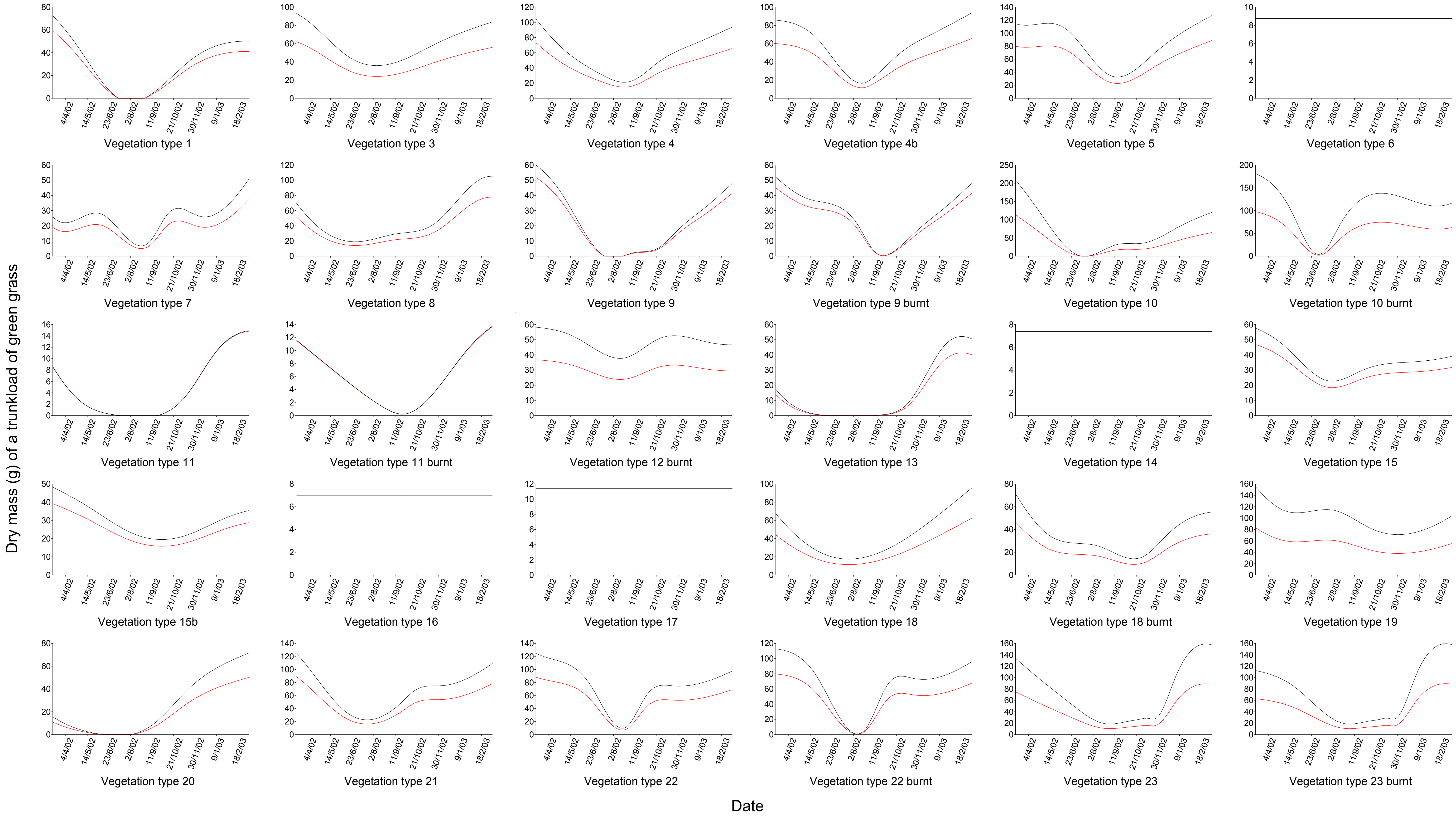
(b)

(c)

Figure 4.33 Histogram and kernel density distributions of the circumference (cm) of *Setaria incrassata* tufts of (a) the *Setaria incrassata* population (b) *Setaria incrassata* tufts selected by adult bulls and (c) *Setaria incrassata* tufts selected by individuals of a cow herd. The mean tuft circumference (cm) is given for each data set.

Table 4.10 Raw average tuft basal area (cm^2) and average tuft basal area (cm^2) adjusted for the selection preferences of bulls and cows for the dominant perennial grass species in each vegetation type. The overall weighted average tuft basal area (cm^2) adjusted for the selection preferences of bulls and cows is also given for each vegetation type. When calculating the weighted average, % aerial cover was used to weight the tuft basal area for each grass species. For a key to vegetation type numbers see Figure 3.1

Vegetation type	Average tuft basal area (cm^2)																																																			Weighted av. of adjusted tuft basal area (cm^2)	
	Aristida scurius			*Bothriochloa radicans*			*Cenchrus ciliaris*			*Digitaria eriantha*			*Enneapogon scoparius*			*Enteropogon macrostachyus*			*Eragrostis lehmanniana*			*Eragrostis superba*			*Heteropogon contortus*			*Ischaemum afrum*			*Panicum maximum*			*Panicum coloratum*			*Sehima galpinii*			*Setaria incrassata*			*Sporobolus consimilis*			*Sporobolus ioclados*			*Urochloa mosambicensis*				
	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Raw	Bulls	Cows	Bulls	Cows
1																															31	29	22																18	17	15	23	19
3										19	18	16																			116	58	32																			31	21
4										25	23	18																			92	62	33																			30	21
5																															62	42	26																45	37	27	38	26
7										22	21	18																			40	33	21																26	21	15	23	17
8																															30	26	19																			26	19
9																																																	23	22	19	22	19
10																															66	50	27																			50	27
11																																																	9	9	9	9	9
12																												53	35	21				59	42	26							61	38	24	31	27	19				36	23
13																															29	28	22																			28	22
15																																																	18	17	14	17	14
18																															80	53	29																33	30	22	37	24
19																			13	13	12										125	65	32																85	59	32	52	28
20																21	21	18							20	20	19				47	39	24																52	44	28	34	24
21																						86	57	33																									29	27	21	32	23
22																									44	39	28																						36	32	22	34	24
23				135	58	30							150	69	34										17	17	16																						8	8	8	44	25
24																															70	51	28																			51	28
25																															42	36	25																15	15	14	17	15
26																																																	25	23	18	23	18
27																															46	40	27																14	14	14	16	15
28																																					43	35	22													35	22
29																															116	61	32																46	41	27	44	28
30																												355	87	37										237	85	38										86	38
31	96	58	32							28	27	22																																								41	27
32							235	78	37																						59	45	28																51	42	27	46	29
33																															222	89	39																24	20	17	42	23
34	208	77	36																																		146	79	37													79	37
35																27	27	24													50	45	29																28	26	20	38	26
36																																					46	38	24													38	24
37																															106	68	34				97	63	34	216	77	35							58	38	24	67	33
38																																																	19	18	16	18	16



Vegetation type 1
Vegetation type 3
Vegetation type 4
Vegetation type 4b
Vegetation type 5
Vegetation type 6
Vegetation type 7
Vegetation type 8
Vegetation type 9
Vegetation type 9 burnt
Vegetation type 10
Vegetation type 10 burnt
Vegetation type 11
Vegetation type 11 burnt
Vegetation type 12 burnt
Vegetation type 13
Vegetation type 14
Vegetation type 15
Vegetation type 15b
Vegetation type 16
Vegetation type 17
Vegetation type 18
Vegetation type 18 burnt
Vegetation type 19
Vegetation type 20
Vegetation type 21
Vegetation type 22
Vegetation type 22 burnt
Vegetation type 23
Vegetation type 23 burnt

Figure 4.34 Daily estimates of the dry mass (g) of a trunkload of green grass for adult bulls (—) and cows (—) during the study period for vegetation types 1 – 23. Grass cover in vegetation type 2 was insignificant. For a key to vegetation type numbers see Figure 3.1.

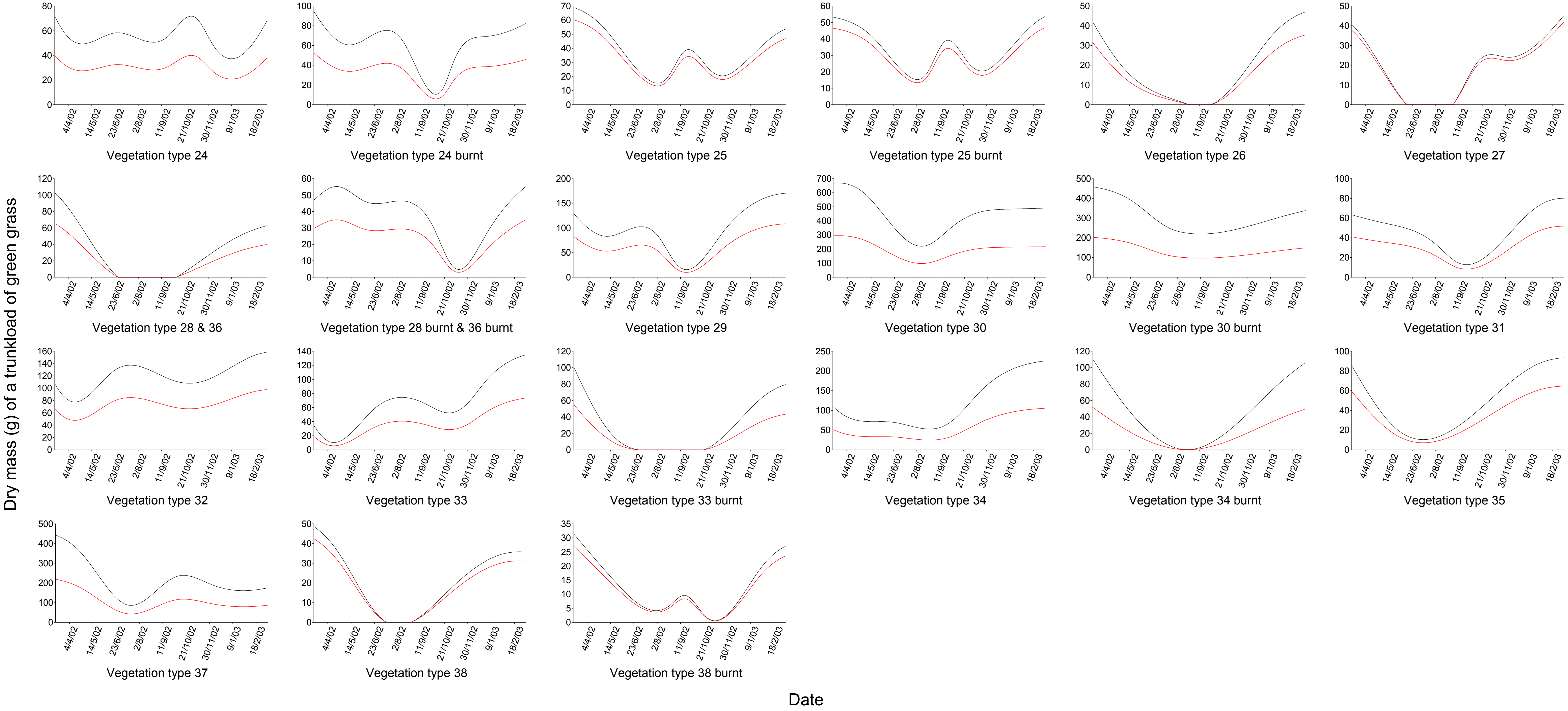
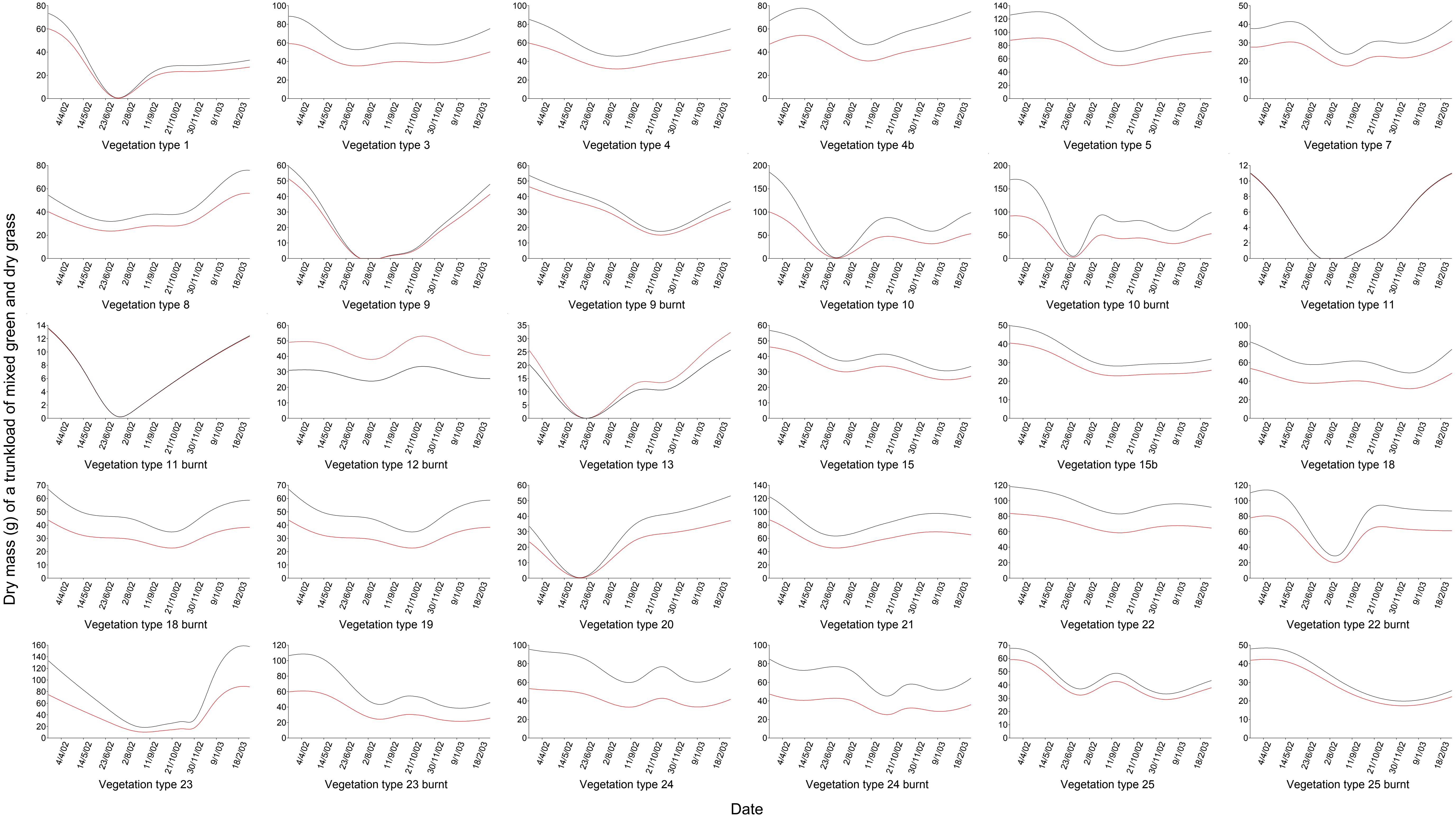


Figure 4.35 Daily estimates of the dry mass (g) of a trunkload of green grass for adult bulls (—) and cows (—) during the study period for vegetation types 24 – 38. For a key to vegetation type numbers see Figure 3.1.



Vegetation type 1
Vegetation type 3
Vegetation type 4
Vegetation type 4b
Vegetation type 5
Vegetation type 7
Vegetation type 8
Vegetation type 9
Vegetation type 9 burnt
Vegetation type 10
Vegetation type 10 burnt
Vegetation type 11
Vegetation type 11 burnt
Vegetation type 12 burnt
Vegetation type 13
Vegetation type 15
Vegetation type 15b
Vegetation type 18
Vegetation type 18 burnt
Vegetation type 19
Vegetation type 20
Vegetation type 21
Vegetation type 22
Vegetation type 22 burnt
Vegetation type 23
Vegetation type 23 burnt
Vegetation type 24
Vegetation type 24 burnt
Vegetation type 25
Vegetation type 25 burnt

Figure 4.36 Daily estimates of the dry mass (g) of a trunkload of mixed green and dry grass grass for adult bulls (—) and cows (—) during the study period for vegetation types 1 – 25. Grass cover in vegetation type 2 was insignificant. For a key to vegetation type numbers see Figure 3.1.

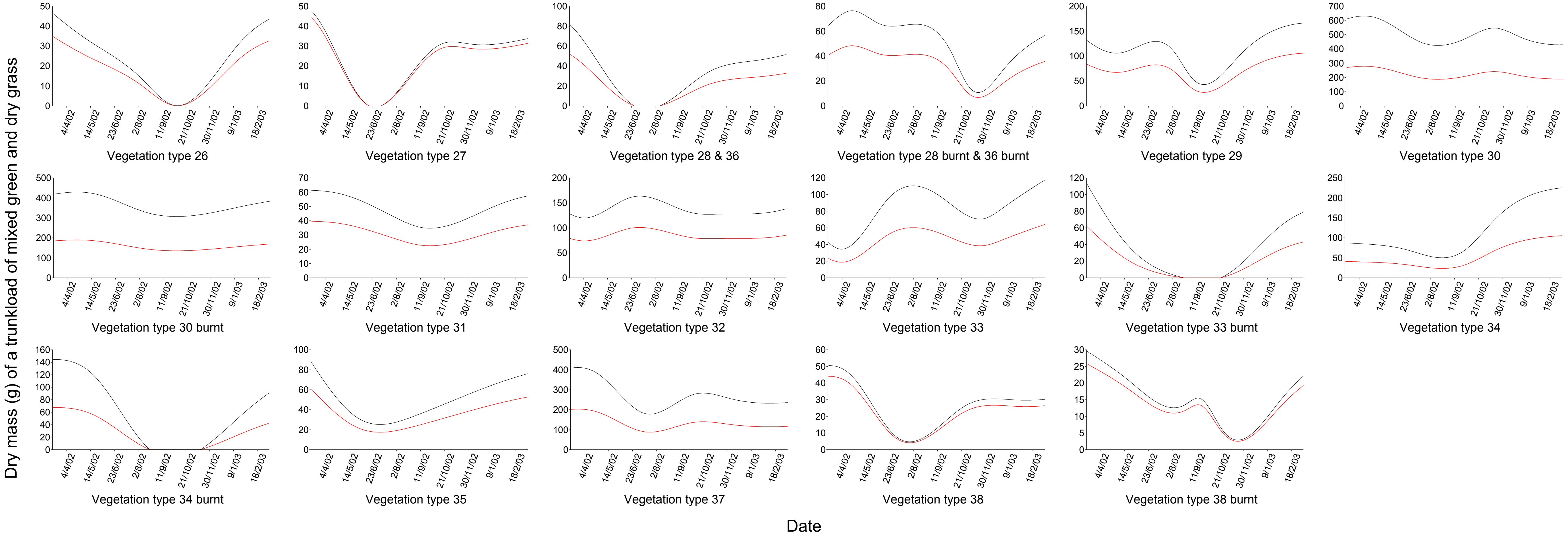


Figure 4.37 Daily estimates of the dry mass (g) of a trunkload of mixed green and dry grass for adult bulls (—) and cows (—) during the study period for vegetation types 26 – 38. For a key to vegetation type numbers see Figure 3.1.

Values for the traits of the grass species used to calibrate regression tree models for the prediction of the crude protein content of green and dry grass plants are shown in Table 4.11.

Table 4.11 Traits of grass species used to calibrate regression tree models for the prediction of crude protein (%) of green and dry grass plants. The crude protein of dry plants was not measured for the annual species

Species	Annual	Maximum plant height (mm)	Maximum width of leaf blade (mm)	Specific area of leaf blade (cm^2/g)	Crude protein (%)	
					Green	Dry
Panicum maximum	0	2000	20	173.33	12.1	4.5
Chloris virgata	1	750	6	126.69	10	-
Digitaria eriantha	0	1400	14	113.02	4.6	3.4
Setaria incrassata	0	2000	14	102.40	5.1	4.5
Urochloa mosambicensis	0	1500	20	140.06	5.3	3.3
Aristida scurius	0	1400	3	134.85	3.2	3.8
Dactyloctenium giganteum	1	1140	12	192.65	10.5	-
Brachiaria eruciformis	1	500	6	161.99	10.8	-
Sehima galpinii	0	1800	6	156.56	5.4	3.6
Sporobolus ioclados	0	1000	12	109.93	5.3	4.4
Heteropogon contortus	0	1000	8	152.02	3.6	2.2

The proportional reduction in error and improvement for each split of the regression model for the prediction of the crude protein content of green grass is shown in Table 4.12. The tree diagram is shown in Figure 4.38. The model used three traits and four splits to explain 97.7 % of the variation in the crude protein content of the calibration data set.

Table 4.12 Proportional reduction in error and improvement of fit for each split of the regression tree model for predicting the crude protein (%) of green grass plants

Split	Variable	Proportional reduction in error	Improvement
1	Specific area of leaf blade (cm^2/g)	0.702	0.702
2	Maximum width of leaf blade (mm)	0.715	0.013
3	Annual	0.954	0.239
4	Maximum width of leaf blade (mm)	0.977	0.023

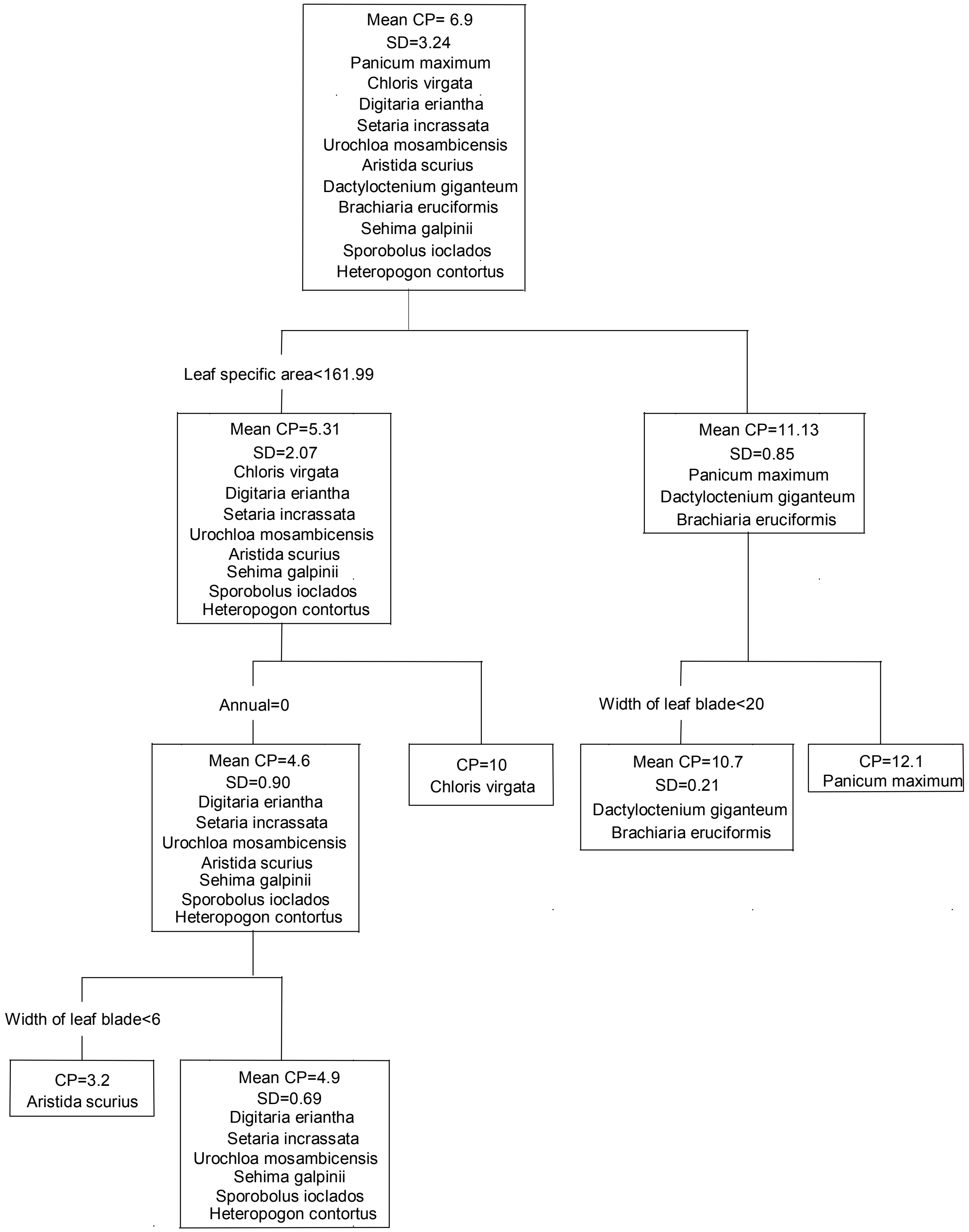


Figure 4.38 Regression tree model for predicting the crude protein (%) of green grass plants.

The specific area of the leaf blade, which was positively correlated with crude protein content, explained the greatest proportion of variance (70.2 %). Other important traits were whether the plant was an annual (23.9 % of the variance) and the maximum width of the leaf blade (3.6 % of the variance). Both of these traits were positively correlated with crude protein content.

The proportional reduction in error and improvement for each split of the regression model for the prediction of the crude protein content of dry grass is shown in Table 4.13. The tree diagram is shown in Figure 4.39. The model used three traits and four splits to explain 99.4 % of the variation in the crude protein content of the calibration data set.

Table 4.13 Proportional reduction in error and improvement of fit for each split of the regression tree model for predicting the crude protein (%) of dry grass plants

Split	Variable	Proportional reduction in error	Improvement
1	Maximum height of plant	0.386	0.386
2	Specific area of leaf blade	0.638	0.252
3	Maximum height of plant	0.966	0.328
4	Maximum width of leaf blade	0.994	0.028

The maximum height of the plant, which was positively correlated with crude protein content, explained the greatest proportion of variance (71.4 %). Other important traits were the specific area of the leaf blade (25.2 % of the variance) and the maximum width of the leaf blade (2.8 % of the variance). Both of these traits were positively correlated with crude protein content.

Values for the traits and regression tree predictions of percent crude protein for green and dry plants are shown, for the common grass species, in Table 4.14. The crude protein content of grass species ranged from 3.2 to 12.1 % when green, and from 2.7 to 6.4 % when partially green (mixed). With the exception of *Panicum maximum*, which had a crude protein content of 12.1 % when green, the annual grass species had higher estimates of crude protein content than the perennial species. Within species estimates of the crude protein content for mixed grass were lower than those for green grass.

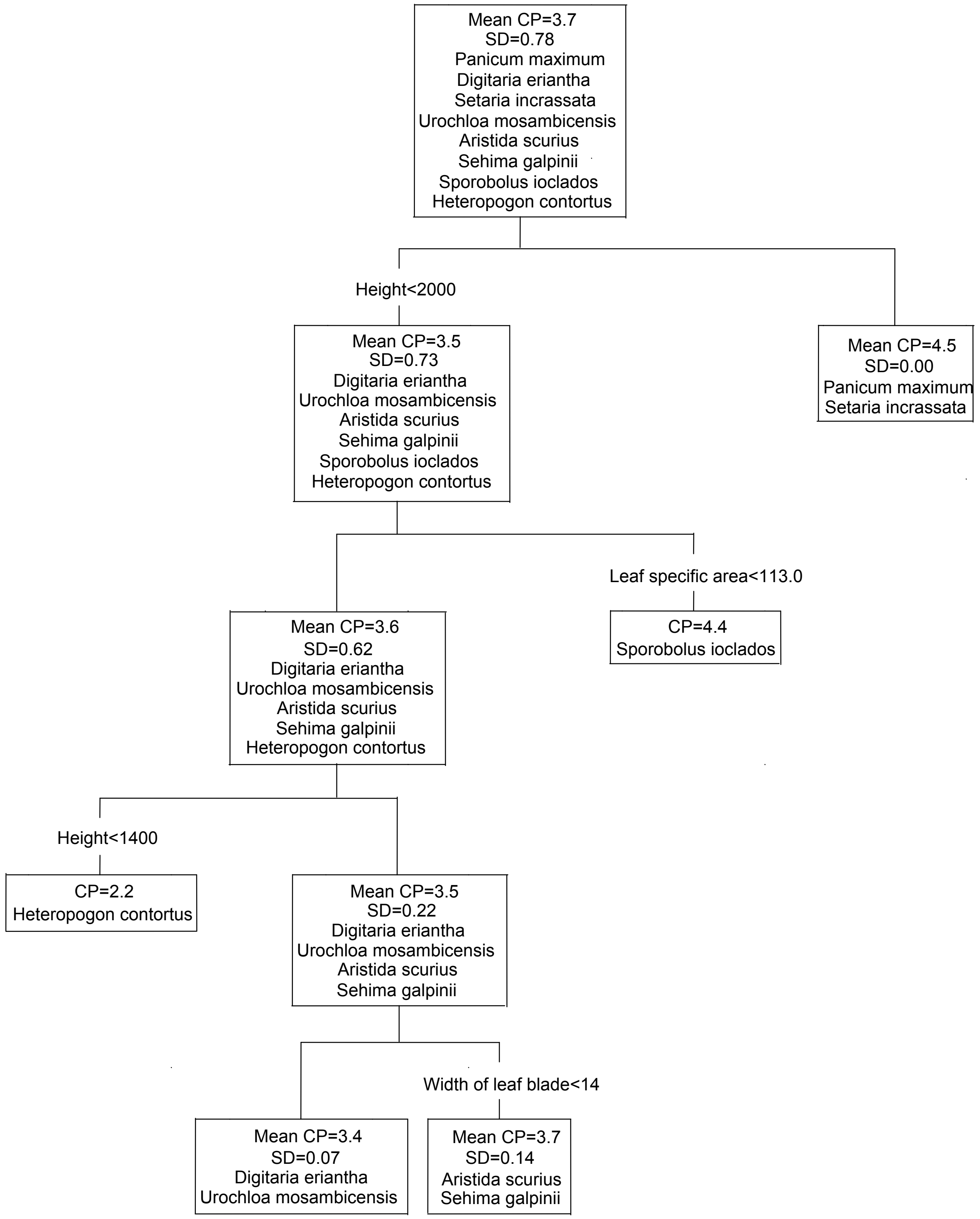


Figure 4.39 Regression tree model for predicting the crude protein (%) of dry grass plants.

Table 4.14 Values for traits and regression tree predictions of percent crude protein for green and dry grass plants. The percent crude protein of plants with a mixture of green and dry material was estimated as the average of the crude protein for green and dry plants. Crude protein was not estimated for dry and mixed plants of annual grass species

Species	Annual	Maximum height of plant (mm)	Maximum width of leaf blade (mm)	Specific area of leaf blade (cm^2/g)	Predicted crude protein (%)		
					Green	Dry	Mixed
Andropogon fastigiatus	1	500	4	223.52	10.7	-	-
Aristida adscensionis	1	1200	3	138.94	10.0	-	-
Aristida congesta	0	900	5	157.68	3.2	2.2	2.7
Bothriochloa radicans	0	700	6	188.54	10.7	2.2	6.4
Brachiaria deflexa	1	700	22	222.37	12.1	-	-
Cenchrus ciliaris	0	1000	8	104.67	4.9	4.4	4.6
Dactyloctenium aegyptium	1	750	8	218.95	10.7	-	-
Dichanthium annulatum	0	1000	7	169.72	10.7	2.2	6.4
Enneapogon cenchroides	1	1000	8	182.82	10.7	-	-
Enneapogon scoparius	0	650	3	152.83	3.2	2.2	2.7
Enteropogon macrostachyus	0	1200	7	118.86	4.9	2.2	3.5
Eragrostis lehmanniana	0	600	2.8	184.98	10.7	2.2	6.4
Erarostis rigidior	0	1000	5	143.27	3.2	2.2	2.7
Eragrostis superba	0	1000	10	120.91	4.9	2.2	3.5
Eriochloa stapfiana	0	1700	8	154.07	4.9	3.7	4.3
Ischaemum afrum	0	1500	8	81.45	4.9	4.4	4.6
Linntonia nutans	0	900	5	129.48	3.2	2.2	2.7
Melinis repens	1	1200	11	120.40	10.0	-	-
Melinis tenuissima	1	1100	6	357.86	10.7	-	-
Panicum coloratum	0	1500	10	134.43	4.9	3.7	4.3
Perotis patens	1	600	12	233.16	10.7	-	-
Pogonarthria squarrosa	0	1400	5.5	152.27	3.2	3.7	3.5
Rottboellia cochinchinensis	1	3000	30	215.14	12.1	-	-
Schmidtia pappophoroides	0	900	7	115.38	4.9	2.2	3.5
Setaria incrassata	0	2000	14	102.40	5.1	4.5	4.8
Setaria sagittifolia	1	800	11	346.15	10.7	-	-
Sorghum versicolor	1	1200	8	176.11	10.7	-	-
Sporobolus consimilis	0	1600	10	74.36	4.9	4.4	4.6
Sporobolus panicoides	1	960	6	289.63	10.7	-	-
Tricholaena monachne	0	1000	3.5	141.75	3.2	2.2	2.7

The weighted average crude protein content of grass plants in green patches ranged from 4.44 % in the *Brachystegia glaucescens – Albizia petersiana* open woodland to 11.01 % in the *Acacia tortilis – Philenoptera violacea* shrub tall woodland (Table 4.15). In mixed patches, the average crude protein ranged from 2.29 % in the *Colophospermum mopane – Brachiaria eruciformis* open woodland to 7.11 % in the *Acacia tortilis – Philenoptera violacea* shrub tall woodland.

In most landscape units, the mass of protein in trunkloads of green grass declined during the dry season and then increased with the onset of the rains (Figure 4.40 & Figure 4.41). However, across landscape units there was considerable variation in this general trend. In vegetation types with an herbaceous layer dominated by annual grasses, the mass of protein per trunkload was assumed to be constant over the growing season. The mass of protein in trunkloads gathered by bulls was always greater than or equal to that in trunkloads gathered by members of family units. The disparity between bulls and family units was greater in some landscape units than in others. Exceptionally high mass of protein per trunkload was estimated for the *Setaria incrassata* grassland (vegetation type 30). However, because *Setaria incrassata* is a very robust grass species, the protein is probably enclosed within thick cell walls and may, therefore, be of limited utility to elephants.

The mass of protein in trunkloads of mixed grass followed a similar temporal trend to that of green grass (Figure 4.42 & Figure 4.43). However, during the wet season the mass of protein per trunkload of mixed grass was generally lower than that from trunkloads of green grass, and the absolute decline in protein mass during the dry season was generally less marked for trunkloads of mixed grass.

Table 4.15 Percent aerial cover and the weighted average crude protein content (%) of grass plants in green and mixed grass patches for each vegetation type. Grass cover in vegetation type 2 was insignificant. The weighted average crude protein content of mixed grass patches was not calculated for vegetation types whose herbaceous layer was dominated by annual grasses. For a key to vegetation type numbers see Figure 3.1

Vegetation type	Aerial cover (%)																																			Weighted average CP (%)	
	Andropogon fastigiatus	*Aristida adscensionis*	*Aristida congesta*	*Aristida sciurus*	*Bothriochloa radicans*	*Brachiara deflexa*	*Brachiaria eruciformis*	*Cenchrus ciliaris*	*Chloris virgata*	*Dactyloctenium aegyptium*	*Dactyloctenium giganteum*	*Dichanthium annulatum*	*Digitaria eriantha*	*Enneapogon scoparius*	*Enneopogon cenchroides*	*Enteropogon macrostachyus*	*Eragrostis lehmanniana*	*Eragrostis rigidior*	*Eragrostis superba*	*Eriochloa stapfiana*	*Heteropogon contortus*	*Ischaemum afrum*	*Lintonia nutans*	*Panicum coloratum*	*Panicum maximum*	*Perotis patens*	*Rottboellia cochinchinensis*	*Sehima galpinii*	*Setaria incrassata*	*Setaria sagittifolia*	*Sorghum versicolor*	*Sporobolus consimilis*	*Sporobolus iocladus*	*Sporobolus panicoides*	*Tricholaena monachne*	*Urochloa mosambicensis*	Green grass patches	Mixed grass patches
1		0.45				0.95			2.26		0.14		3.57			0.05		12.54							44.37					0.05						33.87	8.14	5.62
3			7.21			0.10			0.02				55.45		0.19		3.87								26.47	1.27									1.90	3.43	6.81	5.06
4													71.23				0.01	7.25							14.09	0.03									0.87	6.45	5.59	4.52
5		0.83	0.05			0.10					0.03		7.03		0.03		4.72								14.16	0.99										71.12	6.52	4.82
6		8.60				27.23							0.09		0.09										2.47					0.34						13.79	5.23	
7		0.30	0.21			0.19					0.11		38.24		0.07		7.43								14.67	1.57				0.01						34.80	6.42	4.73
8						2.35					0.03		3.02												80.08					1.03						12.60	10.89	7.31
9						0.02			0.46									1.68	0.02						4.22											93.60	5.57	4.42
10		0.01				2.97			0.03		3.60		6.59					0.01							78.43					0.59						7.77	11.01	7.11
11		0.03				2.52			3.77	3.65	0.75		7.79					10.52							5.42					0.47						61.14	5.79	3.68
12						0.16				0.16		3.80								1.71	1.11	21.08		14.93	0.90				6.93			33.11	15.95				5.24	4.69
13		4.54	0.03			2.02			30.65	0.10	0.65		0.24		0.07			0.68							40.49					0.03						17.80	9.73	4.15
14		16.89				40.47		1.92	0.20				5.01		12.39	0.71		0.05							0.35					15.68				0.71			10.07	
15			0.06			0.11				0.03			0.03					0.06			0.03				1.68											97.51	5.39	4.34
16		11.60	0.28			30.74			1.76	0.05	0.05		10.35		0.09	0.69		22.26							1.80					0.23				11.23		0.32	7.76	
17		19.34	32.86		5.48	37.43							0.08		0.33	0.17		0.58	0.08						0.08									0.41		1.24	8.29	
18		2.56	2.14			1.10			0.08						0.12	0.38	0.39	0.18			0.06				24.90					0.79	0.01		7.65			59.05	7.18	5.08
19		1.25	0.03			0.79	0.03		0.06		0.03					0.21	17.27	7.66							36.95								13.23			20.83	8.61	5.93
20	1.72	11.50	3.59		6.23	5.70			0.04	0.01			0.01	6.14	2.24	9.39		0.33		0.01	12.52				7.59					0.18	0.36			0.15	2.74	26.33	6.64	3.20
21		9.71	0.43		2.66	6.89							1.08	1.48	0.67	0.08	1.18		8.43		5.18				4.63						0.05					50.26	6.23	3.34
22	0.51	0.26			0.60	0.07							0.01	0.75	0.11						33.70				1.89						0.05					61.79	4.91	3.85
23	5.36	6.41	0.08		13.04	2.81	4.54	0.87	0.06				0.20	20.57	8.33	0.05					13.28							6.65	0.13		4.75				2.51	9.88	6.99	2.63
24		1.05				23.36	22.53	6.32						0.18	6.94	1.76						1.05			34.08			0.09	0.53	0.09	0.09					0.88	10.78	3.30
25		0.57				0.02	0.75	5.06											0.05				0.02		10.82			0.09	0.41							82.17	6.08	4.69
26		5.15	4.16			3.40			0.24	0.02					0.74		0.39	1.82							1.62					0.15						80.26	5.73	3.77
27		1.65				0.27							4.14		0.13	0.08	0.30		0.66		2.08				6.74					0.01				0.38	1.31	82.24	5.80	4.40
28	0.96	1.06				0.47	28.07							0.30	0.98						1.20		4.94				0.12	61.29			0.59					0.02	7.00	2.93
29		0.17	0.03						0.12	0.02								0.03							14.94								4.47			80.21	6.33	4.91
30					0.12							9.10	0.99									42.15			1.01				46.52							0.12	5.58	4.91
31			1.84	37.94		0.04							44.38												3.19	4.51									7.96	0.04	4.44	3.63
32		1.96	0.17		1.33	1.20	4.32	9.68					1.90	3.80	0.15				1.12		5.09	1.06			9.34			0.01	0.27		0.05				0.01	58.52	6.19	4.26
33		1.78				1.05	19.92	2.37															0.55		24.31		1.14	23.04	0.27						0.38	25.18	8.27	4.29
34		1.27				1.71	31.40	9.84					3.39									2.34			3.85		5.43	35.55	5.07		0.02					0.10	7.78	2.87
35		9.06				8.03			0.07						0.80	14.27									49.25					0.50						17.96	9.63	5.37
36	0.59	6.85			0.50	1.26	39.68	4.28	0.01						0.16								3.93		5.74		3.77	29.42	0.84		0.31					2.64	8.55	2.29
37		0.27					0.57	0.44					5.68								0.16	1.56			12.17		9.76	12.57	43.75		0.12					12.95	6.72	4.56
38	8.86	25.54	4.06		4.95	5.39	8.17							0.52	7.08						8.30							0.35			0.56			0.13		24.84	8.17	1.77

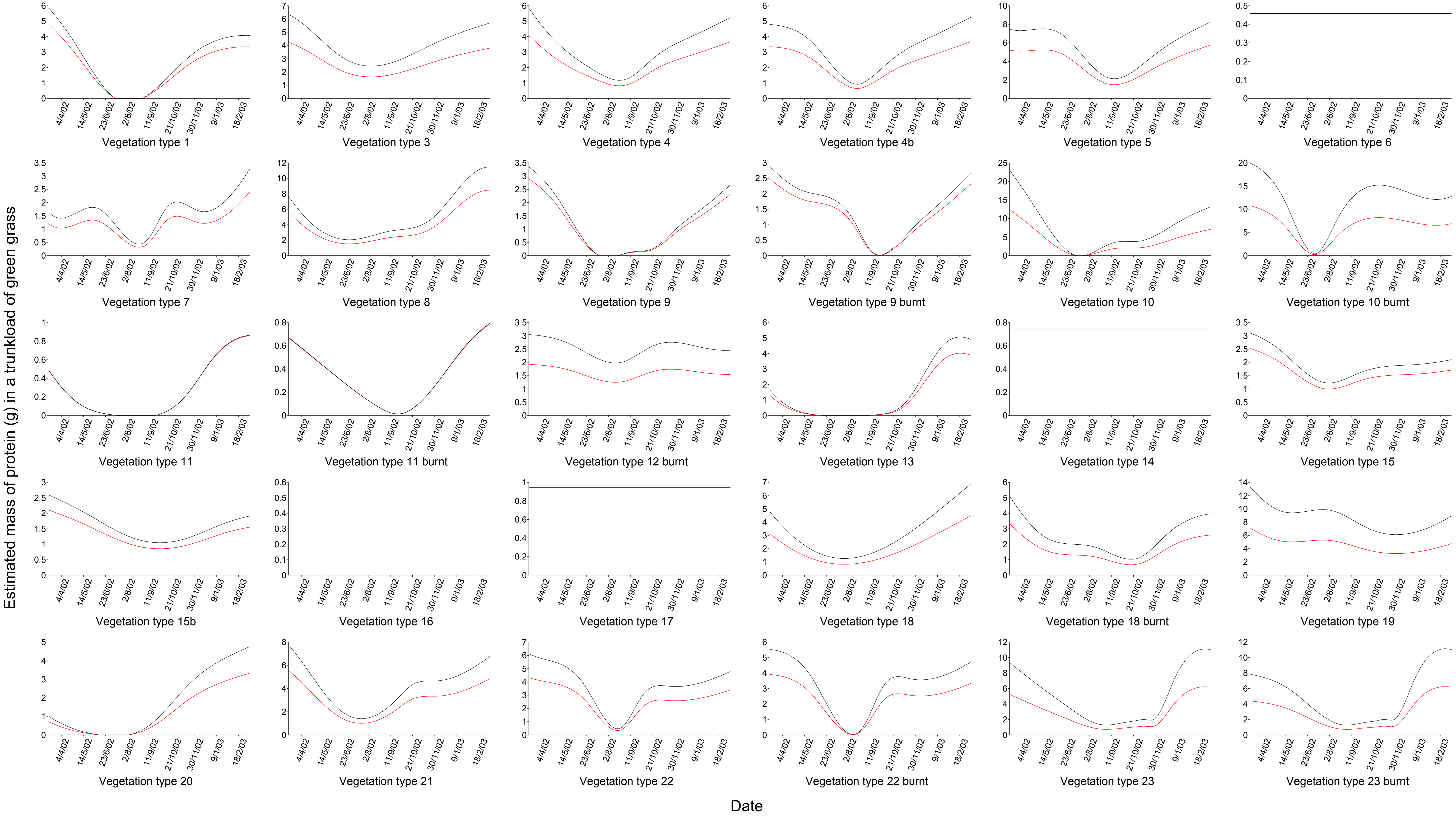
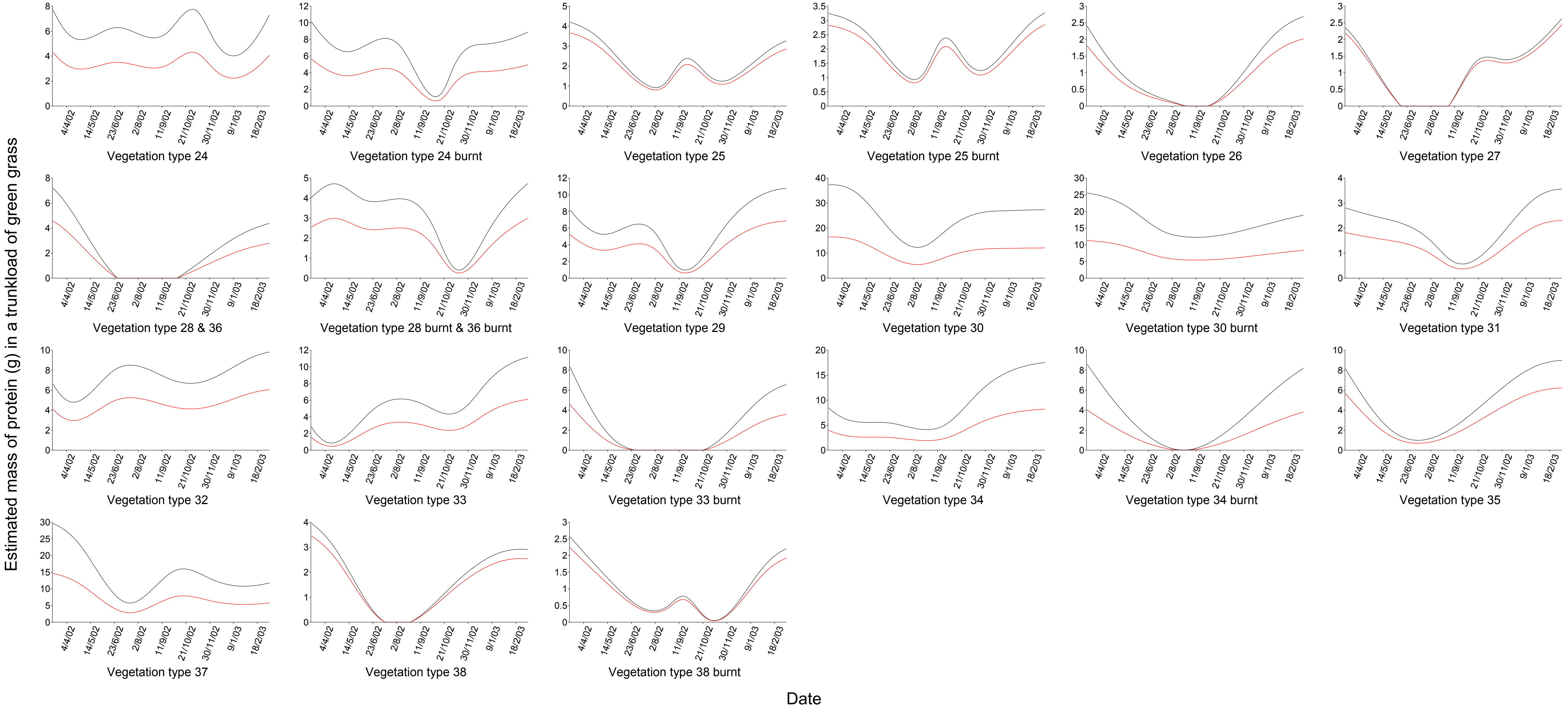


Figure 4.40 Daily estimates of the mass of protein (g) in a trunkload of green grass for adult bulls (—) and cows (—) during the study period for vegetation types 1 – 23. For a key to vegetation type numbers see Figure 3.1.



Vegetation type 24

Vegetation type 24 burnt

Vegetation type 25

Vegetation type 25 burnt

Vegetation type 26

Vegetation type 27

Vegetation type 28 & 36

Vegetation type 28 burnt & 36 burnt

Vegetation type 29

Vegetation type 30

Vegetation type 30 burnt

Vegetation type 31

Vegetation type 32

Vegetation type 33

Vegetation type 33 burnt

Vegetation type 34

Vegetation type 34 burnt

Vegetation type 35

Vegetation type 37

Vegetation type 38

Vegetation type 38 burnt

Figure 4.41 Daily estimates of the mass of protein (g) in a trunkload of green grass for adult bulls (—) and cows (—) during the study period for vegetation types 24 – 38. For a key to vegetation type numbers see Figure 3.1.

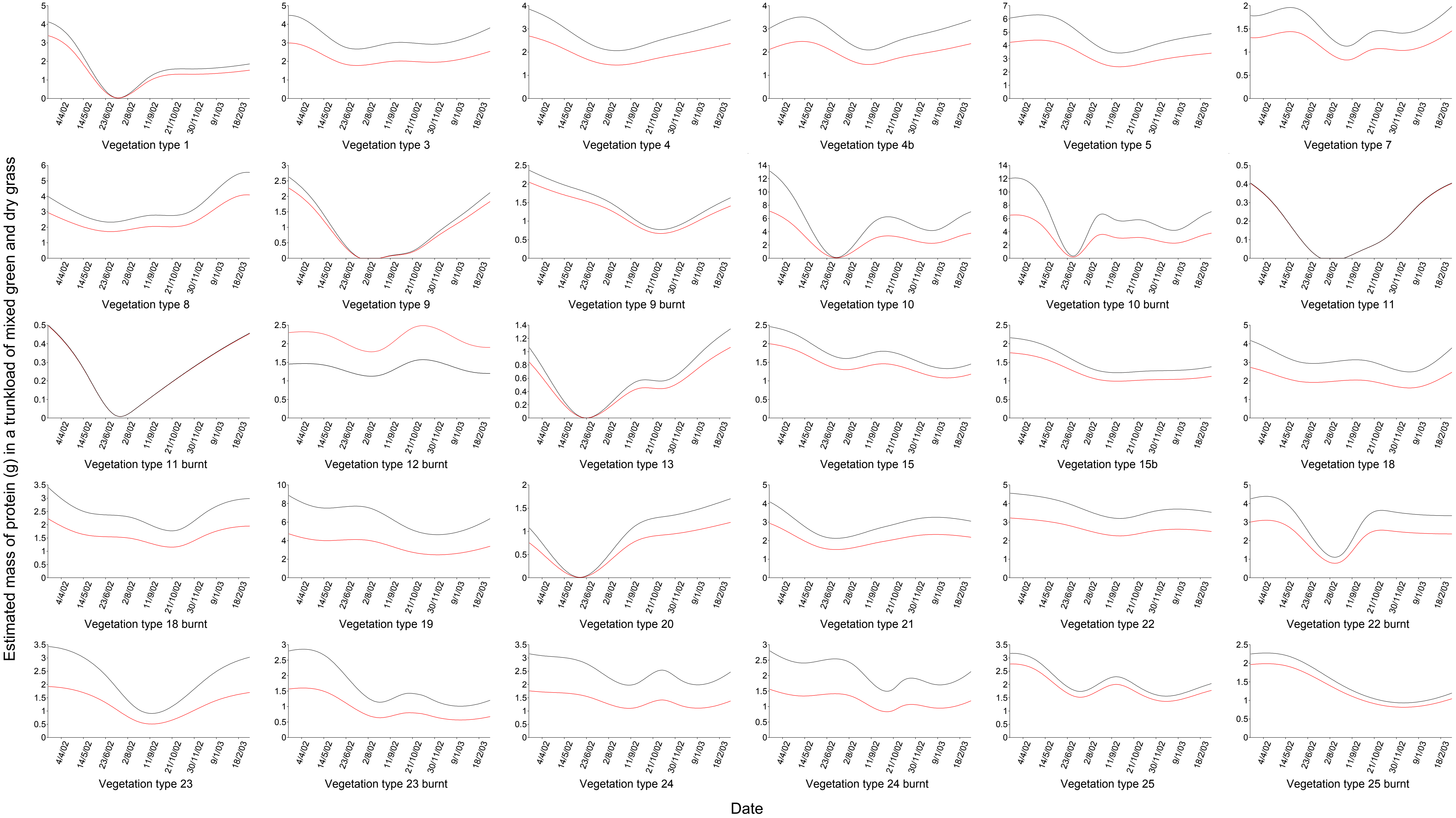


Figure 4.42 Daily estimates of the mass of protein (g) in a trunkload of mixed green and dry grass for adult bulls (——) and cows (——) during the study period for vegetation types 1 – 25. For a key to vegetation type numbers see Figure 3.1.

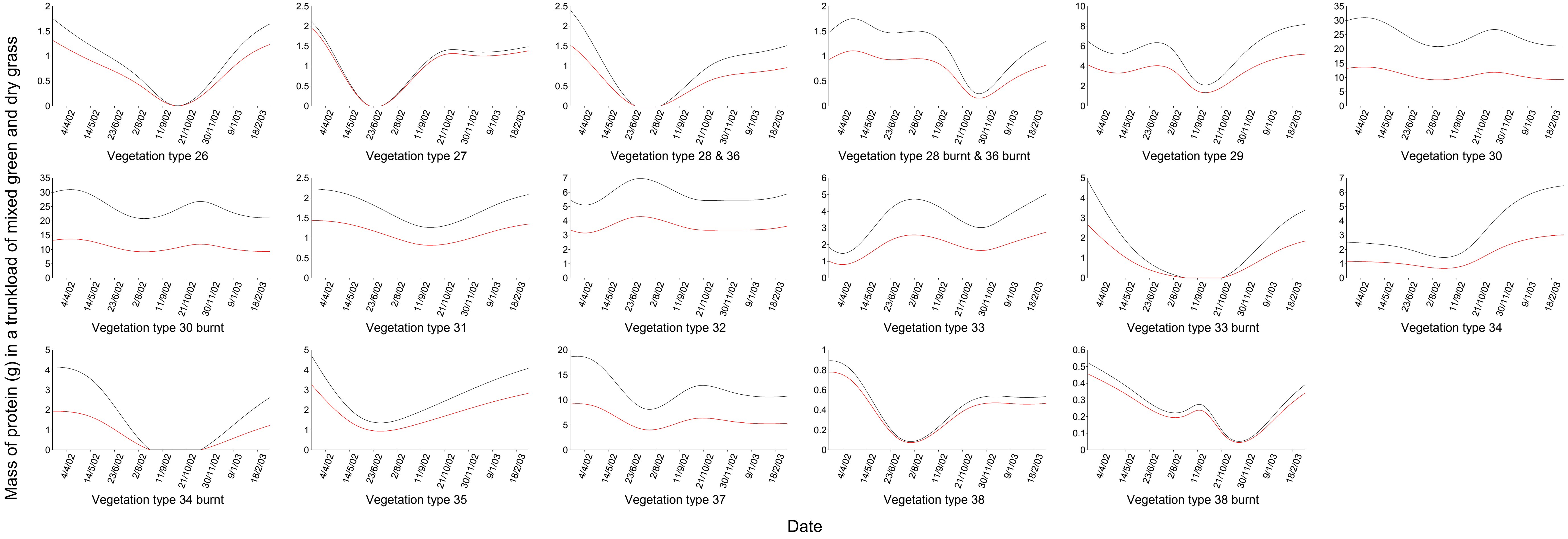


Figure 4.43 Daily estimates of the mass of protein (g) in a trunkload of mixed green and dry grass for adult bulls (—) and cows (—) during the study period for vegetation types 26 – 38. For a key to vegetation type numbers see Figure 3.1.

Forbs

The average dry mass of the stems, leaves and whole plant of each forb species is given in Table 4.16, and the weighted average dry mass of a fully developed, unbrowsed forb plant is given for each vegetation type in Table 4.17. The average dry mass of an unbrowsed forb plant ranged from 14 g in the *Setaria incrassata* grassland to 150 g in the *Combretum imberbe – Urochloa mosambicensis* wooded grassland.

Values for the traits of the forb species used to calibrate a regression tree model for predicting the crude protein content of forbs are given in Table 4.18. The regression tree model (Figure 4.44) used 10 splits and 3 traits to explain 97.3 % of the variation in the crude protein content of the forb species in the calibration data set (Table 4.19). Leaf specific area explained the greatest proportion of variance (51.2 %), followed by the force to crush stem (35.4 %), and the leaf-to-stem ratio (10.7 %). Both leaf specific area and the force to crush stem showed a nonlinear relationship with crude protein content (at some splits there was positive correlation, while at others there was negative correlation). Leaf-to-stem ratio was negatively correlated with crude protein content.

Values for the traits and regression tree predictions of crude protein content for each forb species are given in Table 4.20. The crude protein content of forbs ranged from 7.8 to 19.5 %, and was generally higher than that of green grass species (see Table 4.14).

The average mass of protein in a fully developed, unbrowsed forb plant ranged from 1.5 g in the *Setaria incrassata* grassland to 18.2 g in the *Combretum imberbe – Urochloa mosambicensis* wooded grassland (Figure 4.45).

Estimates of the daily average height of the tallest forb plant in green forb patches are shown for each landscape unit in Figure 4.46 and Figure 4.47. In general, the temporal trend was a decline in height of green forbs as the dry season progressed, presumably due to browsing, followed by an increase from the start of the rainy season. The *Acacia galpinii* - *Croton megalobotrys* forest, *Colophospermum mopane – Enneapogon scoparius* open woodland, *Colophospermum mopane – Commelina kotschyi* shrub open woodland and *Colophospermum mopane – Brachiaria eruciformis* open woodland were conspicuous in that average forb height was well below maximum for an extended period during the dry season.

Table 4.16 Average (n = 5) dry mass (g) of the stems, leaves and whole plant of each forb species

Species	**Average dry mass (g)**		
	Stems	**Leaves**	**Whole plant**
Abutilon austro-africanum	138	35	173
Abutilon indicum subsp. *guineense*	34	24	58
Acathospermum hispiula	14	14	28
Achyranthes aspera	21	10	31
Agathisanthemum bojeri	38	25	63
Ageratum conyzoides	5	5	10
Alternanthera pungens	5	34	39
Anisotes formosissimus	90	29	119
Aspilia natalensis	110	38	148
Asystasia gangetica	16	6	22
Barleria elegans	61	24	85
Barleria lanciflora	64	47	111
Barleria prionitis	51	18	69
Barleria spinulosa	26	16	42
Blepharis maderaspatensis	6	5	11
Boerhavia erecta	23	13	35
Calostephane divaricata	19	11	30
Celosia trigyna	7	3	10
Commelina benghalensis	13	9	22
Commelina kotschyi	9	5	14
Corchorus asplenifolius	5	4	9
Corchorus confusus	12	17	29
Crabbea velutina	4	7	11
Cucumis zeyheri	6	9	25
Cyathula lanceolata	184	60	244
Dicerocaryum eriocarpum	51	29	81
Dicliptera spinulosa	1	1	2
Dicoma tomentosa	7	9	16
Duosperma quadrangulare	62	55	117
Elytraria acaulis	2	3	6
Endostemon obtusifolius	18	8	26
Endostemon tenuiflorus	6	4	10
Evolvulus alsinoides	1	1	2
Heliotropium steudneri	12	8	19
Hermannia glanduligera	25	6	31
Hermbstaedtia odorata	21	8	29
Indigofera daleoides	21	18	39
Indigofera schimperi	234	184	418
Indigofera trita	97	9	107
Ipomoea coscinosperma	12	16	28
Justicia flava	60	12	72
Justicia striata	4	2	6
Launaea cornuta	16	7	22
Leucas glabrata	34	8	42
Megalochlamys revoluta	245	28	273
Melhania acuminata	105	52	157
Nidorella microcephala	5	2	7
Ocimum urticifolium	38	16	54
Oxygonum sp.	4	2	6
Pavonia procumbens	16	12	29
Phyllanthus parvulus var. *parvulus*	1	2	3
Phyllanthus maderaspatensis	7	3	10
Plumbago zeylanica	46	17	64
Pupalia lappacea	68	19	87
Rhynchosia albissima	47	25	72
Rhynchosia minima	6	9	16
Ruellia patula	4	3	7
Seddera suffruticosa	23	7	30
Sida cordifolia	67	18	85
Spermacoce arvensis	7	12	18
Tephrosia villosa	92	97	189
Tephrosia longipes	59	8	66
Tephrosia purpurea	39	26	65
Tragia okanyua	17	14	30
Vernonia steetziana	13	6	19
Waltheria indica	10	7	17

Table 4.17 Percent aerial cover of forb species and weighted average dry mass (g) of a forb plant in each vegetation type. For a key to vegetation type numbers see Figure 3.1

Species	Vegetation type																																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Abutilon austro-africanum	0.020							0.010	0.053	0.133		0.093	0.050	0.120		0.020	0.100	0.018	0.032	0.296	0.033		0.056	0.293	1.280			2.856		0.067		0.495	0.806	1.120	0.100	2.862	0.413	0.070
Abutilon indicum subsp. *guineense*								0.300				0.413	0.030																				0.034	0.940				
Acathospermum hispidula	0.010									0.007	0.650					0.010				0.004																		
Achyranthes aspera	0.710	0.048		0.016	0.040	2.133	0.075	0.780		0.660	0.250		0.440	0.956		0.730	1.047	0.098	0.024	0.337	0.287		0.032	0.040		0.192	0.008					0.005	0.051		0.040	0.009		0.020
Agathisanthemum bojeri				0.032												0.780																						
Ageratum conyzoides								0.690																														
Alternanthera pungens	3.010										1.490		0.020			0.520		0.027																				
Anisotes formosissimus	5.575													0.524																								
Aspilia natalensis			0.527		0.093	1.067																																
Asystasia gangetica			0.047				0.205	4.010																							3.387							
Barleria elegans	0.070									0.547							0.073																					
Barleria lanciflora																							0.508															
Barleria prionitis	1.050								0.200				0.310	0.600		0.010	0.947		0.744	0.149															0.060			
Barleria spinulosa							0.125							0.347		0.020	0.053		0.072	1.933	0.053										0.160				0.070			
Blepharis maderaspatensis				0.408	0.080		0.005				0.010									0.004											1.200				0.110			
Boerhavia erecta	0.200							0.010	0.173	0.067	0.390		0.810	0.071		0.400	0.467	0.080	0.056	0.131	0.080					0.184						0.050	0.006					
Calostephane divaricata	0.780			0.040				0.010						0.013					0.008	0.040			0.004															
Celosia trigyna	0.070		0.107	0.032	0.053	0.107	0.725	0.060	0.013	0.073	0.410		0.240	0.004		0.050		0.022	0.008							0.008					1.080	0.005			0.140			
Commelina benghalensis	0.390	0.624	0.127	0.112	0.027	0.720	0.480	0.020	0.053	0.753	0.420		0.375	0.154	0.013	0.230	0.367	0.004	0.272	0.047	0.013					0.352			0.093		0.280				1.860			
Commelina kotschyi																				0.007			0.164		0.010			6.344		0.027		0.115	0.509	0.360		1.347	0.107	
Corchorus asplenifolius	0.130	0.056	0.133	0.032		0.080	0.090	0.010	0.013	0.007	0.100		0.450	0.711	0.307	0.010	0.160	0.116	0.104	0.616	1.247	0.048	0.100			0.176	0.678	0.008	0.707		0.053	0.010			0.020			0.040
Corchorus confusus		0.008					0.005		0.067			0.160						0.080		0.011		0.008	0.244	0.427	0.030	0.152		0.160		0.080		0.530	0.291	0.310		0.284	0.453	
Crabbea velutina																0.720				0.007	0.160						0.150											
Cucumis zeyheri					0.027	0.933	0.210			0.013	0.060					0.070	0.007			0.018	0.007	0.008				0.032	0.008		0.027				0.069	0.140		0.170	0.093	0.060
Cyathula lanceolata																		0.720							0.510													
Dicliptera spinulosa								1.060		0.160				0.009																								
Dicoma tomentosa																				0.011			0.788						0.013									
Dicerocaryum eriocarpum			0.200		0.107		0.350																								5.000							
Duosperma quadrangulare																									0.700								0.291	8.410		1.209		
Elytraria acaulis														0.036	0.040		0.180	0.120	0.064	0.258	0.573			0.013			0.091									0.027		0.010
Endostemon obtusifolius	0.210						0.005	0.150	0.080	0.240	0.030			0.267			0.027		0.088	0.782	1.100					0.048	0.058								0.020			2.610
Endostemon tenuiflorus	0.260								0.853				0.250	0.013		3.030	0.007	0.031		0.556	0.007					0.280						0.005			0.020			4.110
Evolvulus alsinoides	0.030	0.176		0.008									0.020	0.036	0.667	0.110	0.040	0.018	0.008	0.019	0.061	0.024	0.024			0.072	0.016	0.048	0.107			0.010						0.070
Heliotropium steudneri																		0.600																				
Hermannia glanduligera	0.020		0.107	0.272	0.320	0.427	2.650				0.560		0.010								0.007		0.012			0.016	0.016	0.040			1.587							0.010
Hermbstaedtia odorata			0.007		1.280	0.560	0.670		0.253	0.027	0.380		0.010		0.280	0.160	0.067	0.062	0.288	0.025						0.664			0.013		0.200							
Indigofera daleoides							0.005													0.055			1.418					0.008				0.155			0.010			0.240
Indigofera schimperi												0.080					0.047	0.004			0.027		0.392	0.040				0.288				0.030	0.331	0.230		1.289		0.640
Indigofera trita																				0.007	1.507																	
Ipomoea coscinosperma																							0.212		0.010			0.048				0.030	0.034	0.540		0.022	0.187	
Justicia flava	0.790			0.032			0.100	0.020	0.027	0.560	0.750		0.050	0.253	0.240	0.720	1.047	0.431	0.352	0.091	0.327			0.107		0.040	0.008		0.013									
Justicia striata		0.536								0.020				0.036						0.042	0.027	0.040					0.008					0.015						
Launaea cornuta									0.040					0.004										0.013	0.040			0.048		0.093		0.080		2.470			0.013	
Leucas glabrata	0.520		0.253	0.016	0.187	8.573	2.235				0.500		0.850	0.369		0.010	0.260	0.111	0.280	0.018								0.072			0.013							
Megalochlamys revoluta	1.230													0.169																								
Melhania acuminata	0.060	0.304	0.013	0.024	0.347	1.107	1.240			0.140	0.090			0.653	0.333	0.110	0.400	0.631	0.536	1.211	0.574	0.512	0.296	0.027		0.016	0.659					0.533			0.080	0.004		0.600
Nidorella resedifolia	0.020										0.690																											
Ocimum urticifolium	0.060													0.027															0.707									
Oxygonum sp.																															0.573							
Pavonia procumbens	0.230			0.008		0.533	0.010							0.142	0.027		0.040	0.004	0.128	0.325	0.353	0.016	0.492	0.027			0.450				0.013	0.075			0.110			
Phyllanthus parvulus			0.007	0.008	0.027	0.013	0.025		0.013		0.030	0.120		0.027	0.013		0.020	0.022		0.113	0.053		0.056	0.053	0.310		0.016	0.352	0.107	0.507		0.080		0.130		0.142	0.080	0.090
Phyllanthus maderaspatensis		0.112		0.032					0.027	0.013				0.089	0.013	0.040	0.053	0.004	0.008	0.204	0.227	0.104	0.740	0.173		0.056	0.171	0.032	0.013		0.067	0.150	0.080	0.330	0.050	0.284	0.240	0.190
Plumbago zeylanica								0.140		0.907	0.060															0.056												
Pupalia lappacea	1.240	0.064	0.253	0.344	2.333	18.45	3.535	0.560	0.307	1.413	0.550		3.140	3.524	0.080	1.270	6.310	1.987	1.192	3.287	4.787		0.120	1.133	0.010	2.256	1.209		0.013		0.760	0.590	0.749	0.190	1.720	0.342		
Rhynchosia albissima												1.240							0.008					0.053						1.800		0.600	0.480	1.870		0.009	5.160	
Rhynchosia minima										0.007				0.196					0.008	0.568	0.860	0.296	2.720		0.010		0.083					0.915				0.027		0.370
Ruellia patula	0.540		0.027	0.064		0.147	0.005		0.480		0.030		1.740	0.402	0.040	0.370	0.433	0.107	0.632	0.440	1.395	0.072	0.028			0.152	0.138		0.013			0.030				0.004		
Seddera suffruticosa var suffruticosa														0.276		0.010	0.147	0.013		0.418	0.133	0.024	1.680									0.290						0.050
Sida cordifolia	0.120		0.007	0.168			0.290		0.080		0.070			0.004																	2.760							
Spermacoce arvensis	0.090	0.072	0.453	0.040	0.707	0.493	0.820				1.290		0.010	0.022		0.030			0.120	0.004				0.013		0.008					0.200							
Tephrosia longipes																											0.777					0.155						
Tephrosia purpurea subsp leptostachya var pubescens		0.200		0.032			0.730			0.013	0.020	0.013	0.130	0.049	1.693	0.140	0.067		0.024	0.022					0.040	0.512					0.067				0.030		0.013	0.340
Tephrosia purpurea subsp leptostachya var leptostachya	0.130		1.000	0.088	0.267	0.040	0.320				0.230		0.210	0.018		0.020		0.053		0.116	0.167	0.280	0.088			0.296	0.381		0.133		0.013	0.035				0.004		0.510
Tephrosia villosa														0.058		0.190				0.247																		1.960
Tragia okanyua						0.987	0.225					0.133	0.010							0.040		0.096		0.213			0.281	0.008				0.100						0.020
Vernonia steetziana		0.016	0.093	0.008	0.240		0.065																								0.747							
Waltheria indica	0.080	0.552	0.648	0.712	0.840	0.027	0.835			0.013			0.130	0.169		0.300			0.016	0.004				0.013							5.173							
Weighted average dry mass (g) of a forb plant	**90**	**19**	**58**	**39**	**59**	**70**	**60**	**18**	**36**	**66**	**39**	**69**	**47**	**74**	**57**	**35**	**76**	**100**	**40**	**73**	**61**	**71**	**51**	**79**	**150**	**53**	**48**	**57**	**32**	**14**	**36**	**65**	**117**	**94**	**56**	**160**	**62**	**52**

Table 4.18 Traits of forb species used to calibrate a regression tree model for the prediction of the crude protein content (%) of forbs

Species	Leaf specific area (cm^2/g)	Leaf:stem ratio	Force to crush stem (Nm)	Crude protein (%)
Abutilon indicum	125.90	0.68	6.70	12.70
Achyranthes aspera	285.90	0.50	1.90	19.50
Aspilia natalensis	174.30	0.35	1.60	11.00
Boerhavia erecta	151.60	0.56	3.40	12.70
Dicerocaryum eriocarpum	307.60	0.58	1.60	10.90
Duosperma quadrangulare	97.50	0.89	3.80	10.00
Hermbstaedtia odorata	135.30	0.36	2.00	10.40
Indigofera schimperi	104.30	0.79	7.00	10.40
Justicia flava	220.90	0.20	1.70	15.90
Justicia striata	343.40	0.45	3.10	8.20
Leucas glabrata	306.90	0.23	1.90	9.10
Melhannia acuminata	105.60	0.49	8.50	11.10
Pupalea lappacea	127.10	0.28	1.30	14.40
Rhynchosia albissima	131.40	0.53	2.60	7.40
Waltheria indica	85.10	0.77	4.90	7.90

Table 4.19 Proportional reduction in error and improvement of fit for each split of the regression tree model for predicting the crude protein (%) of forb species

Split	Variable	Proportional reduction in error	Improvement
1	Force to crush stem (Nm)	0.280	0.280
2	Leaf specific area (cm^2/g)	0.527	0.247
3	Leaf specific area (cm^2/g)	0.538	0.011
4	Leaf specific area (cm^2/g)	0.708	0.170
5	Leaf specific area (cm^2/g)	0.753	0.045
6	Leaf specific area (cm^2/g)	0.792	0.039
7	Force to crush stem (Nm)	0.854	0.062
8	Leaf:stem ratio	0.885	0.031
9	Leaf:stem ratio	0.961	0.076
10	Force to crush stem (Nm)	0.973	0.012

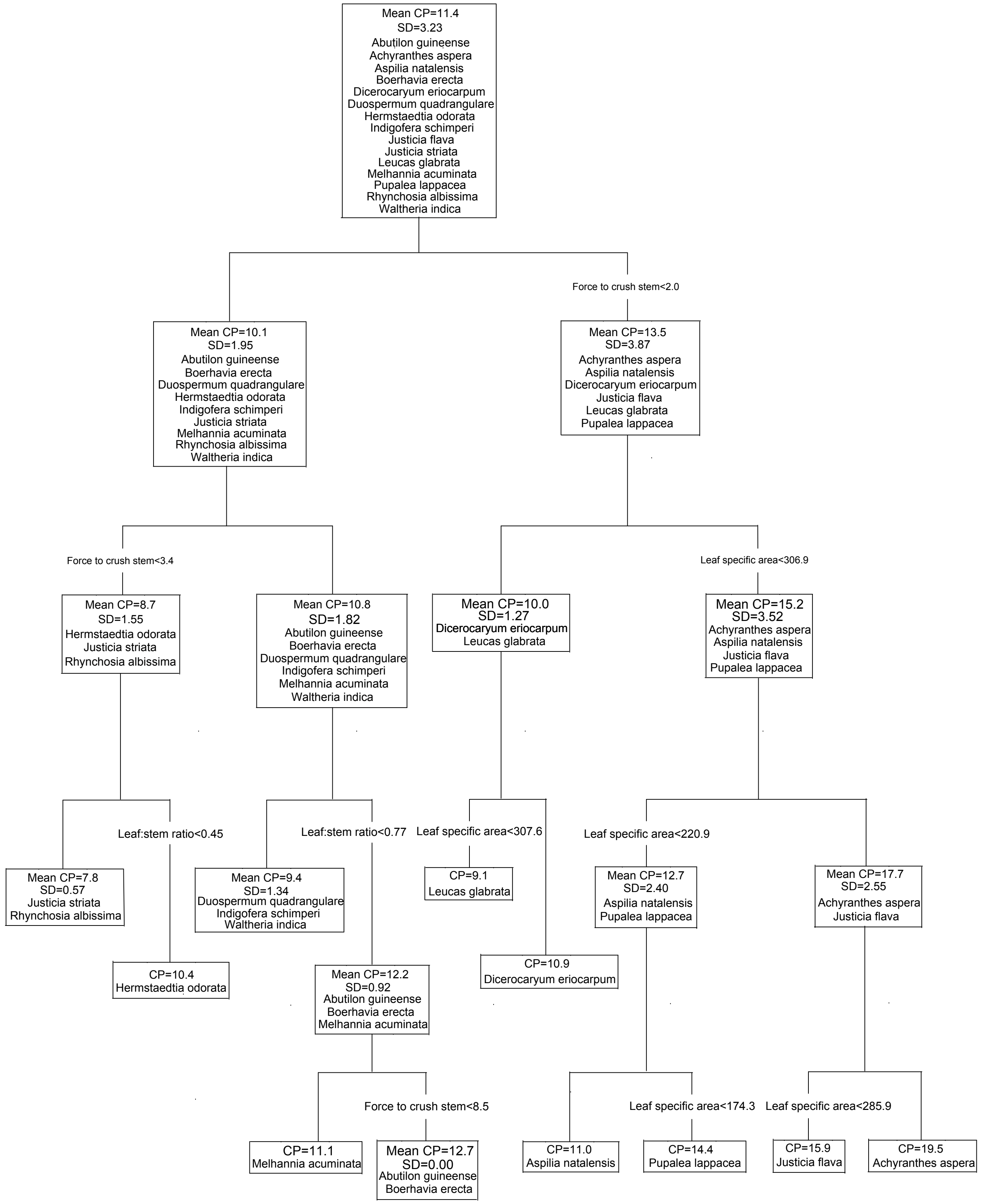


Figure 4.44 Regression tree model for predicting the crude protein content (%) of forb species.

Table 4.20 Values for traits and regression tree predictions of crude protein content (%) for each forb species

Species	Leaf specific area (cm^2/g)	Leaf:stem ratio	Force to crush stem (Nm)	Predicted crude protein (%)
Abutilon austro-africanum	102.80	0.25	5.60	12.70
Acathospermum hispidula	180.40	0.95	2.40	7.80
Agathisanthemum bojeri	118.50	0.64	3.10	7.80
Ageratum conyzoides	359.70	0.87	2.50	7.80
Alternanthera pungens	113.50	7.13	1.90	14.40
Anisotes formosissimus	127.70	0.33	20.40	11.10
Asystasia gangetica	118.30	0.41	2.10	10.40
Barleria elegans	154.40	0.39	13.30	11.10
Barleria lanciflora	139.10	0.73	6.10	12.70
Barleria prionitis	108.70	0.36	6.90	12.70
Barleria spinulosa	169.70	0.62	13.30	11.10
Blepharis maderaspatensis	209.30	0.86	1.30	11.00
Calostephane divaricata	343.00	0.61	1.30	10.90
Celosia trigyna	280.60	0.47	1.20	15.90
Commelina benghalensis	282.60	0.72	2.50	7.80
Commelina kotschyi	231.20	0.61	1.20	15.90
Corchorus asplenifolius	111.70	0.82	4.10	9.40
Corchorus confusus	131.20	1.46	3.50	9.40
Crabbea velutina	160.10	1.59	2.00	7.80
Cucumis zeyheri	209.50	1.50	3.70	9.40
Cyathula lanceolata	79.80	0.33	9.20	11.10
Dicliptera spinulosa	526.00	1.25	1.10	10.90
Dicoma tomentosa	120.40	1.21	2.10	7.80
Endostemon obtusifolius	239.10	0.47	5.10	12.70
Endostemon tenuiflorus	177.20	0.70	1.60	11.00
Evolvulus alsinoides	177.10	0.74	1.00	11.00
Heliotropium steudneri	63.30	0.65	7.70	12.70
Hermannia glanduligera	161.40	0.23	5.30	12.70
Indigofera daleoides	81.00	0.85	4.60	9.40
Indigofera trita	161.30	0.10	5.80	12.70
Ipomoea coscinosperma	180.20	1.37	4.30	9.40
Launaea cornuta	200.70	0.42	1.00	11.00
Megalochlamys revoluta	188.80	0.11	6.70	12.70
Nidorella resedifolia	143.20	0.39	1.60	14.40
Ocimum urticifolium	183.00	0.42	9.80	11.10
Oxygonum sp.	182.30	0.40	1.20	11.00
Pavonia procumbens	197.50	0.75	5.90	12.70
Phyllanthus maderaspatensis	118.00	0.37	7.00	12.70
Phyllanthus parvulus	228.10	1.86	1.40	15.90
Plumbago zeylanica	135.10	0.37	3.10	10.40
Rhynchosia minima	199.50	1.43	2.30	7.80
Ruellia patula	90.50	0.81	2.80	7.80
Seddera suffruticosa var suffruticosa	129.80	0.30	3.40	12.70
Sida cordifolia	104.20	0.27	5.40	12.70
Spermacoce arvensis	213.10	1.81	3.90	9.40
Tephrosia longipes	110.80	0.13	5.20	12.70
Tephrosia purpurea	180.60	0.66	5.00	12.70
Tephrosia villosa	162.70	1.06	6.10	9.40
Tragia okanyua	121.90	0.82	1.80	14.40
Vernonia steetziana	174.40	0.48	1.80	11.00

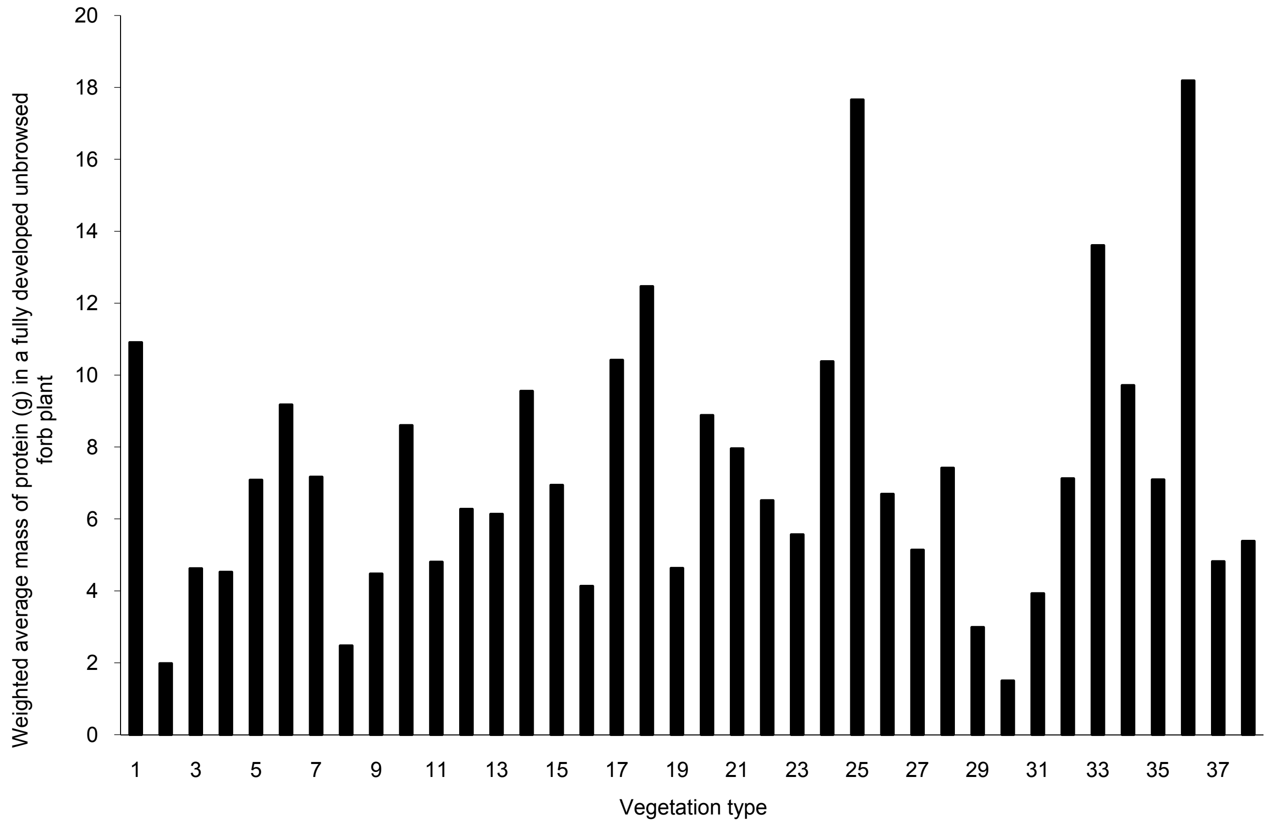


Figure 4.45 Weighted average mass of protein (g) in fully developed, unbrowsed forb plants of each vegetation type. For a key to vegetation type numbers see Figure 3.1.

Daily estimates of the mass of protein in a trunkload of green forbs are given for each landscape unit in Figure 4.48 and Figure 4.49. There was considerable variation among landscape units, but the general temporal trend was a decline in the mass of protein per trunkload during the dry season followed by an increase from the onset of the rainy season. The *Combretum imberbe – Urochloa mosambicensis* wooded grassland, *Acacia nigrescens – Acacia nilotica* open woodland, and *Colophospermum mopane – Brachiaria eruciformis* open woodland offered a very high mass of protein per trunkload of green forbs during the rainy season relative to the other vegetation types. In contrast, the mass of protein per trunkload of green forbs was consistently low in the *Brachystegia glaucescens – Androstachys johnsonii* dense shrub open tall woodland and the *Acacia galpinii - Croton megalobotrys* forest.

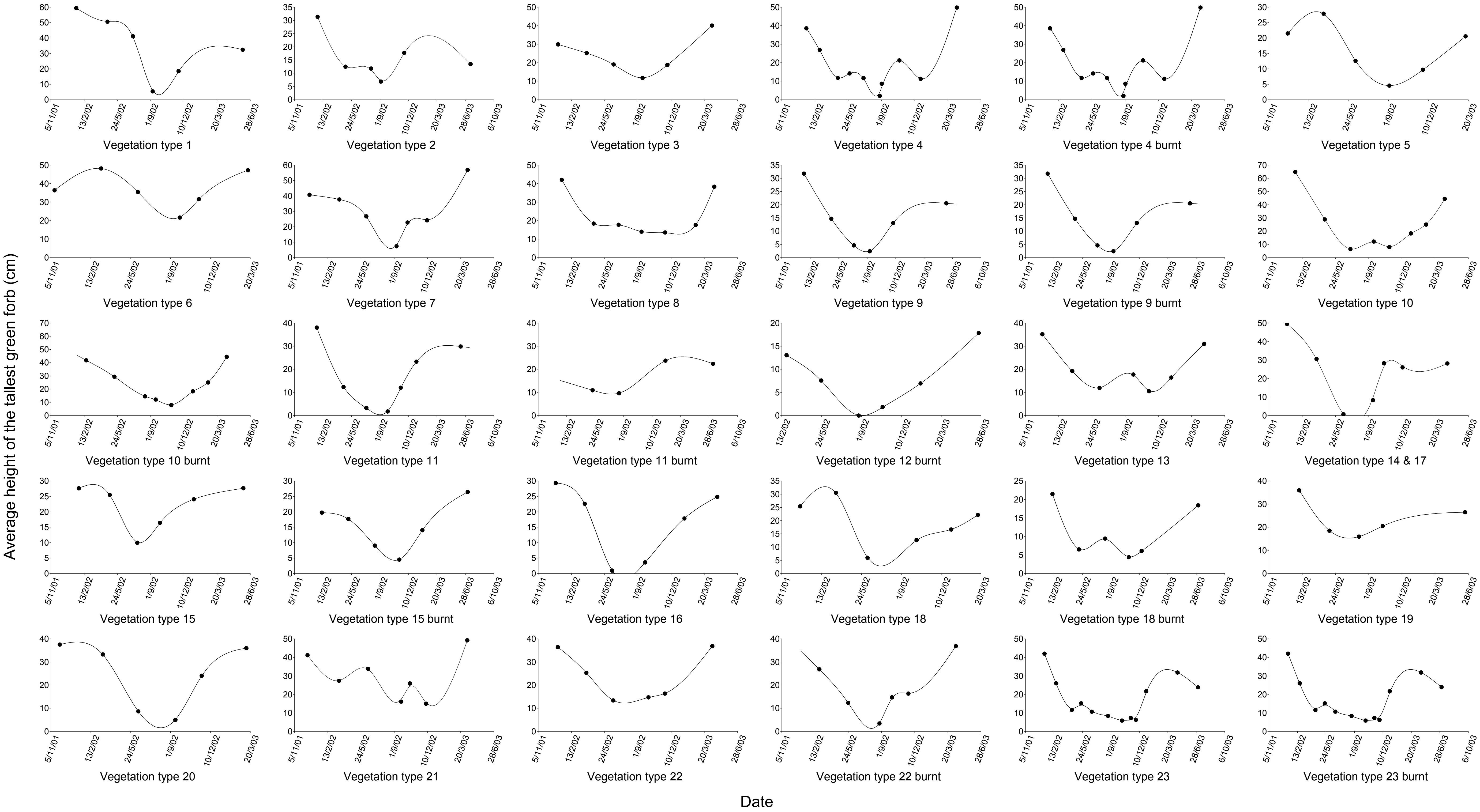


Figure 4.46 Interpolation between estimates of the average height (cm) of the tallest forb in patches of green forbs using smoothing spline regression for vegetation types 1-23. For a key to vegetation type numbers see Figure 3.1.

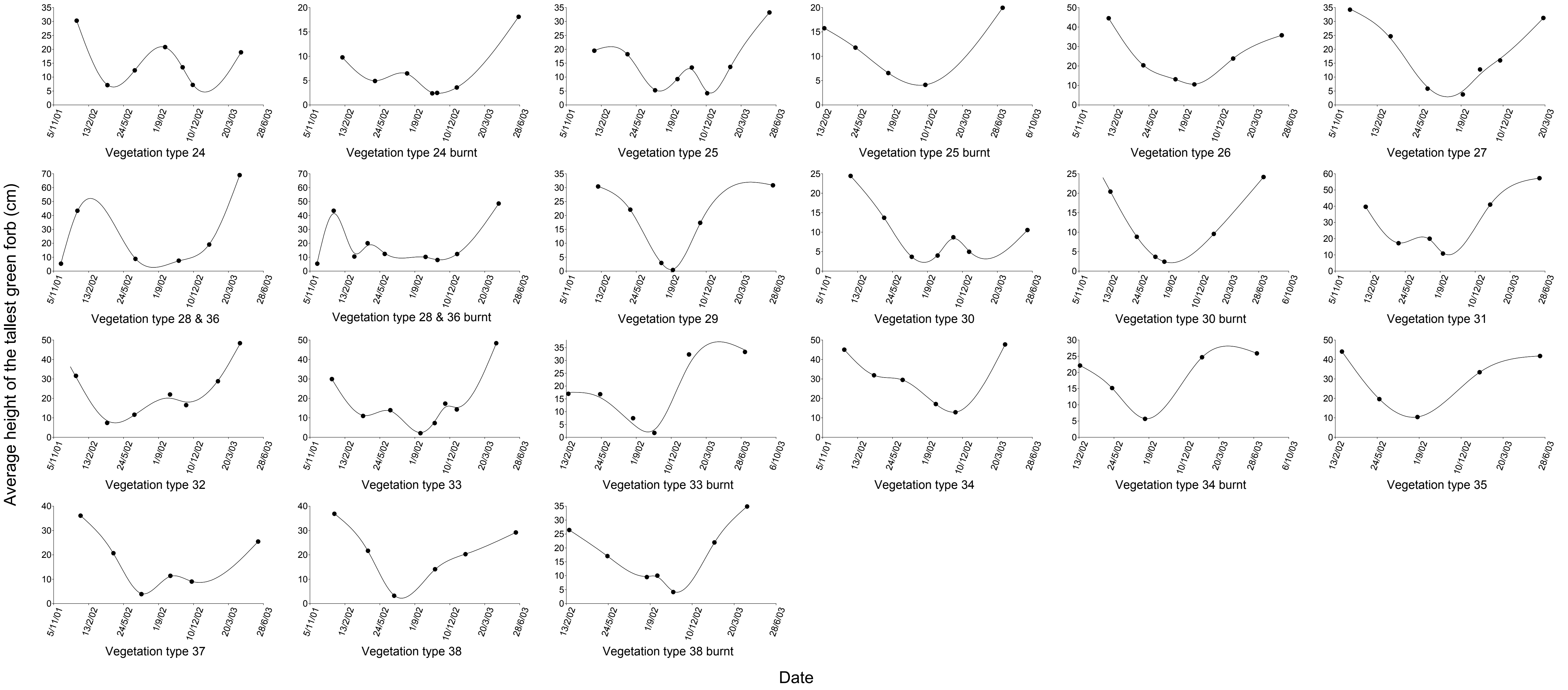


Figure 4.47 Interpolation between estimates of the average height (cm) of the tallest forb in patches of green forbs using smoothing spline regression for vegetation types 24-38. For a key to vegetation type numbers see Figure 3.1.

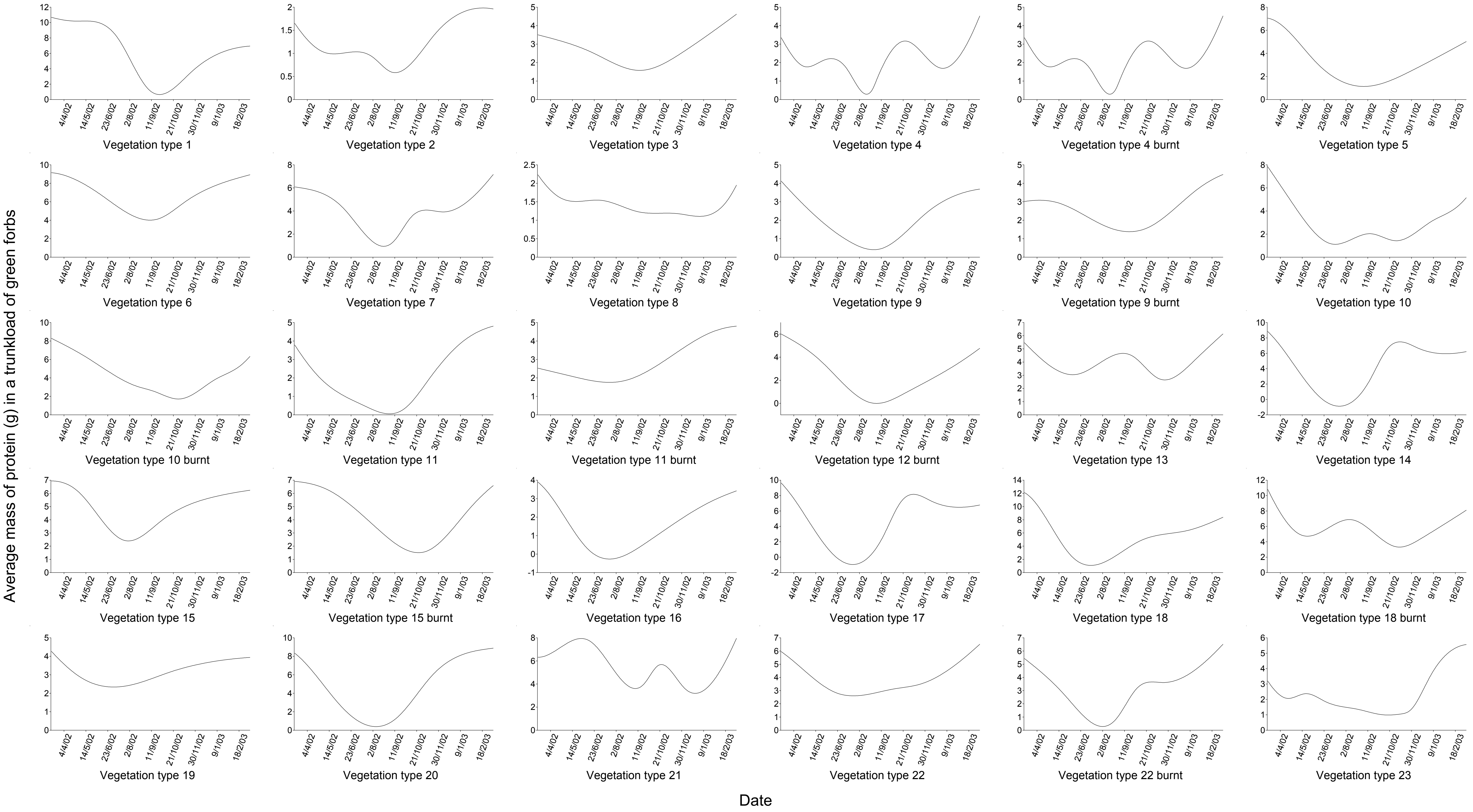
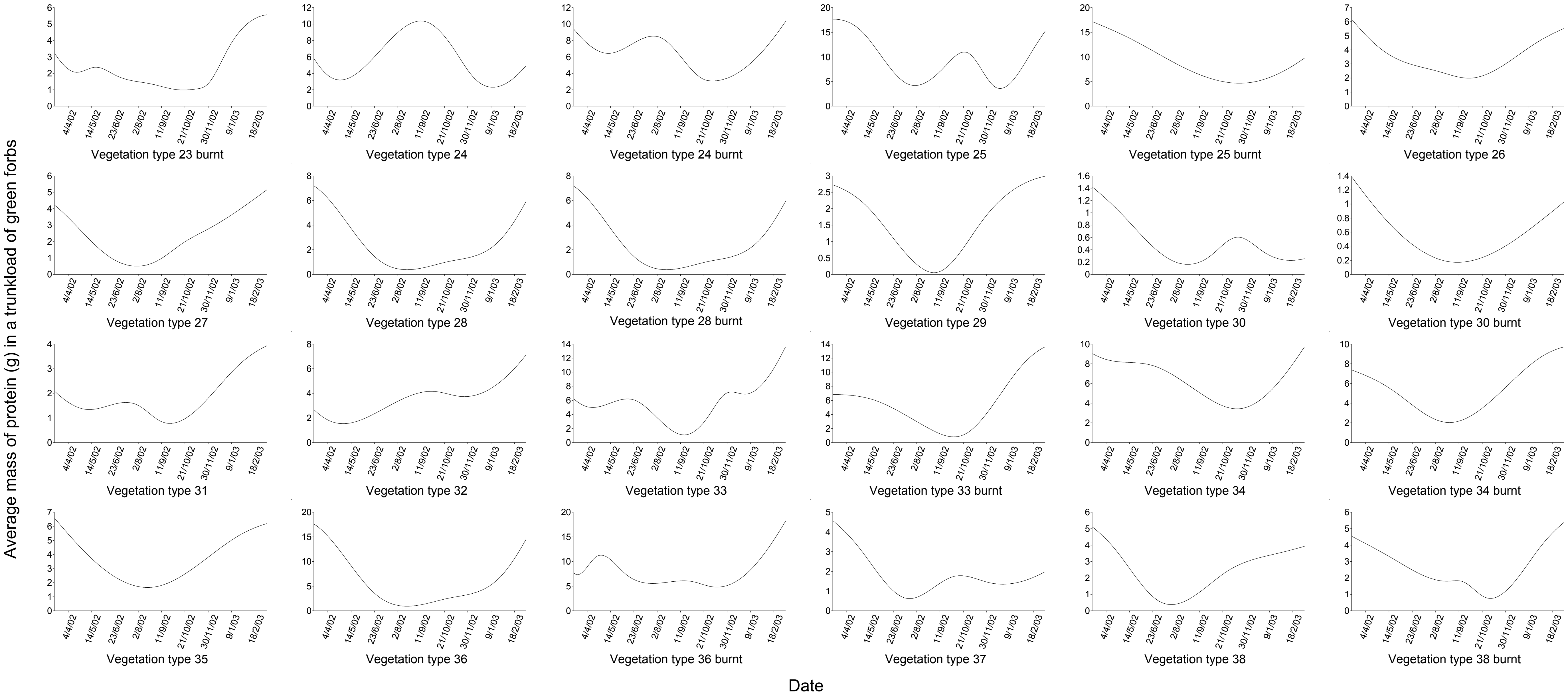


Figure 4.48 Daily estimates of the mass of protein (g) in a trunkload of green forbs during the study period for vegetation types 1 – 23. For a key to vegetation type numbers see Figure 3.1.



Vegetation type 23 burnt

Vegetation type 24

Vegetation type 24 burnt

Vegetation type 25

Vegetation type 25 burnt

Vegetation type 26

Vegetation type 27

Vegetation type 28

Vegetation type 28 burnt

Vegetation type 29

Vegetation type 30

Vegetation type 30 burnt

Vegetation type 31

Vegetation type 32

Vegetation type 33

Vegetation type 33 burnt

Vegetation type 34

Vegetation type 34 burnt

Vegetation type 35

Vegetation type 36

Vegetation type 36 burnt

Vegetation type 37

Vegetation type 38

Vegetation type 38 burnt

Figure 4.49 Daily estimates of the mass of protein (g) in a trunkload of green forbs during the study period for vegetation types 23 – 38. For a key to vegetation type numbers see Figure 3.1.

Leaves

The data used to calibrate the relationship between the dry mass of a trunkload of green leaves and the dry mass of a leaf unit for adult bulls and members of family units are shown in Table 4.21. The dry mass of a trunkload of leaves increased linearly with increasing dry mass of a leaf unit for both adult bulls (R^2 = 0.786, n = 15, P = 0.000001) and members of family units (R^2 = 0.869, n = 18, P = 0.0000001) (Figure 4.50). The linear equation for members of family units had a lower y-intercept and slope compared to that of adult bulls. This indicated that members of family units take smaller trunkloads of leaves than adult bulls and that this disparity becomes greater with increasing mass of a leaf unit.

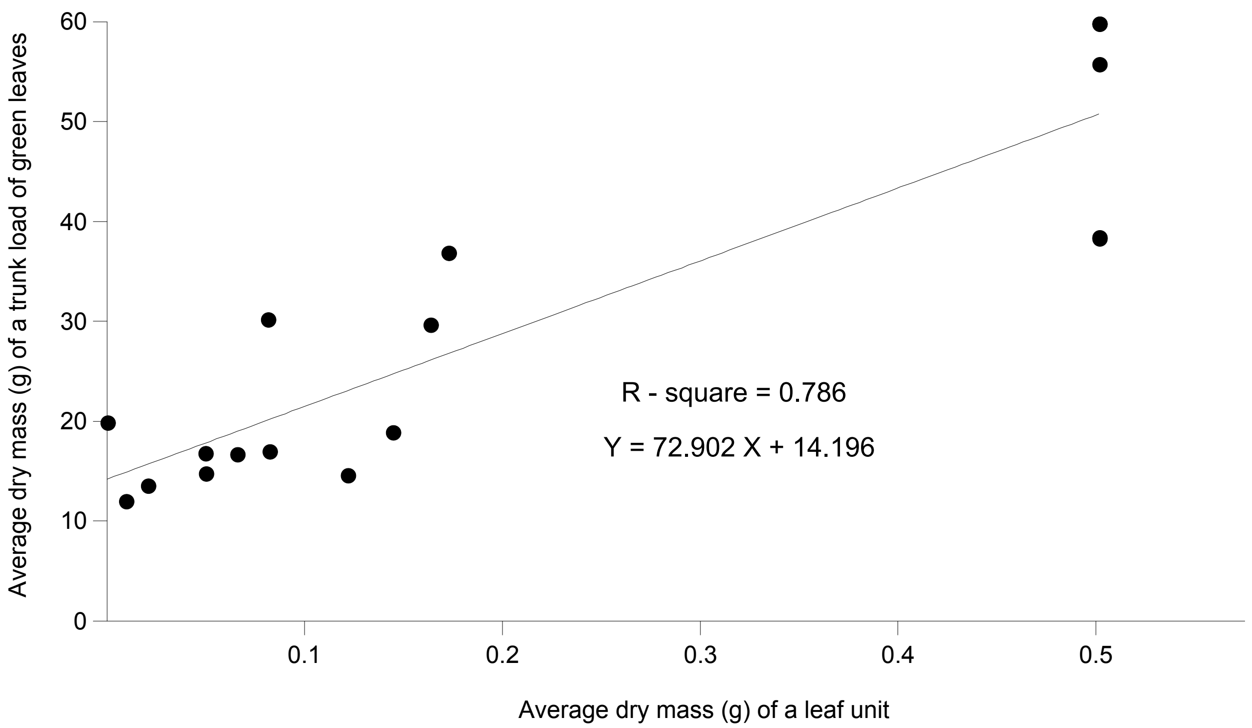
There was a positive linear relationship (R^2 = 0.969, n = 18, P = 0.0000001) between leaf specific area and leaf crude protein content (Figure 4.51).

The dry mass of a leaf unit, predicted crude protein content, and the dry mass and protein content of a trunkload of green leaves for adult bulls and members of family units is given for each woody species in Table 4.22. The heaviest trunkloads of leaves were predicted from *Ficus abutilifolia* (148.2 g for adult bulls and 145.4 g for members of family units) and the lightest from the microphyllous *Acacia* species (17.3 g for adult bulls and 8.8 g for members of family units). The estimates of the crude protein content of green leaves of *Markhamia zanzibarica* (46.8 %) and *Grewia lepidopetilata* (42.3 %) were unrealistically high indicating a failure of the linear relationship to correctly predict crude protein content at very high values of leaf specific area. Possibly, at high levels of leaf specific area a threshold is reached beyond which there is no further increase in leaf crude protein content. However, the effect of these unrealistic estimates was considered insignificant because *Markhamia zanzibarica* and *Grewia lepidopetilata* made up a very small fraction of the available browse. When the unrealistic estimates were excluded, the crude protein content of green leaves ranged from 5.5 % for *Euclea natalensis* to 30.2 % for *Grewia caffra*. The highest mass of protein per trunkload of green leaves was estimated for *Ficus abutilifolia* (19.9 g for adult bulls and 19.5 g for members of family units) and the lowest for *Maerua parvifolia* (1.4 g for adult bulls and 0.7 g for members of family units).

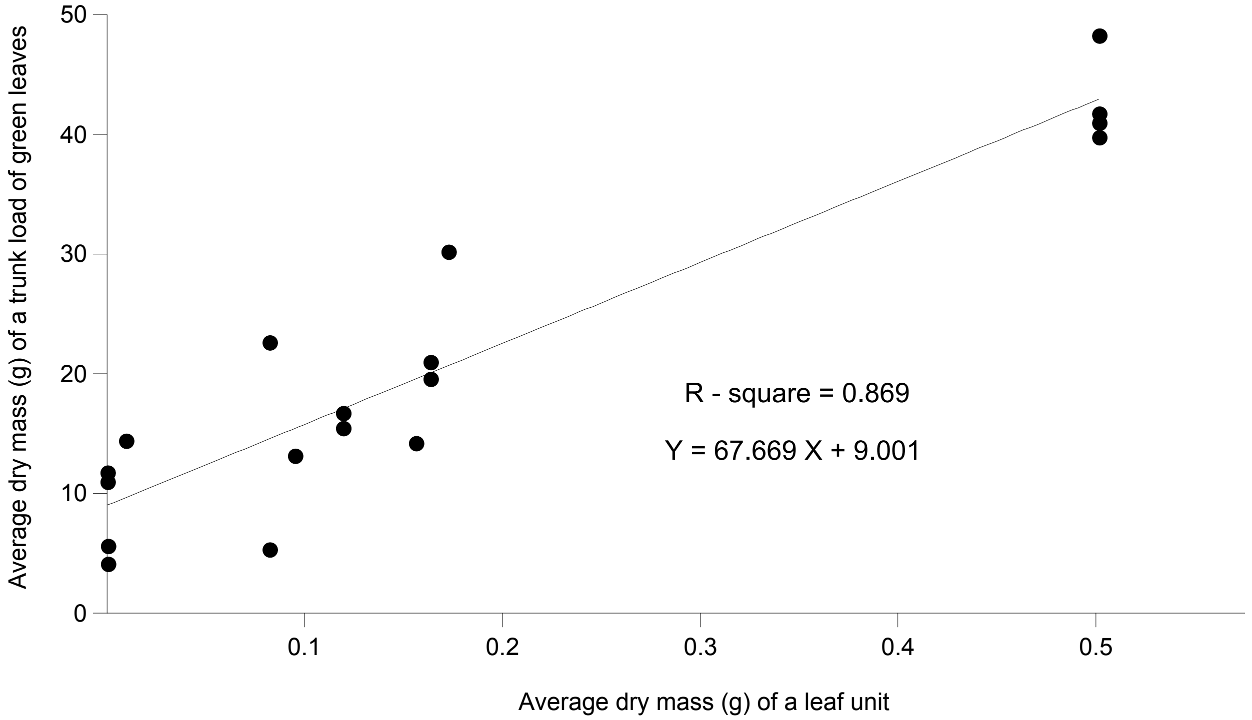
Daily estimates of the weighted average dry mass of a trunkload of green leaves for adult bulls and members of family units are shown for each landscape unit in Figure 4.52 and Figure 4.53. Estimates for adult bulls were never lower than those for members of family units. Differences in trunkload mass between adult bulls and members of family units were larger for some vegetation types than others. In general, the mass of a trunkload of green leaves declined during the driest part of the year. However, for some vegetation types, particularly those on heavy soils, the mass of a trunkload of green leaves increased during the driest part of the year.

Table 4.21 Data used to calibrate the linear relationship between the dry mass (g) of a trunkload of green leaves and the dry mass (g) of a leaf unit for adult bulls and adult cows and subadults

Elephant		Species of woody plant	Average dry mass of a leaf unit (g)	Average (n=5) dry mass of a trunkload of green leaves (g)
Age	Sex			
adult	bull	*Albizia petersiana*	0.0094	12.1
adult	bull	*Albizia versicolor*	0.0813	30.3
adult	bull	*Brachystegia glaucescens*	0.0205	13.6
adult	bull	*Colophospermum mopane*	0.5015	55.8
adult	bull	*Colophospermum mopane*	0.5015	38.4
adult	bull	*Colophospermum mopane*	0.5015	59.9
adult	bull	*Colophospermum mopane*	0.5015	38.5
adult	bull	*Colophospermum mopane*	0.5015	59.9
adult	bull	*Colophospermum mopane*	0.0658	16.8
adult	bull	*Dichrostachys cinerea*	0.0002	19.9
adult	bull	*Grewia bicolor*	0.1635	29.8
adult	bull	*Grewia flavescens*	0.0821	17.1
adult	bull	*Grewia sulcata*	0.1216	14.7
adult	bull	*Lecaniodiscus fraxinifolius*	0.1443	18.9
adult	bull	*Pappea capensis*	0.1726	36.9
adult	bull	*Pteleopsis myrtifolia*	0.0497	14.8
adult	bull	*Senna petersiana*	0.0496	16.9
subadult	unknown	*Albizia harveyi*	0.0004	5.7
subadult	unknown	*Albizia harveyi*	0.0004	4.1
subadult	bull	*Albizia petersiana*	0.0094	14.4
adult	cow	*Colophospermum mopane*	0.5015	41.8
adult	cow	*Colophospermum mopane*	0.5015	41.0
adult	cow	*Colophospermum mopane*	0.5015	39.8
subadult	bull	*Colophospermum mopane*	0.5015	48.3
subadult	unknown	*Dichrostachys cinerea*	0.0002	11.0
subadult	bull	*Dichrostachys cinerea*	0.0002	11.8
adult	cow	*Grewia bicolor*	0.1635	19.6
subadult	bull	*Grewia bicolor*	0.1635	21.0
subadult	unknown	*Grewia flavescens*	0.0821	5.4
subadult	bull	*Grewia flavescens*	0.0821	22.7
adult	cow	*Hippocratea indica*	0.1192	16.8
subadult	cow	*Hippocratea indica*	0.1192	15.5
adult	cow	*Julbernardia globiflora*	0.1562	14.3
adult	cow	*Pappea capensis*	0.1726	30.2
adult	cow	*Spirostachys africana*	0.0949	13.2



(a)



(b)

Figure 4.50 Relationship between the average dry mass (g) of a leaf unit and the average dry mass (g) of a trunkload of green leaves for (a) adult bulls and (b) adult cows and subadults. The corrected R^2 values are given.

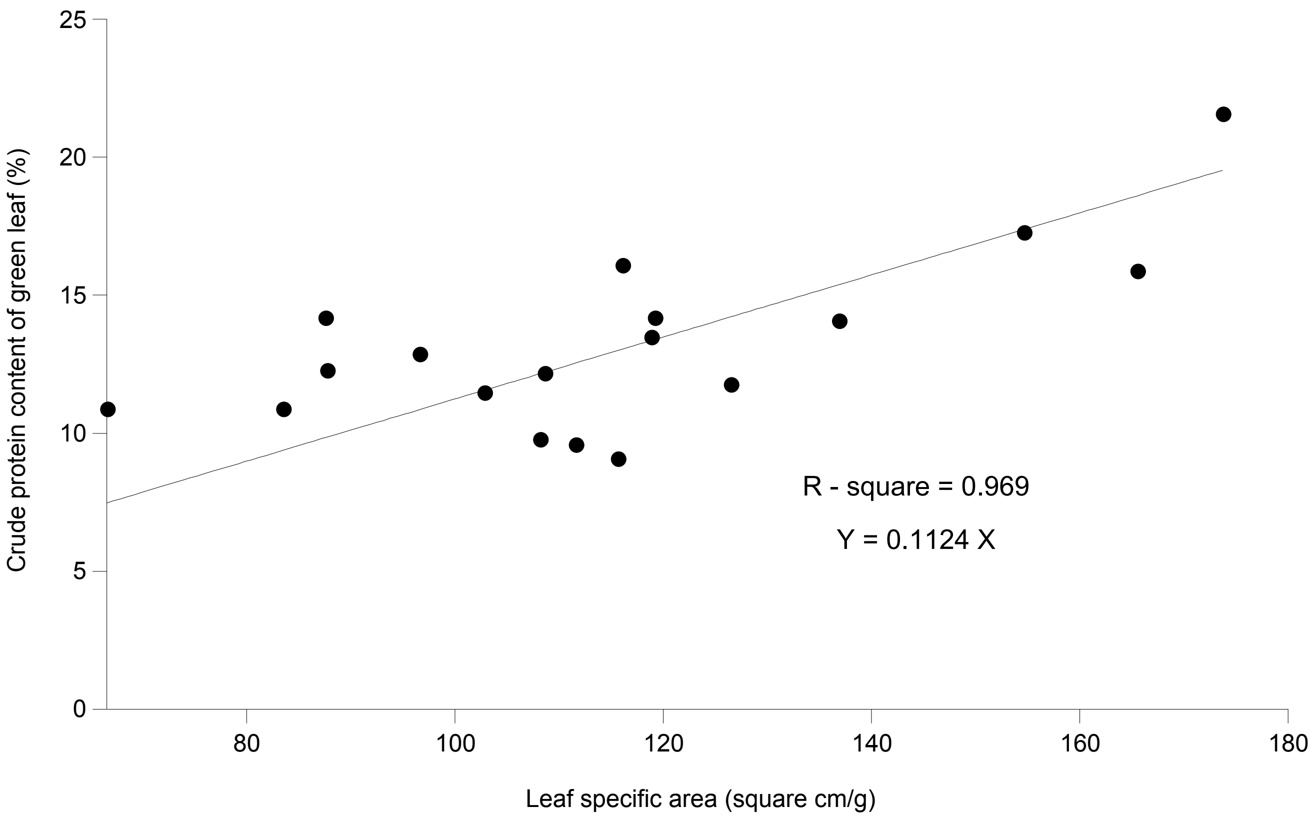


Figure 4.51 Relationship between leaf specific area (cm^2/g) and leaf crude protein content (%). The corrected R^2 value is given.

Daily estimates of the weighted average dry mass of protein in a trunkload of green leaves for adult bulls and members of family units are shown for each landscape unit in Figure 4.54 and Figure 4.55. The general temporal trend was similar to that of trunkload mass, with a decline during the driest part of the year in most vegetation types and an increase during the driest part of the year in vegetation types with heavy soils.

Table 4.22 Dry mass (g) of a leaf unit, predicted crude protein content (%), and the dry mass (g) and protein content (%) of a trunkload of green leaves for adult bulls and cows and subadults for each woody species

Species	Dry mass of leaf unit (g)	Leaf specific area (cm^2/g)	Dry mass of a trunkload of green leaves (g)		Crude protein content (%)	Mass of protein in a trunkload of green leaves (g)	
			Bulls	Cows		Bulls	Cows
Acacia borleae	2.200E-08	113.0	17.3	8.8	12.7	2.2	1.1
Acacia erubescens	3.196E-08	158.3	17.3	8.8	17.8	3.1	1.6
Acacia galpinii	6.824E-08	150.4	17.3	8.8	16.9	2.9	1.5
Acacia gerradii var.gerradii	5.622E-08	104.5	17.3	8.8	11.7	2.0	1.0
Acacia nigrescens	3.904E-02	119.2	19.9	11.6	14.2	2.8	1.6
Acacia nilotica	1.975E-04	141.4	17.3	8.9	15.9	2.7	1.4
Acacia robusta	6.243E-08	111.4	17.3	8.8	12.5	2.2	1.1
Acacia schweinfurthii	4.758E-08	187.3	17.3	8.8	21.0	3.6	1.9
Acacia tortilis	7.313E-05	173.7	17.3	8.8	21.6	3.7	1.9
Acacia welwitschii	4.782E-03	90.9	17.6	9.2	10.2	1.8	0.9
Adansonia digitata	2.023E-01	101.1	30.8	23.0	11.4	3.5	2.6
Afzelia quanzensis	7.887E-02	223.5	22.5	14.4	25.1	5.7	3.6
Albizia anthelmintica	1.541E-02	157.8	18.3	9.9	17.7	3.2	1.8
Albizia harveyi	4.236E-04	136.9	17.3	8.9	14.1	2.4	1.3
Albizia petersiana	9.426E-03	154.6	17.9	9.5	17.3	3.1	1.6
Albizia versicolor	8.125E-02	142.5	22.7	14.5	16.0	3.6	2.3
Alchornea laxifolia	1.934E-01	211.0	30.2	22.4	23.7	7.2	5.3
Allophylus rubifolius	3.440E-02	105.3	19.6	11.2	11.8	2.3	1.3
Androstachys johnsonii	3.160E-01	81.4	38.4	30.9	9.1	3.5	2.8
Anisotes rogersii	6.609E-02	193.7	21.7	13.5	21.8	4.7	2.9
Artabotrys brachypetalus	1.770E-01	107.7	29.1	21.2	12.1	3.5	2.6
Balinites maughamii	1.071E-01	78.0	24.4	16.3	8.8	2.1	1.4
Bauhinia tomentosa	8.721E-02	228.3	23.1	14.9	25.7	5.9	3.8
Berchemia discolor	1.613E-01	147.3	28.1	20.1	16.6	4.6	3.3
Boscia angustifolia	1.017E-01	66.9	24.1	15.9	7.5	1.8	1.2
Brachysetgia glaucescens	2.049E-02	153.1	18.6	10.3	17.2	3.2	1.8
Bridelia mollis	4.034E-01	158.2	44.3	37.0	17.8	7.9	6.6
Cadaba termitaria	3.951E-02	105.7	19.9	11.6	11.9	2.4	1.4
Canthium glaucum	2.925E-02	179.8	19.2	10.9	20.2	3.9	2.2
Canthium setiflorum	2.990E-02	72.1	19.3	10.9	8.1	1.6	0.9
Capparis sepiaria	9.043E-02	97.6	23.3	15.2	11.0	2.6	1.7
Capparis tomentosa	1.731E-01	77.3	28.8	20.9	8.7	2.5	1.8
Cassia abreviata	7.315E-02	117.7	22.2	14.0	13.2	2.9	1.8
Catunaregum swynnertonii	7.544E-02	74.6	22.3	14.1	8.4	1.9	1.2
Cephalocroton puchellii	7.621E-02	103.6	22.4	14.2	11.6	2.6	1.6
Cissus cornifolia	1.035E-01	161.3	24.2	16.1	18.1	4.4	2.9
Cleistochlamys kirkii	1.166E-01	187.2	25.1	17.0	21.0	5.3	3.6
Cleistanthus schleteri	8.285E-02	140.7	22.8	14.6	15.8	3.6	2.3
Cocculus hirsutis	1.185E-01	232.4	25.2	17.1	26.1	6.6	4.5
Coffea racemosa	4.767E-02	125.6	20.4	12.2	14.1	2.9	1.7
Colophospermum mopane	5.015E-01	87.7	50.8	43.9	12.3	6.3	5.4
Combretum adenogonium	1.088E+00	91.3	90.2	84.9	10.3	9.3	8.7
Commiphora africanum	2.448E-02	93.7	18.9	10.6	10.5	2.0	1.1
Combretum apiculatum	1.323E-01	108.5	26.1	18.1	12.2	3.2	2.2
Combretum celastroides	1.756E-01	138.8	29.0	21.1	15.6	4.5	3.3
Commiphora edulis	1.299E-01	210.5	26.0	17.9	23.7	6.1	4.2
Combretum hereroense	7.513E-02	112.9	22.3	14.1	12.7	2.8	1.8
Combretum imberbe	6.579E-02	102.8	21.7	13.4	11.5	2.5	1.5
Combretum microphyllum	1.620E-01	172.8	28.1	20.2	19.4	5.5	3.9
Commiphora mollis	3.187E-02	124.4	19.4	11.1	14.0	2.7	1.5
Combretum mossambicense	1.730E-01	139.5	28.8	20.9	15.7	4.5	3.3
Commiphora glandulosa	5.694E-02	179.9	21.1	12.8	20.2	4.3	2.6
Combretum zeyheri	4.249E-01	96.6	45.7	38.5	12.9	5.9	5.0
Crossopteryx febrifuga	2.443E-01	105.4	33.6	25.9	11.8	4.0	3.1
Croton megalobotrys	3.044E-01	195.8	37.6	30.1	22.0	8.3	6.6
Croton pseudopulchellus	4.324E-02	139.2	20.1	11.9	15.6	3.2	1.9
Dalbergia arbutifolia	3.250E-02	165.6	19.4	11.1	18.6	3.6	2.1
Dalbergia melanoxylon	4.894E-02	72.3	20.5	12.3	20.2	4.1	2.5
Dichrostachys cinerea	2.211E-04	165.5	17.3	8.9	15.9	2.7	1.4
Diospyros lyciodes	6.757E-02	148.0	21.8	13.6	16.6	3.6	2.3
Diospyros mespiliformis	2.587E-01	90.9	34.6	26.9	10.2	3.5	2.8
Diospyros squarrosa	2.703E-01	132.7	35.4	27.7	14.9	5.3	4.1
Diospyros loureiriana	2.988E-01	148.6	37.3	29.7	16.7	6.2	5.0
Dombeya kirkii	1.751E-01	241.0	29.0	21.1	27.1	7.8	5.7
Dovyalis hispidula	7.148E-02	129.0	22.0	13.8	14.5	3.2	2.0
Drypetes mossambicensis	2.111E-01	115.6	31.4	23.6	9.2	2.9	2.2
Elephantorrihza goetzii	5.728E-08	182.3	17.3	8.8	20.5	3.5	1.8
Ehretia amoena	1.259E-01	83.5	25.7	17.6	10.9	2.8	1.9
Erythrococca trichogyne	2.806E-02	186.4	19.1	10.8	20.9	4.0	2.3
Euclea divinorum	1.233E-01	79.1	25.5	17.5	8.9	2.3	1.6
Euclea natalensis	3.220E-01	49.0	38.8	31.3	5.5	2.1	1.7
Ficus abutilifolia	1.955E+00	119.2	148.2	145.4	13.4	19.9	19.5
Ficus tettensis	2.460E-01	110.3	33.7	26.0	12.4	4.2	3.2
Friesodielsia obovata	1.882E-01	206.7	29.9	22.0	23.2	6.9	5.1
Garcinia livingstonii	2.875E-01	73.2	36.5	28.9	8.2	3.0	2.4
Gardenia resinifolia	9.463E-02	160.3	23.6	15.5	18.0	4.2	2.8
Gardenia volkensii	1.001E-01	147.2	24.0	15.8	16.5	4.0	2.6
Grewia bicolor	1.635E-01	108.6	28.2	20.3	12.2	3.4	2.5
Grewia flavescens	8.209E-02	118.8	22.7	14.6	13.5	3.1	2.0
Grewia caffra	2.792E-02	269.1	19.1	10.8	30.2	5.8	3.3
Grewia inaequilatera	1.622E-01	200.4	28.1	20.2	22.5	6.3	4.5
Grewia monticola	3.618E-01	116.1	41.5	34.1	16.1	6.7	5.5
Grewia lepidopetilata	4.831E-02	376.2	20.5	12.2	42.3	8.7	5.2
Grewia sulcata	1.216E-01	167.5	25.4	17.3	18.8	4.8	3.3
Grewia villosa	2.532E-01	210.7	34.2	26.5	23.7	8.1	6.3
Heinzia crinita	4.799E-02	169.1	20.5	12.2	19.0	3.9	2.3
Hibiscus ovalifolius	1.261E-01	229.0	25.7	17.6	25.7	6.6	4.5
Hippocratea buchananii	3.051E-01	173.1	37.7	30.2	19.5	7.3	5.9
Hippocratea crenata	5.792E-02	112.2	21.1	12.9	12.6	2.7	1.6
Hippocratea indica	1.192E-01	126.5	25.2	17.2	11.8	3.0	2.0
Hymenocardia ulmnoides	5.049E-02	152.1	20.6	12.4	17.1	3.5	2.1
Hyphaene petersiana	4.606E-01	91.0	48.1	41.0	10.2	4.9	4.2
Julbernardia globiflora	1.562E-01	108.1	27.7	19.8	9.8	2.7	1.9
Kigelia africana	3.856E-01	83.1	43.1	35.8	9.3	4.0	3.3
Kirkia acuminata	5.828E-02	149.5	21.2	12.9	16.8	3.6	2.2
Lannea schweinfurthii	1.619E-01	111.6	28.1	20.1	9.6	2.7	1.9
Lecaniodiscus fraxinifolius	1.443E-01	153.1	26.9	18.9	17.2	4.6	3.3
Philonoptera violacea	6.241E-01	87.1	59.1	52.4	9.8	5.8	5.1
Maclura africana	7.966E-02	145.7	22.6	14.4	16.4	3.7	2.4
Maerua angolensis	1.398E-01	101.9	26.6	18.6	11.4	3.0	2.1
Maerua edulis	4.123E-02	74.8	20.0	11.7	8.4	1.7	1.0
Maerua parvifolia	9.118E-03	67.7	17.9	9.5	7.6	1.4	0.7
Manilkara mochisia	7.259E-02	77.2	22.1	13.9	8.7	1.9	1.2
Markhamia zanzibarica	3.009E-01	416.0	37.4	29.9	46.8	17.5	14.0
Margaritaria discoides	4.753E-02	136.3	20.4	12.2	15.3	3.1	1.9
Gymnosporia pubescens	6.043E-02	66.6	21.3	13.1	10.9	2.3	1.4
Gymnosporia putterlikioides	6.020E-02	137.4	21.3	13.0	15.4	3.3	2.0
Gymnosporia senegalensis	2.686E-01	64.2	35.2	27.6	7.2	2.5	2.0
Millettia usaramensis	5.099E-02	259.5	20.7	12.4	29.2	6.0	3.6
Monodora junodii	2.525E-01	166.3	34.2	26.5	18.7	6.4	4.9
Mundulea sericea	1.889E-02	146.8	18.5	10.2	16.5	3.1	1.7
Newtonia hilderbrantii	5.419E-08	138.9	17.3	8.8	15.6	2.7	1.4
Ochna barbosae	1.145E-01	90.7	24.9	16.8	10.2	2.5	1.7
Ochna inermis	7.274E-02	128.1	22.1	13.9	14.4	3.2	2.0
Ormocarpum trichocarpum	3.028E-07	89.7	17.3	8.8	10.1	1.7	0.9
Pappea capensis	1.726E-01	124.8	28.8	20.9	14.0	4.0	2.9
Pavetta gracillima	4.569E-02	180.2	20.3	12.0	20.3	4.1	2.4
Phyllanthus pinnatus	1.180E-02	182.9	18.0	9.7	20.6	3.7	2.0
Phyllanthus reticulatus	2.060E-02	196.4	18.6	10.3	22.1	4.1	2.3
Psydrax livida	1.856E-01	108.4	29.7	21.8	12.2	3.6	2.7
Ptaeroxylon obliquum	3.438E-02	111.4	19.6	11.2	12.5	2.4	1.4
Pterocarpus brenanii	7.401E-01	135.4	66.8	60.5	15.2	10.2	9.2
Pterocarpus lucens	4.173E-02	116.5	20.0	11.8	13.1	2.6	1.5
Pteleopsis myrtifolia	4.974E-02	116.9	20.6	12.3	13.1	2.7	1.6
Rhigozum zambesiacum	3.750E-03	80.5	17.5	9.1	9.0	1.6	0.8
Rhoicissus revoilii	1.124E-01	125.3	24.8	16.7	14.1	3.5	2.4
Rhus geinzii	4.520E-02	108.9	20.3	12.0	12.2	2.5	1.5
Salvadora persica	1.416E-01	58.7	26.7	18.7	6.6	1.8	1.2
Sclerocarya birrea	1.162E-01	116.3	25.0	17.0	13.1	3.3	2.2
Schrebera trichoclada	2.406E-01	131.9	33.4	25.6	14.8	4.9	3.8
Flueggea virosa	2.670E-02	156.9	19.0	10.7	17.6	3.4	1.9
Senna petersiana	4.962E-02	140.5	20.6	12.3	15.8	3.2	1.9
Spirostachys africana	9.488E-02	117.2	23.6	15.5	13.2	3.1	2.0
Stadmannia oppositifolia	2.623E-01	97.5	34.8	27.2	11.0	3.8	3.0
Sterculia rogersii	8.089E-02	151.4	22.7	14.5	17.0	3.9	2.5
Strychnos decussata	8.799E-02	89.6	23.1	15.0	10.1	2.3	1.5
Strychnos madagascariensis	5.941E-02	87.5	21.2	13.0	14.2	3.0	1.8
Strychnos potatorum	3.413E-01	158.6	40.1	32.7	17.8	7.2	5.8
Strychnos spinosa	1.521E-01	134.0	27.4	19.5	15.1	4.1	2.9
Tabernaemontana elegans	3.466E-01	192.2	40.5	33.1	21.6	8.7	7.1
Terminalia prunioides	5.650E-02	111.5	21.0	12.8	12.5	2.6	1.6
Terminalia sericea	1.813E-01	92.3	29.4	21.5	10.4	3.0	2.2
Thylacium africanum	3.949E-01	61.7	43.7	36.4	6.9	3.0	2.5
Tinnea rhodesiana	2.550E-02	211.0	19.0	10.6	23.7	4.5	2.5
Tricalysia allenii	1.030E-01	148.9	24.1	16.0	16.7	4.0	2.7
Vangueria infausta	2.131E-01	124.9	31.5	23.7	14.0	4.4	3.3
Vitex mombassae	8.834E-02	123.2	23.2	15.0	13.8	3.2	2.1
Xanthocercis zambesiaca	4.515E-02	156.6	20.3	12.0	17.6	3.6	2.1
Xeroderris stulhmannii	2.445E-01	165.9	33.6	25.9	18.6	6.3	4.8
Ximenia americana	4.312E-02	63.9	20.1	11.9	7.2	1.4	0.9
Ximenia caffra	1.757E-01	69.7	29.0	21.1	7.8	2.3	1.7
Xyllia torreana	1.388E-01	175.8	26.6	18.5	19.8	5.2	3.7
Ziziphus mucronata	1.042E-01	119.6	24.2	16.1	13.4	3.3	2.2

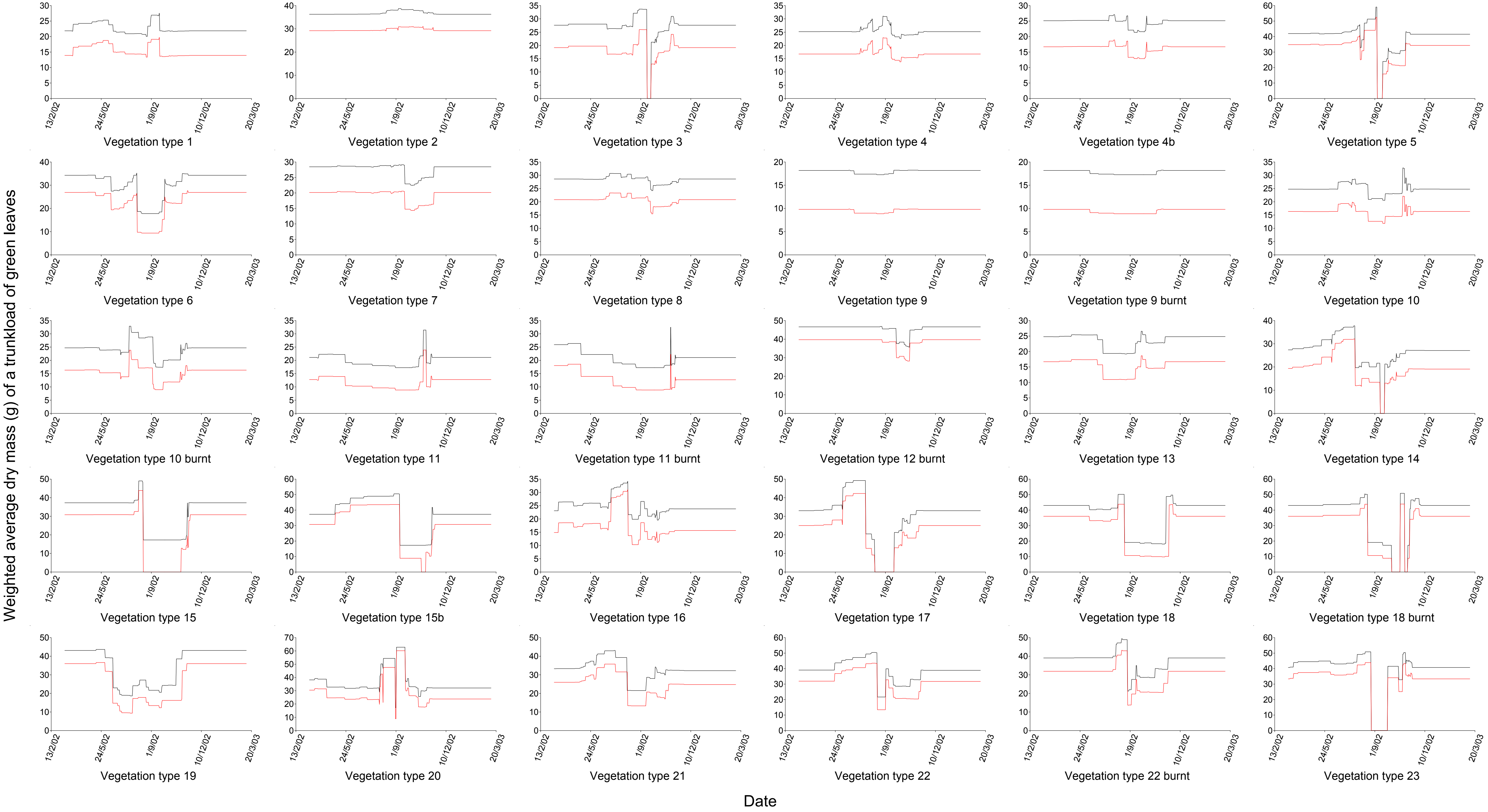
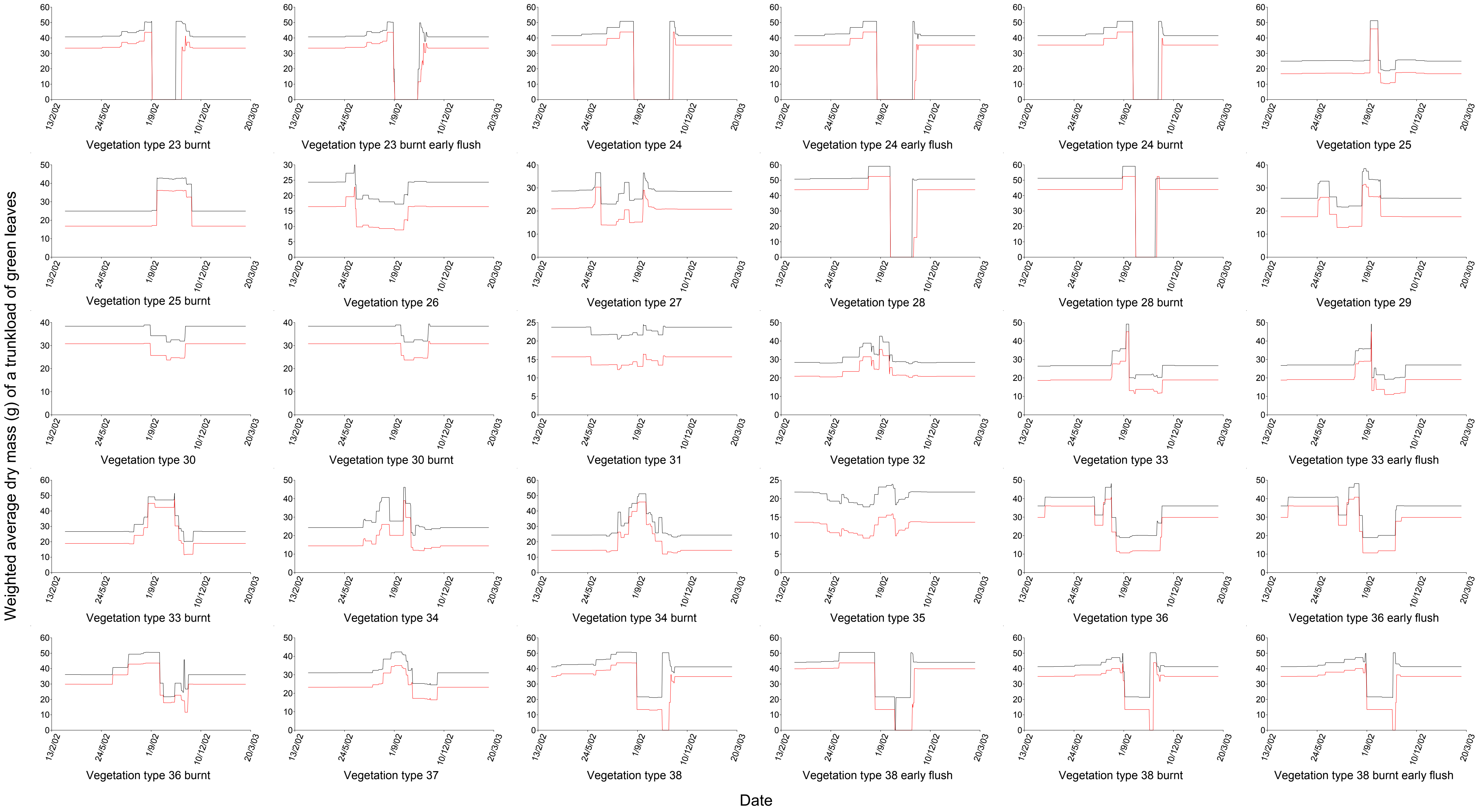


Figure 4.52 Daily estimates of the weighted average dry mass (g) of a trunkload of green leaves for adult bulls (—) and members of family units (—) for vegetation types 1-23. For a key to vegetation type numbers see Figure 3.1.



Vegetation type 23 burnt
Vegetation type 23 burnt early flush
Vegetation type 24
Vegetation type 24 early flush
Vegetation type 24 burnt
Vegetation type 25
Vegetation type 25 burnt
Vegetation type 26
Vegetation type 27
Vegetation type 28
Vegetation type 28 burnt
Vegetation type 29
Vegetation type 30
Vegetation type 30 burnt
Vegetation type 31
Vegetation type 32
Vegetation type 33
Vegetation type 33 early flush
Vegetation type 33 burnt
Vegetation type 34
Vegetation type 34 burnt
Vegetation type 35
Vegetation type 36
Vegetation type 36 early flush
Vegetation type 36 burnt
Vegetation type 37
Vegetation type 38
Vegetation type 38 early flush
Vegetation type 38 burnt
Vegetation type 38 burnt early flush

Figure 4.53 Daily estimates of the weighted average dry mass (g) of a trunkload of green leaves for adult bulls (—) and cows and subadults (—) for vegetation types 23-38. For a key to vegetation type numbers see Figure 3.1.

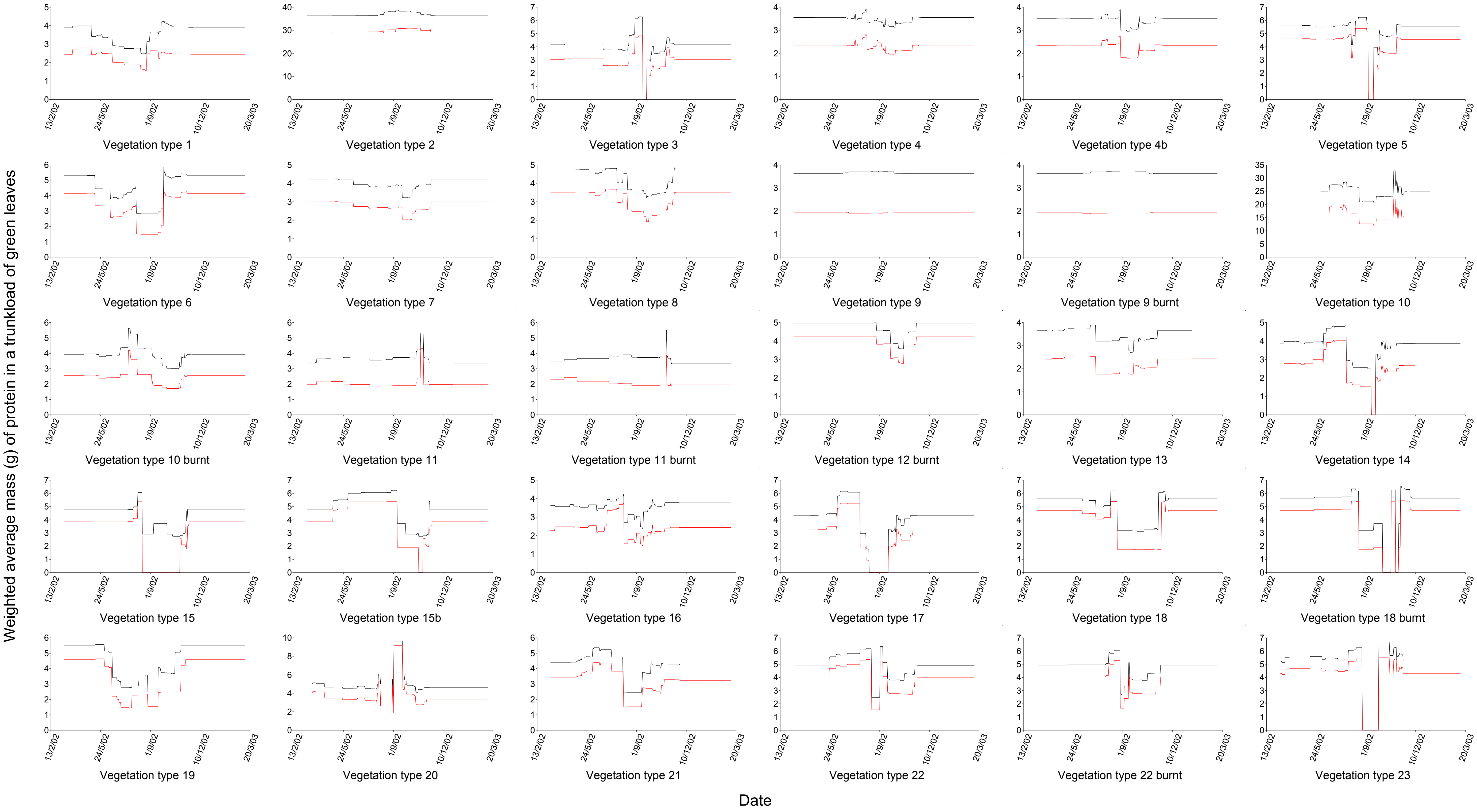
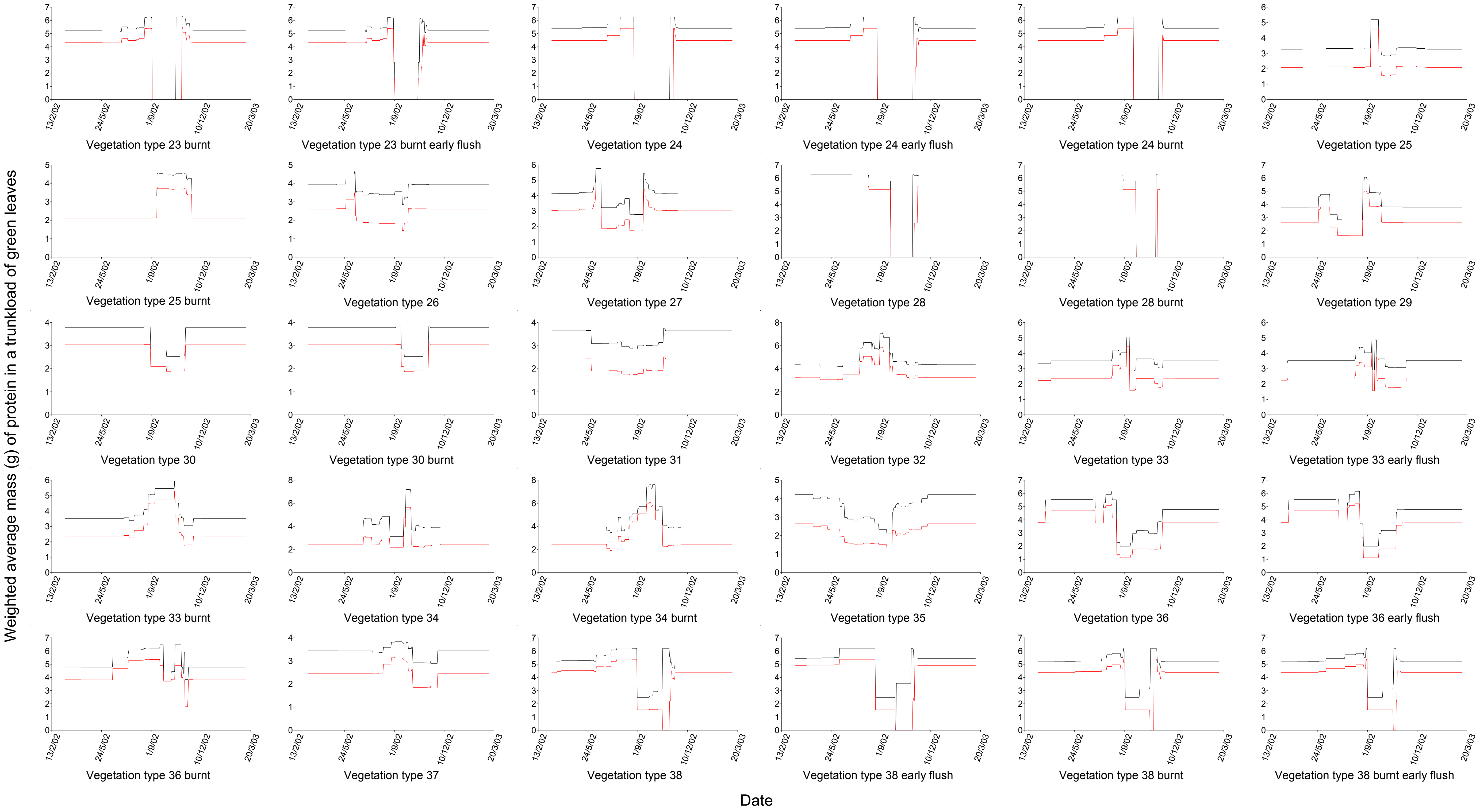


Figure 4.54 Daily estimates of the weighted average mass (g) of protein in a trunkload of green leaves for adult bulls (—) and members of family units (—) for vegetation types 1-23. For a key to vegetation type numbers see Figure 3.1.



Vegetation type 23 burnt
Vegetation type 23 burnt early flush
Vegetation type 24
Vegetation type 24 early flush
Vegetation type 24 burnt
Vegetation type 25
Vegetation type 25 burnt
Vegetation type 26
Vegetation type 27
Vegetation type 28
Vegetation type 28 burnt
Vegetation type 29
Vegetation type 30
Vegetation type 30 burnt
Vegetation type 31
Vegetation type 32
Vegetation type 33
Vegetation type 33 early flush
Vegetation type 33 burnt
Vegetation type 34
Vegetation type 34 burnt
Vegetation type 35
Vegetation type 36
Vegetation type 36 early flush
Vegetation type 36 burnt
Vegetation type 37
Vegetation type 38
Vegetation type 38 early flush
Vegetation type 38 burnt
Vegetation type 38 burnt early flush

Figure 4.55 Daily estimates of the weighted average mass (g) of protein in a trunkload of green leaves for adult bulls (—) and cows and subadults (—) for vegetation types 23-38. For a key to vegetation type numbers see Figure 3.1.

Bark from canopy branches

The crude protein content of bark from canopy branches of the woody plants most commonly utilised for canopy bark is shown in Table 4.23.

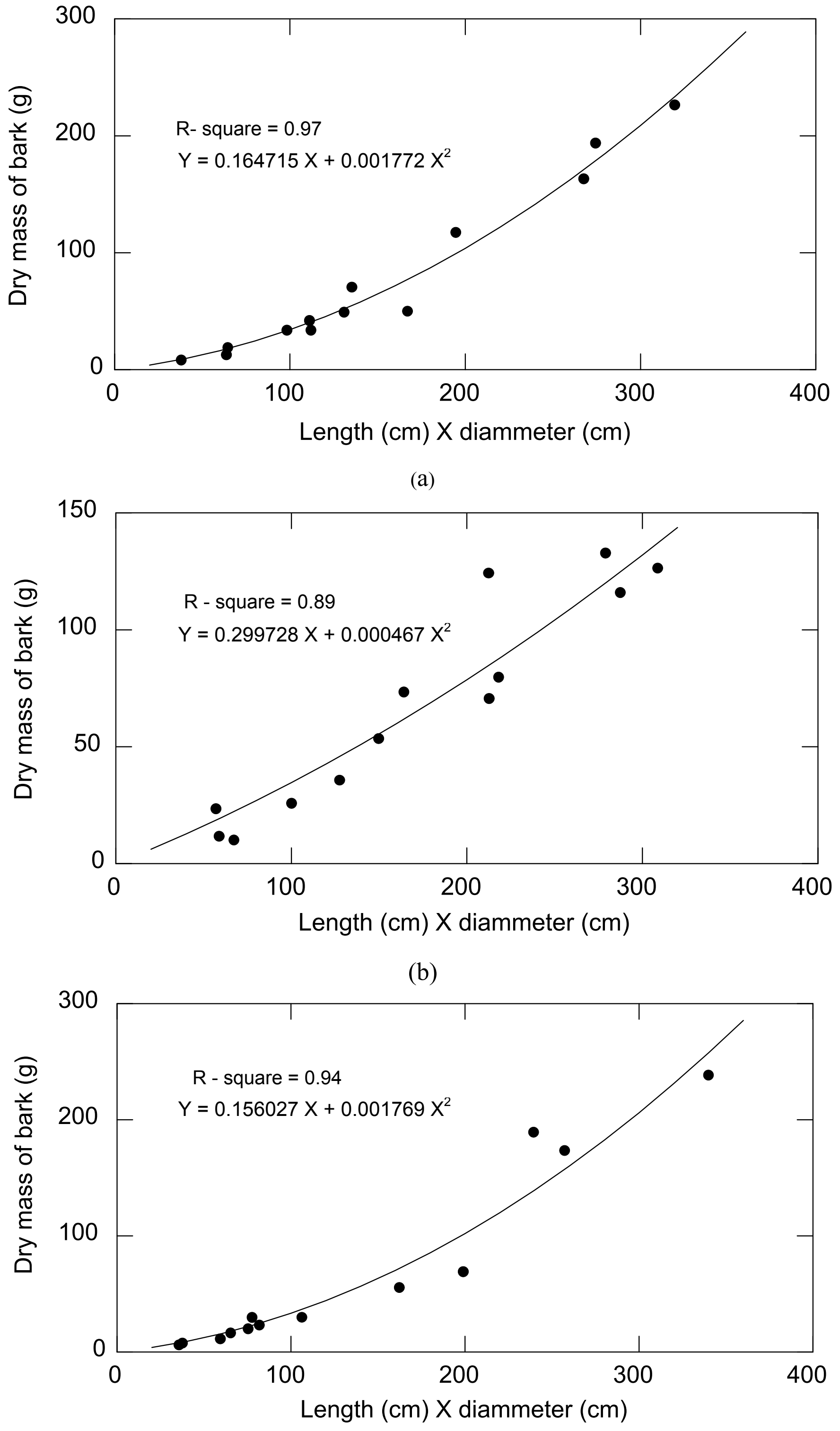
Table 4.23 Crude protein content (%) of bark from canopy branches of the woody plants most commonly utilised for canopy bark. Note that, because elephants consume both the outer and inner bark when feeding from canopy branches, the estimates were based on bark as a whole, and do not relate to the cambium only

Species	Crude protein content of bark from canopy branches (%)
Colophospermum mopane	3.9
Grewia bicolor	4.8
Grewia monticola	4.8

There was a curvilinear relationship between the product of the length and diameter of *Colophospermum mopane* (R^2 = 0.97, n = 13), *Grewia bicolor* (R^2 = 0.89, n = 13) and *Grewia monticola* (R^2 = 0.94, n = 13) branches and the dry mass of bark harvested from them (Figure 4.56). The curvilinear as opposed to linear nature of the relationship was due to an increased coarseness and thickness of the outer bark on thicker (older) branches.

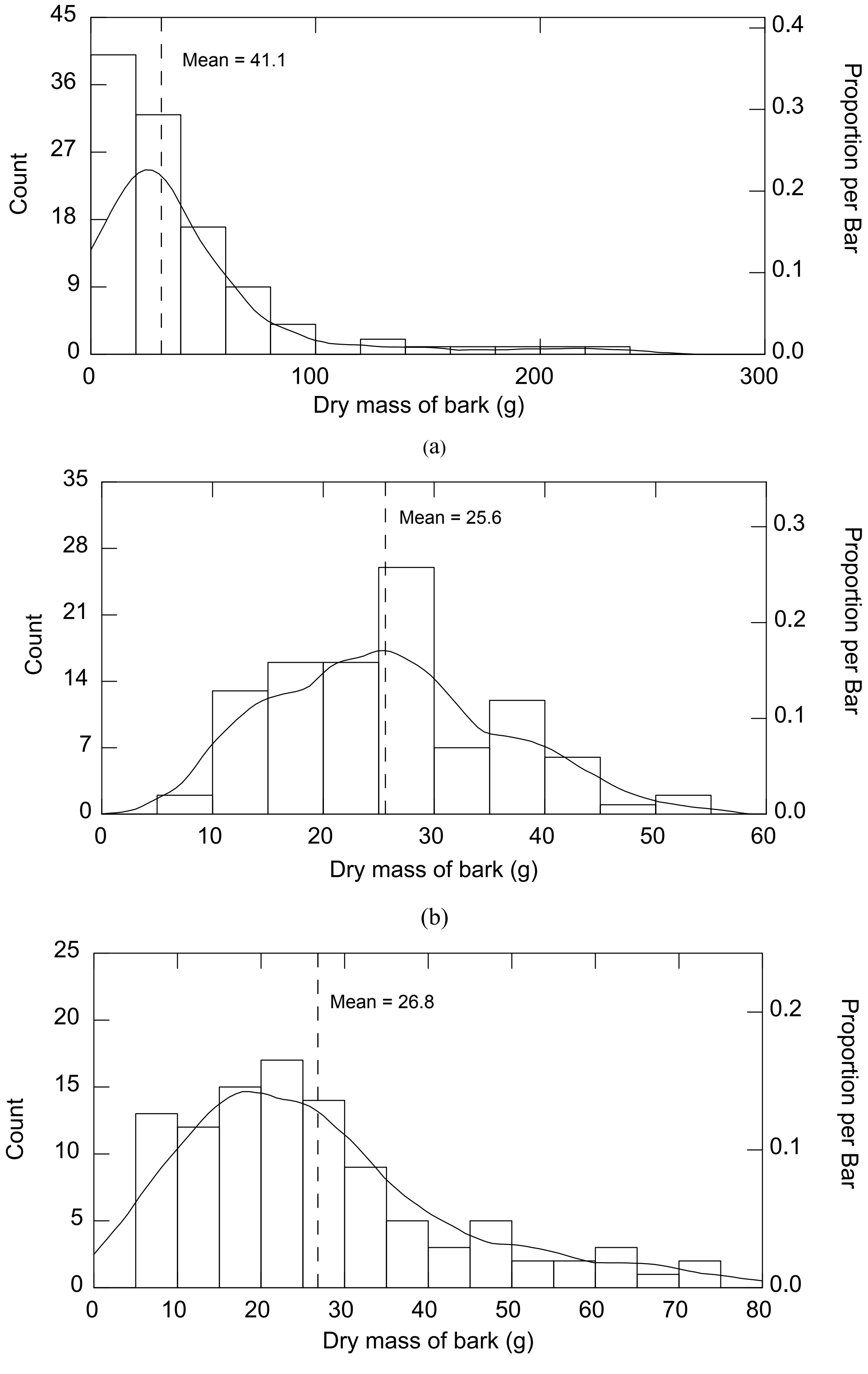
On average, bulls took larger bites of canopy bark (*Colophospermum mopane* = 41.1 g, n = 109; *Grewia bicolor* = 25.6 g, n = 101; *Grewia monticola* = 26.8 g, n = 103) (Figure 4.57) than members of family units (*Colophospermum mopane* = 20.2 g, n = 102; *Grewia bicolor* = 19.8 g, n = 100; *Grewia monticola* = 22.1 g, n = 121) (Figure 4.58).

The weighted average mass of protein in a mouthful of canopy bark taken by adult bulls and members of family units is shown for each vegetation type in Table 4.24 and Table 4.25 respectively. The average mass of protein per mouthful of canopy bark ranged from 1.23 g to 1.60 g for adult bulls and from 0.79 g to 1.06 g for members of family units.



(c)

Figure 4.56 Relationship between the product of the length (cm) and diameter (cm) of (a) *Colophospermum mopane*, (b) *Grewia bicolor* and (c) *Grewia monticola* branches and the dry mass of bark harvested from them.

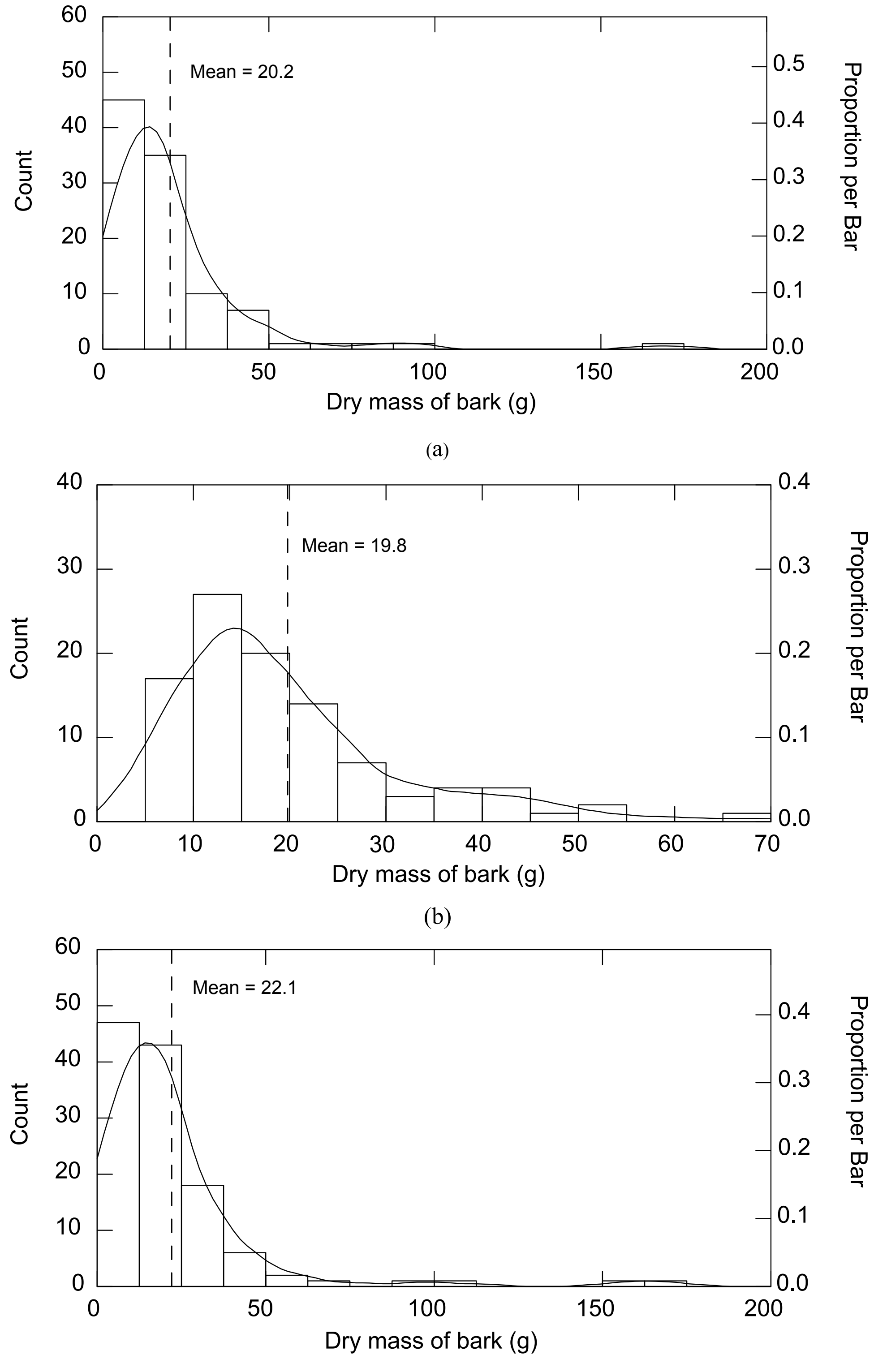


(a)

(b)

(c)

Figure 4.57 Histogram and kernel density distributions of bite mass of canopy bark taken by adult bulls from (a) *Colophospermum mopane*, (b) *Grewia bicolor* and (c) *Grewia monticola* branches.



(a)

(b)

(c)

Figure 4.58 Histogram and kernel density distributions of bite mass of canopy bark taken by members of family units from (a) *Colophospermum mopane*, (b) *Grewia bicolor* and (c) *Grewia monticola* branches.

Table 4.24 Density of *Colophospermum mopane*, *Grewia bicolor* and *Grewia monticola* plants with canopy below 6 m and the weighted average mass (g) of protein in a mouthful of canopy bark taken by adult bulls for each vegetation type. For a key to vegetation type number see Figure 3.1

Vegetation type	Density of *Colophospermum mopane* plants with canopy below 6 m (plants/m^2)	Density of *Grewia bicolor* plants with canopy below 6 m (plants/m^2)	Density of *Grewia monticola* plants with canopy below 6 m (plants/m^2)	Weighted average mass of protein in a mouthful of canopy bark (g)
1		0.02636	0.00520	1.24
2			0.00016	1.29
3			0.00027	1.29
4	0.00008	0.00216	0.00768	1.28
5	0.09472	0.00840	0.00947	1.55
6	0.05000	0.01533	0.00133	1.51
7	0.02640	0.00853	0.00100	1.51
8		0.05560	0.00040	1.23
9		0.00530	0.00036	1.23
10	0.00040	0.04267	0.00516	1.24
11		0.02070	0.00100	1.23
12	0.00978		0.00013	1.60
13	0.00010	0.04800	0.01700	1.24
14	0.04283	0.13733	0.00222	1.32
15	0.07067	0.01720	0.00200	1.52
16	0.02843	0.05240	0.00300	1.36
17	0.04789	0.08247	0.00473	1.36
18	0.05156	0.01877	0.01973	1.46
19	0.14427	0.01040	0.00640	1.57
20	0.04067	0.02400	0.01428	1.43
21	0.08243	0.05183	0.02028	1.44
22	0.02843	0.00363	0.00464	1.53
23	0.04155	0.00254	0.00130	1.57
24	0.25067	0.00267		1.60
25	0.00054			1.60
26	0.00034	0.02440	0.02664	1.26
27	0.00223	0.01752	0.03301	1.28
28	0.05444	0.00016		1.60
29	0.00140	0.01280	0.01520	1.28
30	0.00360	0.00027		1.58
31		0.00013		1.23
32	0.00300	0.00055	0.01345	1.34
33	0.00085	0.00034	0.00023	1.46
34	0.00840	0.00050	0.00005	1.58
35		0.00360	0.00200	1.25
36	0.05051	0.00059		1.60
37	0.00053	0.00027	0.00027	1.43
38	0.03939	0.00703	0.00118	1.54

Table 4.25 Density of *Colophospermum mopane*, *Grewia bicolor* and *Grewia monticola* plants with canopy below 4 m and the weighted average mass (g) of protein in a mouthful of canopy bark taken by members of family units for each vegetation type. For a key to vegetation type numbers see Figure 3.1

Vegetation type	Density of *Colophospermum mopane* plants with canopy below 4 m (plants/m^2)	Density of *Grewia bicolor* plants with canopy below 4 m (plants/m^2)	Density of *Grewia monticola* plants with canopy below 4 m (plants/m^2)	Weighted average mass of protein in a mouthful of canopy bark (g)
1		0.02609	0.00520	0.97
2			0.00016	1.06
3			0.00027	1.06
4	0.00008	0.00216	0.00768	1.03
5	0.09458	0.00840	0.00947	0.82
6	0.04787	0.01533	0.00133	0.83
7	0.02290	0.00853	0.00100	0.84
8		0.05560	0.00040	0.95
9		0.00530	0.00036	0.96
10	0.00007	0.04267	0.00516	0.96
11		0.02070	0.00100	0.96
12	0.00978		0.00013	0.79
13	0.00003	0.04800	0.01700	0.98
14	0.03982	0.13733	0.00222	0.92
15	0.07067	0.01720	0.00200	0.82
16	0.02833	0.05240	0.00300	0.90
17	0.04389	0.08247	0.00473	0.90
18	0.05051	0.01877	0.01973	0.88
19	0.14093	0.01040	0.00640	0.81
20	0.03882	0.02400	0.01428	0.89
21	0.07843	0.05183	0.02028	0.88
22	0.02812	0.00363	0.00464	0.84
23	0.04151	0.00254	0.00130	0.80
24	0.25067	0.00267		0.79
25	0.00042			0.79
26	0.00020	0.02440	0.02664	1.01
27	0.00166	0.01752	0.03301	1.02
28	0.05444	0.00016		0.79
29	0.00127	0.01280	0.01520	1.00
30	0.00333	0.00027		0.80
31		0.00013		0.95
32	0.00273	0.00055	0.01345	1.01
33	0.00067	0.00034	0.00023	0.88
34	0.00330	0.00050	0.00005	0.81
35		0.00360	0.00200	0.99
36	0.04909	0.00059		0.79
37	0.00036	0.00027	0.00027	0.92
38	0.03921	0.00703	0.00118	0.82

4.4.4. *Speed of travel between patches*

The speed of travel between feeding stations was estimated for 73 elephants across 3 age/sex classes. The average speed for each class is shown in Table 4.26.

Table 4.26. Average speed of travel while foraging (km/hr) for adult bulls, adult cows and subadults. The variance of each estimate is given in parentheses

Age & sex	Sample size	Average speed of travel between feeding stations (km/hr)
Adult bull	20	2.96 (0.22)
Adult cow	26	3.05 (0.25)
Subadult	27	2.82 (0.39)

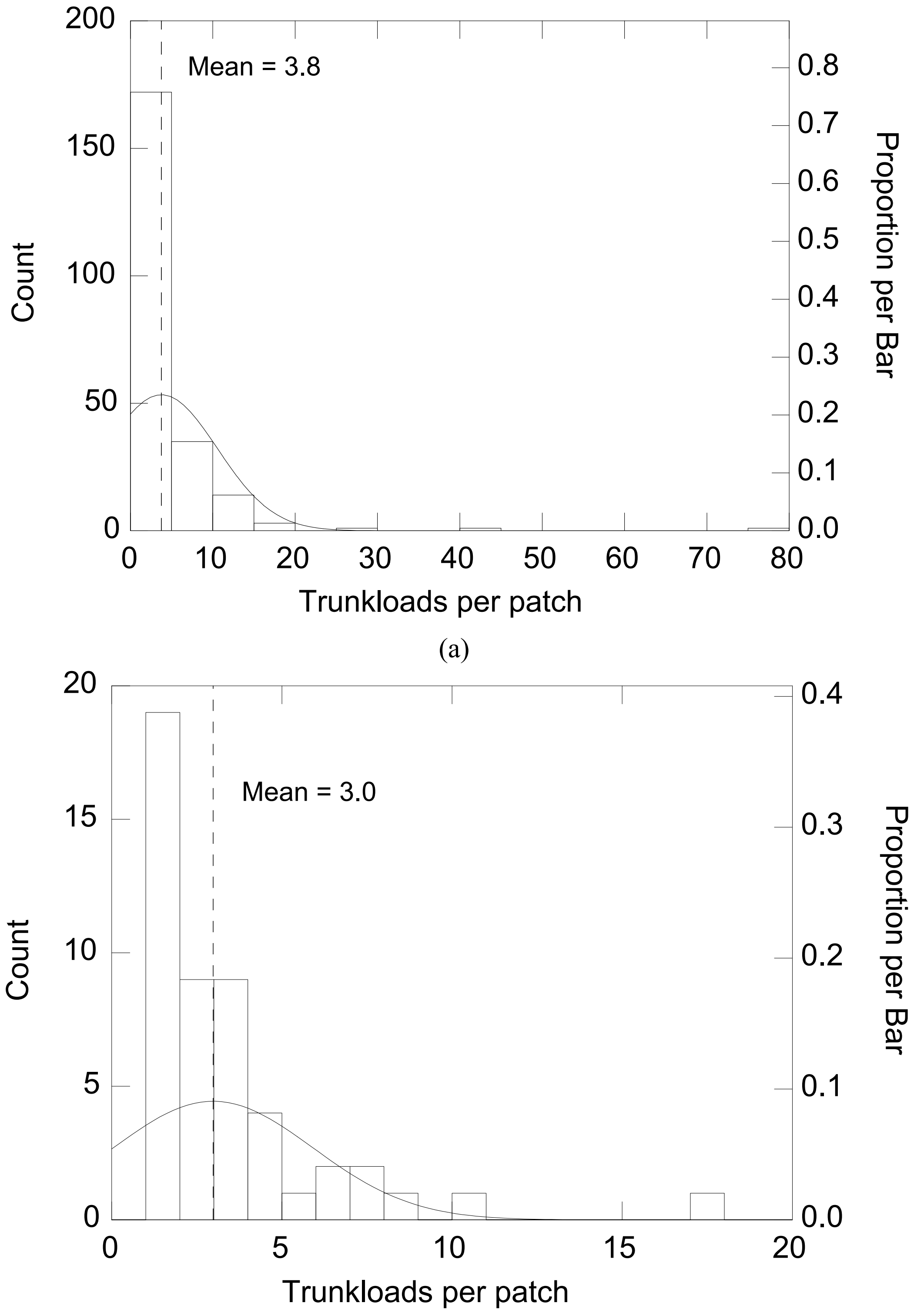
There were no significant differences in speed of travel among the classes (P = 0.332) and, consequently, data were pooled, and the overall average of 2.94 km/hr or 0.817 m/s was used to calculate the rate of protein intake.

4.4.5. *Number of trunkloads per patch*

When feeding on leaves, the average number of trunkloads per woody plant was 3.8 (n = 227) for adult bulls and 3.0 (n = 49) for members of family units (Figure 4.59). When calculating the rate of protein intake these values were rounded to 4.0 and 3.0 for adult bulls and members of family units respectively.

When feeding on canopy bark, the average number of trunkloads per woody plant was 2.5 (n = 62) for adult bulls and 1.9 (n = 24) for members of family units (Figure 4.60). When calculating the rate of protein intake these values were rounded to 2.0 for both adult bulls and members of family units.

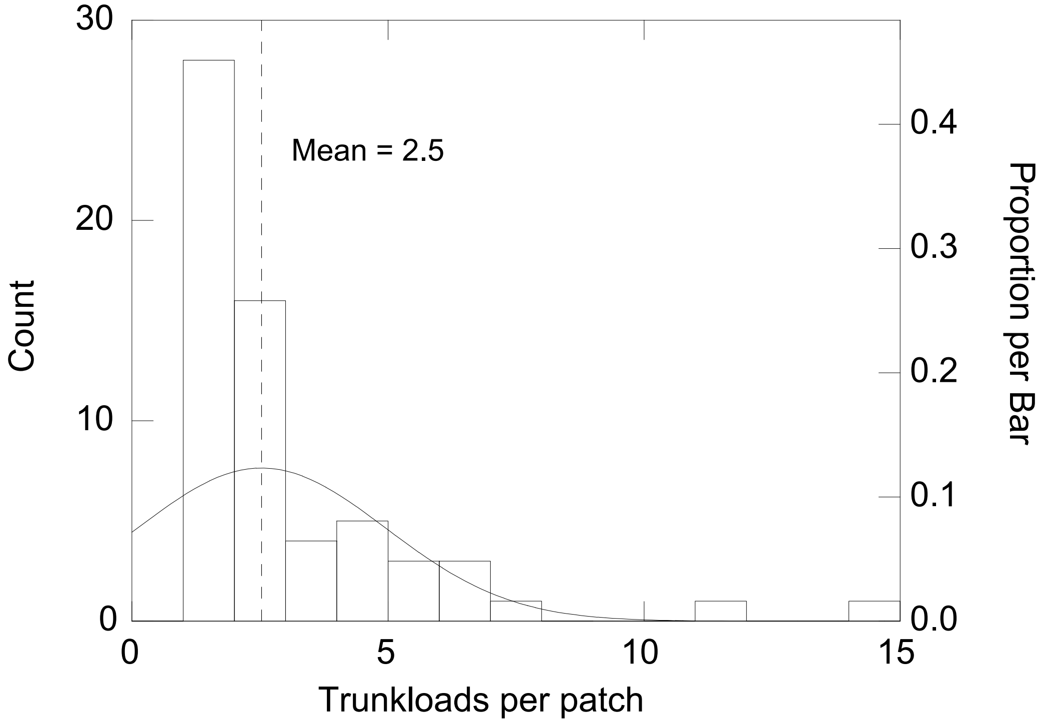
When feeding on grass and forbs the number of trunkloads harvested per patch was set at 1.



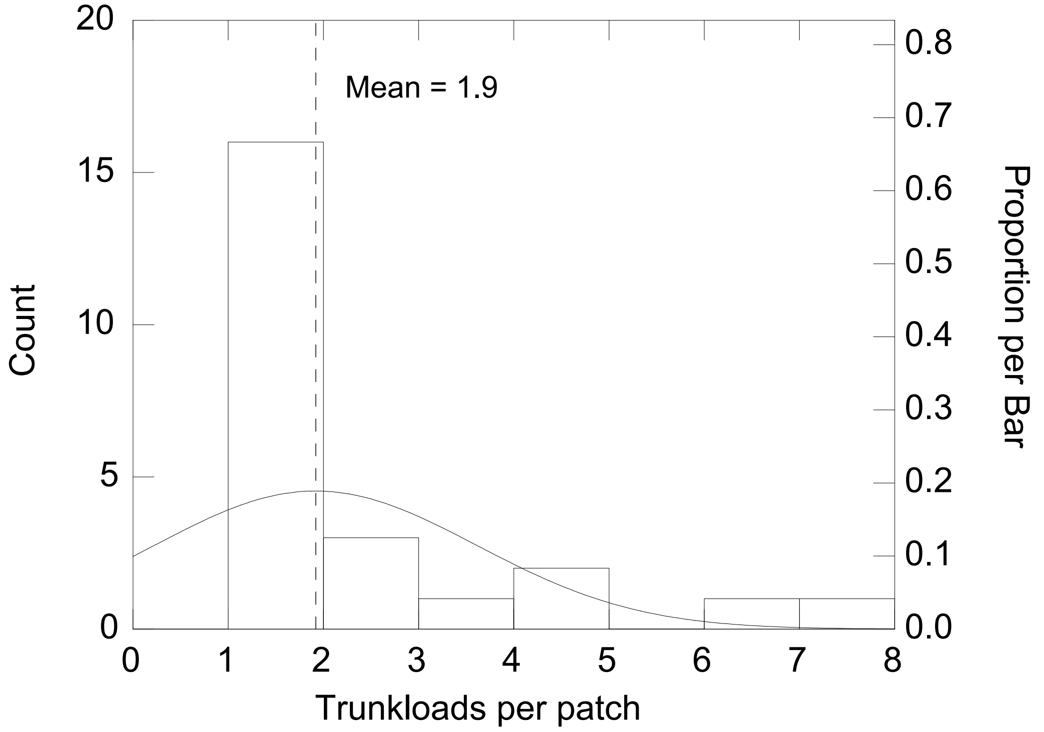
(a)

(b)

Figure 4.59. Histogram and normal density distributions of the number of trunkloads of leaves harvested per patch for (a) adult bulls and (b) members of family units.



(a)



(b)

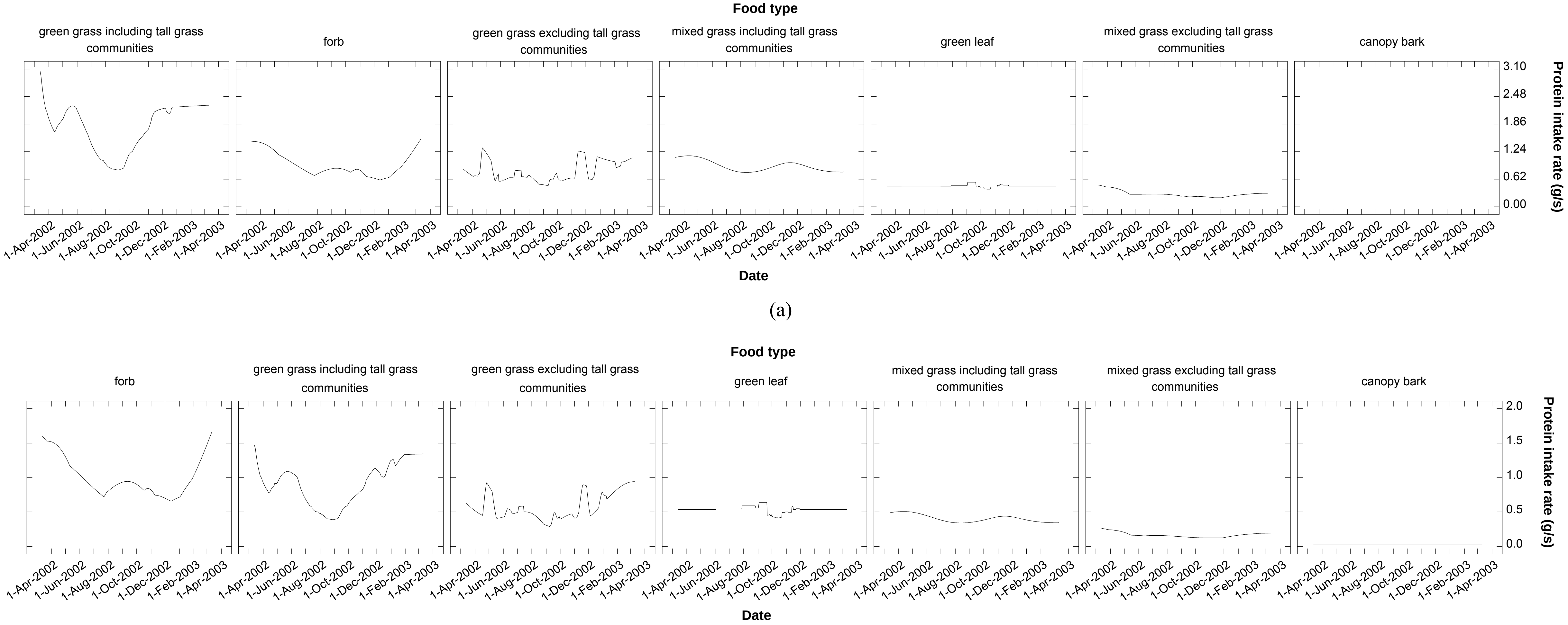
Figure 4.60. Histogram and normal density distributions of the number of trunkloads of canopy bark harvested per patch for (a) adult bulls and (b) members of family units.

4.4.6. *Short-term rate of protein intake*

Time series profiles of the maximum short-term rate of protein intake for each food type are shown for adult bulls and members of family units in Figure 4.61. Because elephants are poor digesters of cell wall material (van Hoven et al., 1981; Meissner et al., 1990) the cell contents of tall, robust grass species such as *Setaria incrassata* and *Ischaemum afrum* that have relatively thick cell walls, are largely inaccessible to elephants. Consequently, the maximum short-term intake rate of protein for green grass and mixed grass was calculated for the study area including the tall grass communities and also for the study area excluding the tall grass communities.

When the tall grass communities were excluded, green forbs provided the highest rate of short-term protein intake for both adult bulls and members of family units. Green grass provided the second highest rate of protein intake, and green leaves the third highest rate. Canopy bark and mixed grass provided the lowest and second lowest rates respectively.

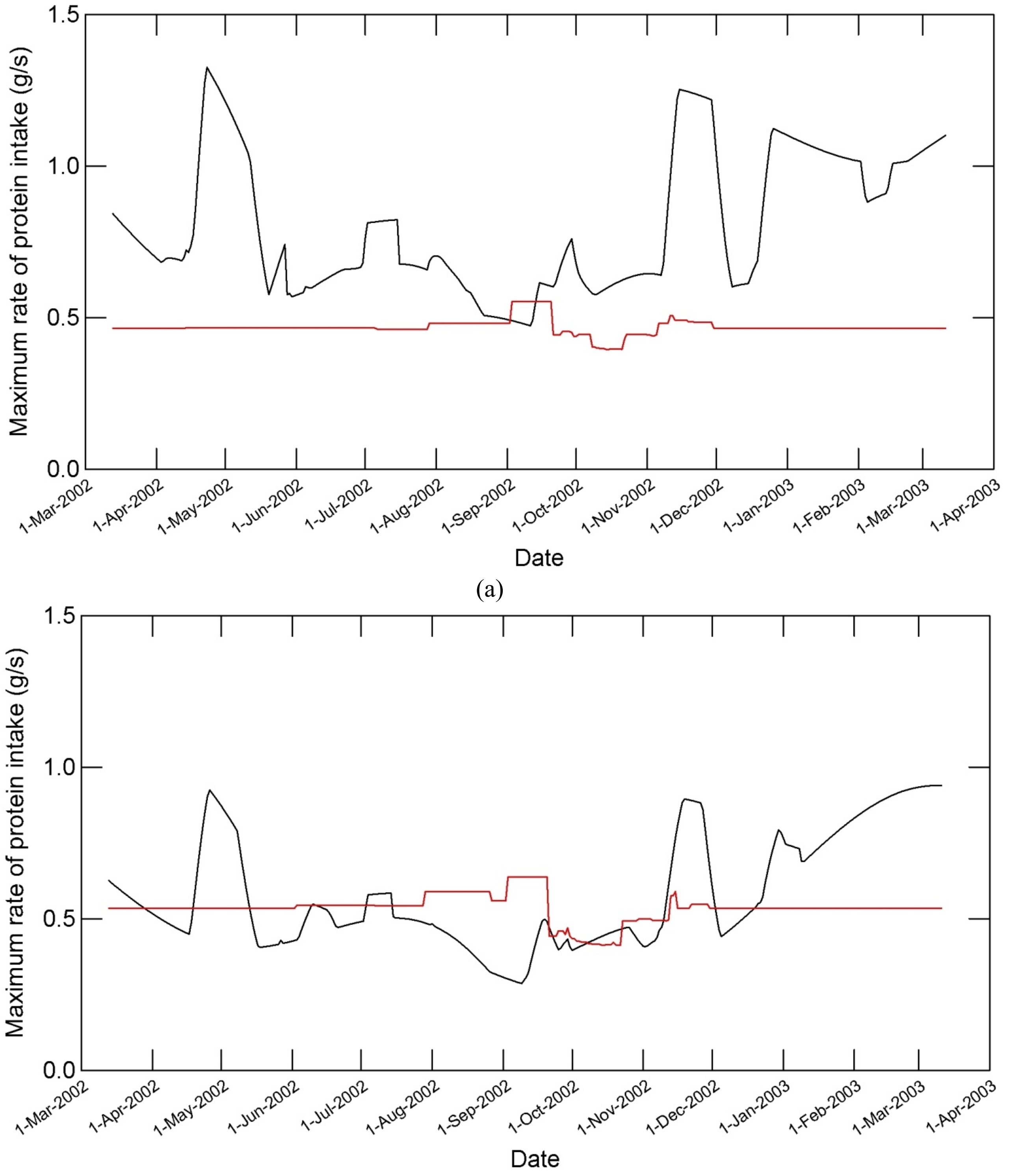
For adult bulls, the maximum rate of protein intake when feeding on grass was higher than when feeding on leaves for most of the study period. Only for a short period during the hot dry season (between September and October 2002) did the maximum rate of protein intake when feeding on leaves supersede that from feeding on green grass (Figure 4.62). In contrast, protein intake by members of family units when feeding on green grass was only higher than when feeding on green leaves during the rainy season. During the cool and hot dry seasons, green leaves provided a higher rate of protein intake than green grass.



(a)

(b)

Figure 4.61. Time series profiles of the maximum short-term rate of protein intake (g/s) for each food type achieved by (a) adult bulls and (b) members of family units. Because elephants are poor digestors of cell wall material the cell contents of robust grass species such as *Setaria incrassata* and *Ischaemum afrum* that have relatively thick cell walls are largely inaccessible to elephants. Consequently, the maximum short-term rate of protein intake (g/s) for green grass and mixed grass is presented for the study area including the tall grass communities and also for the study area excluding the tall grass communities. Food types are arranged in order with types providing the highest rate of protein intake on the left and types with the lowest rates of protein intake on the right.



(a)

(b)

Figure 4.62. Time series profiles of the maximum rate of protein intake (g/s) for green grass excluding the tall grass communities (—) and for green leaves (—) for (a) adult bulls and (b) members of family units.

4.5. Discussion

4.5.1. *Ecological insights*

Foraging mechanics

The results of the model show how forage quality may be influenced, not only by preferences associated with the energy and nutrient content, but also by the costs involved in harvesting and processing food. The model showed that when food with a relatively low energy and nutrient concentration (as measured by the protein intake proxy) can be harvested with large trunkloads and also has short search, prehension, and chewing times, the rate of intake may be higher than that from food rich in energy and nutrients that is more difficult to find and harvest in large quantities per unit time. This may explain why elephants prefer to feed on grass during the rainy season (Buss, 1961; Bax & Sheldrick, 1963; Laws, 1970a; Williamson, 1975; Field & Ross, 1976; Guy, 1976; Barnes, 1982; Owen-Smith, 1988; Kabigumila, 1993; de Boer et al., 2000; Osborn, 2004) despite its lower protein density relative to browse (Field, 1971; Field & Ross, 1976; Topps, 1997).

The mechanistic approach to elephant foraging also highlighted the important role played by the trunk, which allows prehension and chewing of food to occur simultaneously thereby facilitating the high rate of intake essential for the maintainance of an exceptionally large body size.

Seasonal changes in diet

Seasonal changes in the rate of energy and nutrient intake provide a possible explanation for the shift in diet of elephants from a predominantly grazing diet in the wet season to a predominantly browsing diet in the dry season (Buss, 1961; Bax & Sheldrick, 1963; Laws, 1970a; Williamson, 1975; Field & Ross, 1976; Guy, 1976; Barnes, 1982; Owen-Smith, 1988; Kabigumila, 1993; de Boer et al., 2000; Osborn, 2004). Elephants may eat more grass during the rainy season because, at this time, the high patch density, short handling time and large trunkload mass of grass compensate for its low nutrient content to the extent that it has a higher rate of short-term nutrient intake relative to browse. With the onset of the dry season, grass begins to dry out and senesce. This has the effect of lowering its energy and nutrient content, increasing search time, increasing its handling time (because grass tufts must first be shaken to remove dry material before being ingested), and reducing the mass of a trunkload. The net result is a lower short-term rate of energy and nutrient intake from grass relative to browse during the dry season, and hence a possible explanation for the observed shift towards a diet largely composed of browse from woody plants.

Sex related differences in foraging behaviour

Sex related differences in the rate of energy and nutrient intake across food types provide a possible explanation for the sexual segregation of elephants observed during the dry season (Stokke, 1999; Stokke & du Toit, 2000; Stokke & du Toit, 2002). Adult bulls harvest heavier trunkloads of grass relative to cows and, as a result, they are able to maintain a high rate of energy and nutrient intake from grass for longer into the dry season because the large trunkload mass compensates for the decline in grass quality. Consequently, while bulls are able to satisfy their nutritional requirements during the dry season by roaming widely in search of suitable grazing (Stokke & du Toit, 2002), cows must seek habitats with an abundant supply of browse, hence the observed dry season segregation of adult bulls and family units. The absence of segregation during the rainy season may be because the energy and nutrient density of grass is relatively high at this time and, therefore, the limiting effect of the smaller bite mass of cows on the rate of energy and nutrient intake is not as significant.

If maximisation of the short-term rate of energy and nutrient intake is an important determinant of diet selection by elephants, observed differences in the mass of food harvested with each trunkload should result in adult bulls being preferential grazers and members of family units being preferential browsers. This hypothesis is consistent with the observation that when green grass is available it constitutes a large proportion of the diet of bulls (Buss, 1961; Guy, 1976; Owen-Smith, 1988), whereas the diet of cows is dominated by woody browse (Barnes, 1982).

High rates of protein intake for both bulls and members of family units were achieved when feeding on forbs. This suggests that forbs, which have received little attention in the literature, may be a highly profitable food source for elephants.

4.5.2. *Assumptions, limitations and future improvements*

The ingestion model assumed that chewing time was independent of trunkload mass, in other words the time to chew small and large trunkloads was the same. In reality this assumption is unlikely and, therefore, the model possibly over estimated intake rate when large trunkloads were harvested and provided an under estimate when small trunkloads were harvested. To overcome this problem, chewing time could be represented in the model as a function of trunkload mass (see Ginnett & Demment, 1997).

The model also assumed that patches of food were uniformly distributed in space and, consequently, calculated the distance between patches as $\frac{1}{\sqrt{D}}$, where D is the density of patches (patches/m^2) (Clark & Evans, 1954). Although a uniform distribution of patches of food is unrealistic, the alternative – a random distribution – is also unlikely, especially when individual plants are considered patches, because competition between plants for resources precludes a random distribution. However, if a random distribution were chosen, the distance between patches could be modelled as $\frac{1}{2\sqrt{D}}$ (Clark & Evans, 1954) which would in effect halve the distance between patches relative to a uniform distribution. This would serve to further reduce the already negligible influence of search time on intake rate and would, therefore, make very little difference to the results obtained using a uniform distribution.

Ingestion models estimate the rate of intake of food and do not provide a measure of the actual uptake of nutrients from the ingested food i.e. they do not take into account the constraints of digestion. Consequently, when only the intake rate of food material is considered, a false idea of the utility of forage may be gained. For example, in this study the ingestion model estimated very high rates of protein intake by bull elephants when feeding on grass from the tall grass communities. The tall grass communities were dominated by *Setaria incrassata* and *Ischaemum afrum*. Although these species have a relatively high protein density, they are particularly robust and, therefore, have thick cell walls relative to other grass species. Because elephants are poor digesters of cell wall material (van Hoven et al., 1981; Meissner et al., 1990) the overall rate of nutrient uptake from these grass species is likely to be low despite the high rate of intake. A more realistic measure of the utility of food could be obtained by combining the ingestion model with a digestion model to create a single integrated model (for a review of integrated models see Yearsley et al., 2001).

This component of the study has shown that green grass and forbs can provide elephants with a higher rate of energy and nutrient intake than leaves and bark from woody plants. However, the relevance of this finding is dependent on whether elephants consider the rate of energy and nutrient intake to be an important criterion for habitat and diet selection. This is addressed in the next two chapters.

Chapter 5. Habitat selection by elephants: the influence of short-term rate of protein intake and distance from surface water

5.1. Introduction

Elephants are naturally destructive feeders, especially when utilising the stems, bark and roots of woody plants (Laws, 1970b; Anderson & Walker, 1974; Ben-Shahar, 1993; Tchamba, 1995). Impact by elephants on woody vegetation may be important for promoting habitat heterogeneity and increased levels of biodiversity (Gillson & Lindsay, 2003). However, over the past 50 years, the woody vegetation of many protected areas in Africa has come under increasing pressure from elephants, to the extent that local extirpation of woody species has occurred in some reserves and is potentially imminent in others (O'Connor et al., 2007). In addition, elephant-induced transformation of forest and woodland to shrubland and grassland has lead to concern over the loss of animal species that are dependent on forest and woodland habitats for their survival (Laws, 1970a; Herremans, 1995; Cumming et al., 1997; Fenton et al., 1998; Lombard et al., 2001; Fritz et al., 2002; Braswell & Slusar, 2005; Botes et al., 2006).

Management intervention to curtail impacts has been constrained by a limited understanding of the actual mechanisms driving resource selection by elephants (O'Connor et al., 2007). The currency used when deciding where to forage and what to eat has not been identified, and the nature of the interaction between the dietary and non-dietary determinants of habitat selection is poorly understood. Consequently, there is a critical need to test possible predictors and mechanisms of habitat and diet selection by elephants.

In order to decompose the complex process of resource selection into manageable parts, foraging by herbivores has been described as a “top-down”, hierarchical, spatial process from choice of habitat at the coarse scale to choice of plant part at the fine scale (Johnson, 1980; Senft et al., 1987). Within the hierarchy, a selection process will be of higher order than another if it is conditional on the latter. For example, selection of habitat types within a home range of an animal is of higher order than selection of the home range, because the availability of each habitat type is determined by the selection of the home range. Similarly, selection of food items is of higher order than selection of feeding site, for the site delimits the array of food items available to be selected.

Application of this conceptual framework to studies of resource selection by wildlife has shown that selection criteria are not necessarily congruent across scales (McLoughlin et al., 2002; 2004). This is because details of fine-scale processes become insignificant at coarse scales, and processes that operate at coarse scales tend to change too slowly or vary over too large a spatial scale to be perceptible at fine scales (Coughenour, 1991). For example, distance from drinking water may influence the coarse-scale decision of which habitat to forage in, but is unlikely to influence the fine-scale choice of which plants to eat within the selected habitat. Hence, resource selection studies conducted at a number of discrete scales (discrete multi-scale studies) are often more informative than single scale designs (Johnson et al., 2004). For this reason, the discrete multi-scale format has become the commonly used design in the study resource selection by wildlife (Schaefer & Messier, 1995; Rolstad et al., 2000; Rettie & Messier, 2000; McLoughlin et al., 2002; Martinez et al., 2003; Johnson et al., 2004; McLoughlin et al., 2004; Whittingham et al., 2005).

While the discrete multi-scale approach provides useful insights into resource selection at different scales, it is limited by a fundamental flaw in that it ignores the potential for “bottom-up” cross-scale linkages in the selection process (Johnson et al., 2004). In other words, selection at the coarse scale is assumed to be independent of selection at finer scales. In reality, this is unlikely because decisions made at the fine scale can potentially influence resource selection at larger scales (Shipley, 2007). For example, a bird might search a wide area for a tree with the best nesting cavity and then defend a territory around that tree regardless of the coarser-scale characteristics of the territory (Battin & Lawler, 2006).

The realisation that cross-scale relationships are potentially an important part of the selection process led to the development of multi-scale or multi-grain models. These models use predictor variables that are measured at multiple spatial scales and perform better than those developed using discrete multi-scale designs that only include predictor variables measured at a single spatial scale (Johnson et al., 2004; Graf et al., 2005; Meyer & Thuiller, 2006).

Although multi-scale models are an improvement on single-scale models, they are limited in that they are typically based on a statistical regression analysis that does not try to represent the true regulation processes underlying resource selection. Instead, they demonstrate a correlation between environmental variables and the spatial distribution of the target species, and in so doing, provide predictive power without furthering understanding of the actual mechanics driving the selection process (Yearsley et al., 2001).

Furthermore, because multi-scale models rely on regression analysis of numerous predictor variables measured at different scales, they are subject to the problem of cross-scale correlation (Battin & Lawler, 2006). In habitat selection studies, cross-scale correlation occurs when there is an association between habitat variables at two or more scales. If habitat variables are correlated, traditional analytical techniques may reach erroneous conclusions regarding the presence or strength of habitat associations at a particular scale (Battin & Lawler, 2006). Although techniques such as variance decomposition can be used to determine the degree to which cross-scale correlations may influence model interpretation, there is currently no single solution to this problem (Lawler & Edwards, 2006).

In this chapter, habitat selection by elephants is investigated using a modelling approach that functionally represents foraging across multiple spatial scales, and also allows for both "top-down" and "bottom-up" cross-scale linkages. The central idea behind the approach is that instead of multi-scale predictor variables being entered separately into a statistical model, they are first functionally integrated into a single composite predictor through use of a mechanistic submodel. By condensing a number of variables into a single functional predictor, the approach also mitigates the harmful effects of cross-scale correlations.

5.2. Modelling habitat selection by elephants

Given a short foraging time per unit nutrient, a low level of cell wall digestion, and a limited ability to recycle microbial protein, it is hypothesised that elephants take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time to meet their nutritional demands (see Chapter 1). Accordingly, elephants are expected to select habitats that maximize their short-term rate of intake of digestible energy and nutrients. Due to the fact that the level of digestible energy contained within forage is difficult to measure for elephants, the rate of protein intake was assumed to be a surrogate measure of the rate of intake of digestible energy and nutrients (see Chapter 4 for support of this assumption).

Considering that the rate of protein intake represents the functional integration of foraging actions from fine to coarse scales (see Chapter 4), its use as a predictor for habitat selection automatically incorporates both "top-down" and "bottom-up" cross-scale linkages in the process of habitat selection. Furthermore, because the rate of protein intake is the integrated result of a number of variables, its inclusion reduces the number of predictors in the model and, in so doing, lowers the chance of cross-scale correlations amongst covariates.

However, because distance from drinking water is an important constraint restricting use of habitats by elephants (Young, 1970; Western, 1975; Stokke & du Toit, 2002; Conybeare, 2004; de Beer et al., 2006; Chamaillé-Jammes et al., 2007), habitat selection is expected to be the result of a trade-off between distance from water and short-term rate of protein intake, with the nature of the trade-off being governed by sex related differences in resource selection and the spatial distribution of suitable forage resources in relation to surface water.

The aim of this chapter was to test these predictions at the landscape level by determining to what extent short-term rate of protein intake and distance from surface water could be used to explain "presence-only" habitat selection data that were collected from adult bull and adult cow elephants fitted with GPS collars.

5.3. Methods

5.3.1. *Statistical model*

A variety of statistical techniques are available for modelling the geographic distributions of plant and animal species (for recent reviews see Guisan & Zimmermann, 2000; Segurado & Araújo, 2004; Burgman et al., 2005; Wintle et al., 2005; Guisan & Thuiller, 2005; Elith et al., 2006; Pearce & Boyce, 2006; Austin, 2007). These techniques predict geographic distributions by relating presence-only, presence-absence or abundance data of the target species to environmental predictors. The methods vary in how they model the distribution of the response, select relevant predictor variables, define fitted functions for each variable, weight variable contributions, allow for interactions and predict geographic patterns of occurrence (Elith et al., 2006).

Some methods, for example BIOCLIM (Busby, 1991), DOMAIN (Carpenter et al., 1993) and ENFA (Hirzel et al., 2002), only use presence records to derive a model. These methods tend to generate over-optimistic predictions because the lack of absence data results in the target species being predicted at too many locations (Zaniewski et al., 2002; Engler et al., 2004). However, MAXENT (Phillips et al., 2006), a newly introduced presence-only method, out performs many of the established methods and shows considerable promise (Elith et al., 2006).

Modelling techniques that use both presence and absence data generally out perform presence-only methods (Zaniewski et al., 2002; Engler et al., 2004; Brotons et al., 2004; Olivier & Wotherspoon, 2006). Generalised Linear Modelling (GLM, McCullagh & Nelder, 1989) and Generalised Additive Modelling (GAM, Hastie & Tibshirani, 1986) are two regression techniques that require both presence and absence data. They have been used extensively in species distribution modelling (e.g. Guisan et al., 1998; Franklin, 1998; Lehmann, 1998; Guisan et al., 2002; Miller & Franklin, 2002; Bio et al., 2002; Granadeiro et al., 2004; Bustamante & Seoane, 2004; Olivier & Wotherspoon, 2006) because of their strong statistical foundation and ability to realistically model ecological relationships (Guisan et al., 2002). Both make use of the logit transformation (logistic regression) when modelling a binary (presence/absence) response. GAMs use non-parametric, data-defined smoothers to fit non-linear functions and, as a result, are more capable of modelling complex response curves than GLMs, which only fit parametric terms (Yee & Mitchell, 1991).

A disadvantage of using GLMs and GAMs is that model coefficients are difficult to interpret, especially if interactions are present. In addition, as far as logistic regression is concerned, there are few diagnostics for choosing variable transformations and no true goodness of fit test (Chan & Loh, 2004). These problems have been overcome by Logistic Regression Tree Modelling (LRT, Chan & Loh, 2004). This method recursively partitions the presence-absence data and fits a different logistic regression at each partition. This allows complex nonlinear features of the data to be modelled without requiring variable transformations. The binary tree that results from the partitioning process is pruned to minimize a cross-validation estimate of the predicted deviance. This obviates the need for a formal goodness-of-fit test. The LRT model is especially easy to interpret if a simple linear logistic regression is fitted to each partition, because the tree structure and the set of graphs of the fitted functions in the partitions comprise a complete visual description of the model. Thus the model not only provides a prediction formula, but also conveys visually interpretable information about the roles of the predictor variables. In addition, interactions between predictor variables are automatically modelled in the tree structure. Complexity in the data is shared between the tree structure and the regression models in the nodes. This division of labor helps to keeps LRT models simple and easy to interpret.

Methods that require both presence and absence records can be used when absence data are not available by generating "pseudo-absences" (Zaniewski et al., 2002) and using them in the model as absence data for the target species. One way to choose "pseudo-absences" is to generate them at random over the study area (Hirzel et al., 2001; Zaniewski et al., 2002). However, this method runs a risk of generating absences in areas that are, in fact, favourable to the target species. This problem is particularly prevalent when modelling the distribution of rare species (Engler et al., 2004) or in situations where presence data is obtained from a few individuals in the population. To reduce the number of false absences, Engler et al. (2004) proposed a method that uses ENFA to weight the random generation of "pseudo-absences". In this method, "pseudo-absences" are randomly generated only in the parts of the study site that are predicted to be unsuitable by ENFA. Engler et al. (2004) showed that this method produced significantly better results than randomly generating "pseudo-absences" over the entire study site.

The purpose of this study was to test whether the short-term rate of protein intake and distance from surface water are important determinants of habitat selection by elephants. The nature of the interaction between these two predictor variables was of particular interest and because LRT models are easier to interpret when interactions are present than GLMs or GAMs (Chan & Loh, 2004), LRT was chosen as the modelling technique for the study.

Absence data were not available, so it was necessary to generate "psuedo-absences" for use in LRT. Furthermore, presence data for elephants were collected from a few individuals (see section 5.3.2) and, as a result, presence data were not recorded for many areas where elephants were known to occur. Consequently, the method developed by Engler et al. (2004) of weighting the random generation of "pseudo-absences" using an initial habitat suitability (HS) map derived from presence-only data, was used to reduce the number of false absences. However, ENFA could not be used to weight "pseudo-absences" because the requirements of ENFA of normally distributed predictors and unimodal response curves were not met by the data. Consequently, MAXENT as opposed to ENFA models were used to weight the random generation of "pseudo-absences". MAXENT estimates the distribution of the target species by finding the distribution of maximum entropy (i.e. closest to uniform) subject to the constraint that the expected value of each environmental variable (or its transform and/or interactions) under this estimated distribution matches its empirical average (Phillips et al., 2006). MAXENT can model complex response curves and does not require normally distributed predictors.

To integrate choice at multiple spatial scales and also functionally represent trade-off between the rate of protein intake and distance from water, a two-stage approach was used to model monthly habitat selection by elephants. In the first stage, the foraging choices made by elephants at the plant part, individual plant and plant community scales were functionally integrated into a single measure of potential profitability by modelling the short-term rate of protein intake using the mechanistic ingestion model developed in chapter 4. In the second stage, LRT modelling was used to relate monthly presence/"pseudo-absence" data of adult bulls and family units to the rate of protein intake and the cost distance from drinking water.

5.3.2. *Collection of response data and generation of predictor maps*

Elephant presence data and generation of "pseudo-absences"

To collect presence data for elephants, 3 adult bulls and 2 adult cows were fitted with Televilt GPS Simplex collars between the 27th of September and the 5th of October 2001. The collared cows were from the two breeding herds at Malilangwe and, consequently, complete coverage of the distribution of family units was achieved. The collars were programmed to record positions at hourly intervals because gaining a representative sample of space use by the collared animals and sampling habitat use systematically through time were considered more important than ensuring that successive observations were statistically independent (McNay et al., 1994; Otis & White, 1999; Poole & Stuart-Smith, 2006). The positions saved on the collars were downloaded every month on a radio link using a Televilt RX900 receiver and a 4-element Yagi antenna.

On the 12th of November 2001, one of the collared bulls left the study area and travelled approximately 80 km south to the Mabalauta region of the Gonarezhou National Park (Figure 5.1). He returned to the study area on the 18th of January 2002. To prevent further loss of data, the collar was removed from this animal and was fitted to another, hopefully more sedentary, adult bull on the 28th of February 2002.

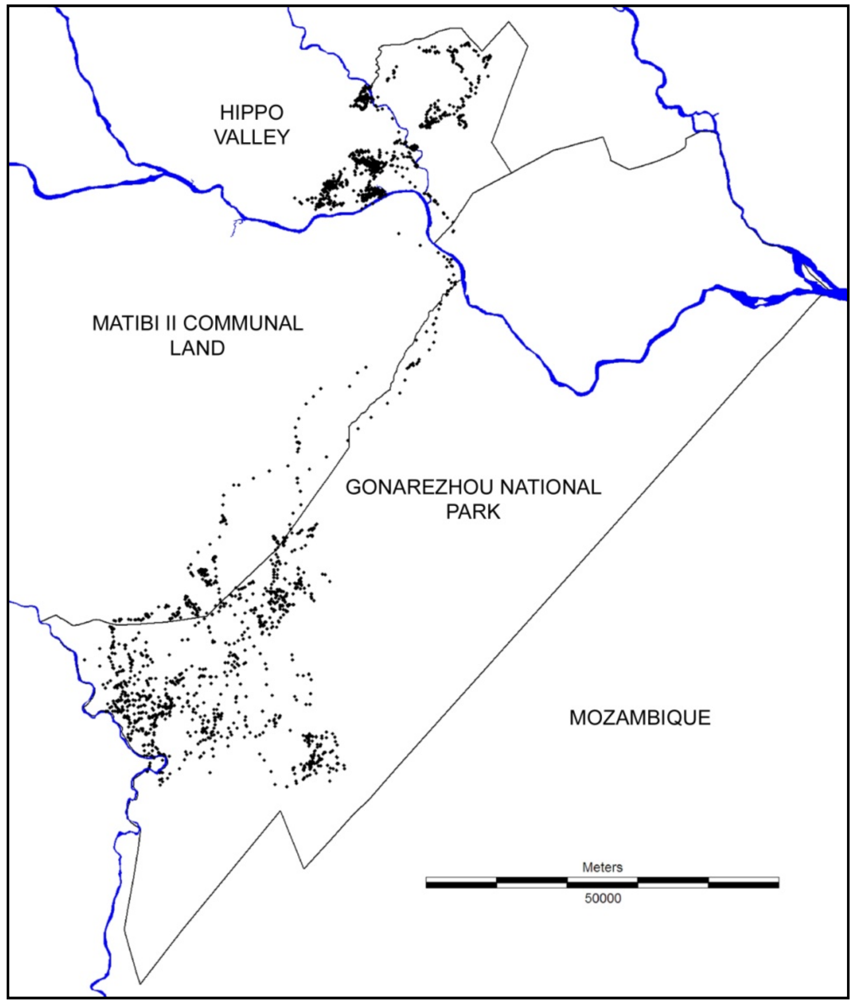


Figure 5.1 Map showing GPS position data (•) from the collared adult bull that made a long distance movement into the southern region of the Gonarezhou National Park between 4th October 2001 and 11th February 2002.

At collar failure, the elephants were immobilised, and the collars removed. The saved positions were downloaded and stored, along with their associated date, time, and sex of the collared animal, in a spatial database using Cartalinx GIS software (Hagan & Eastman, 1998). The objective was to estimate the population level response to variation in habitat and, consequently, the position data from the individual animals were pooled. The pooled data were then filtered by sex and date to produce monthly presence data sets for adult bulls and family herds.

Although no attempt was made to measure the effect of shade on habitat selection, observation of elephants indicated shade to be an important constraint to habitat selection. In general, between 10 am and 3 pm elephants sought shade and avoided open areas. Consequently, to control for the effect of shade, only positions recorded between 4 pm and 9 am were used in the analysis.

Due to the fact that the collars only collected data on the presence of elephants, and because LRT models require both presence and absence data, generation of “pseudo- absences” (Zaniewski et al., 2002; Engler et al., 2004; Pearce & Boyce, 2006; Olivier & Wotherspoon, 2006) was necessary. To do this, MAXENT was used to produce monthly HS maps for adult bulls and family units from the presence-only data, using the short-term rate of protein intake and cost distance from water as predictor variables. Each HS map was reclassed using Idrisi Kilimanjaro GIS software (Eastman, 2003) to a boolean suitability map (suitable = 1, unsuitable = 0) by setting a cutoff such that 95 % of the presence points were included in the area assigned a value of 1. A 95 % cutoff was chosen so as to reduce the effect of unrepresentative occurrences that do not convey reliable information about habitat selection (Titeux, 2006). “Psuedo-absences” were then generated for each boolean HS map by selecting sample points, of equal number to the presence points, within the unsuitable portion of the study site, using a stratified random sampling strategy. The “pseudo-absence” and presence points were then combined to create monthly presence/absence datasets for adult bulls and family units.

Average total short-term rate of protein intake

The diet of elephants is most often composed of a mixture of food types, with the proportion of each type changing seasonally (Field, 1971; Wyatt & Eltringham, 1974; Williamson, 1975; Guy, 1976; de Boer et al., 2000; Osborn, 2004). For this reason, the overall potential profitability of the food resource in each land unit was represented as the sum of the short-term rates of protein intake from each food type. It should be noted that this index does not represent the actual short-term rate of protein intake realised by elephants when feeding in a particular land unit but rather a measure of the potential profitability of the food available in a land unit relative to the others.

Maps depicting the average total short-term rate of protein intake by adult bulls were constructed for each month of the study period by combining the daily coverages of short-term rate of protein intake for each food type that were constructed in Chapter 4 according to the following equation:

$$I_{AvTot,bull} = \frac{\sum_{i=1}^{n} I_{i,ggrass,bull} + I_{i,mgrass,bull} + I_{i,gforb,bull} + I_{i,gleaf,bull} + I_{i,cbark,bull}}{n}$$

where $I_{AvTot,bull}$ is the monthly average total short-term rate of protein intake (g/s) achieved by bulls, $I_{i,ggrass,bull}$ is the short-term rate of protein intake (g/s) achieved by bulls when feeding on green grass on the i^{th} day of the month, $I_{i,mgrass,bull}$ is the short-term rate of protein intake (g/s) achieved by bulls when feeding on mixed grass on the i^{th} day of the month, $I_{i,gforb,bull}$ is the short-term rate of protein intake (g/s) achieved by bulls when feeding on green forbs on the i^{th} day of the month, $I_{i,gleaf,bull}$ is the short-term rate of protein intake (g/s) achieved by bulls when feeding on green leaf on the i^{th} day of the month, $I_{i,cbark,bull}$ is the short-term rate of protein intake (g/s) achieved by bulls when feeding on canopy bark on the i^{th} day of the month, and n is the number of days in the month.

Monthly maps depicting the average total short-term rate of protein intake by members of family units were constructed using the same equation except that the daily intake maps for adult bulls were replaced with those for members of family units.

Sex related differences in the average total rate of short-term rate of protein intake over the study area were measured for each month of the study period by subtracting the map depicting the rate of protein intake achieved by adult bulls from that of cows using the IMAGEDIFF module of Idrisi Kilimanjaro GIS software (Eastman, 2003).

Cost distance from drinking water

Sources of drinking water were divided into point sources, which included pans, springs and dams, and linear sources, which included drainage lines and rivers. The co-ordinates of all significant point sources were mapped from a georeferenced digital aerial photographic mosaic and the boundaries of large dams were mapped using a GPS. The co-ordinates and boundaries were used to create a reference image depicting the spatial positions of the point water sources. Each point water source was visited as soon as possible after rain or otherwise at 2 to 3 week intervals, and the percent full ranked using an eight-point scale (0 %; 1 %; 2-10 %; 11-25 %; 26-50 %; 51-75 %; 76-95 %; 96-100 %). If it was thought the water would dry up before the next visit, the date at which the water was predicted to dry up was estimated, taking into account the prevailing climatic conditions. Because it was often logistically impossible to visit each source immediately after rain, the date of water input was extracted from the daily rainfall surfaces created in chapter 4. The data were used to construct a time series for each point source depicting the percent full at intervals during the study period. To estimate the percent full for each source on a daily basis, a smoothing spline regression was fitted through the observations for each source using the procedures of Kyplot (KyensLab Inc., 2002). To create a daily presence/absence record of water available to elephants, the continuous time series for each source was reclassed to create a boolean dataset by using a cutoff of 5 % full for pans and springs, and 0.5 % cutoff for the larger dams. Below the cutoff water was deemed unavailable to elephant and above the cutoff it was deemed available. Using Idrisi 32 GIS software (Eastman, 2001) the boolean datasets were used to create daily attribute values files that were assigned to the point source reference image to create daily coverages depicting the availability of water in point sources.

To record availability of water in the linear sources, the length of the important rivers and drainage lines was traversed on foot at the middle of each month and the presence of drinking water for elephants was recorded by saving a track on a GPS. The tracks were imported into Cartalinx GIS software (Hagan & Eastman, 1998), which was used to create monthly maps depicting availability of drinking water in the linear sources. Using Idrisi 32 GIS software (Eastman, 2001), the daily point source maps were added to the respective monthly maps of linear sources to create daily images depicting the availability of water in both the point and linear sources.

All parts of the study area were not equally accessible to elephants because of the presence of impassable cliffs in the sandstone hills and along parts of the Chiredzi River. For this reason, it was decided to represent distance from drinking water as a travel cost that took into account the presence of impassable barriers. To do this a slope image of the study area was created from a 5 m digital elevation model (DEM) that was created by interpolating between contours digitised at 10 m intervals. Barriers to movement were mapped from the slope image by defining impassable barriers as areas with a slope greater than 70 %. The 70 % cut-off was chosen by extracting the slope of known barriers to movement from the DEM. Daily cost distance from water maps were then created by running the cost distance module of Idrisi 32 GIS software (Eastman, 2001) using the daily maps depicting the presence of water as feature definition images and the map of the impassable barriers as a friction surface (impassable barriers were assigned an arbitrary friction value of 1000 and all other areas were assigned the base friction value of 1). Distances were measured according to the minimum amount of friction that must be accumulated to move from a given cell to the nearest source of drinking water. Movement was constrained to 8 possible directions from any cell, with diagonal movements producing a cost of 1.41 times the friction value. Monthly maps of the average cost distance from water were created by adding the daily maps for each month and dividing the result by the number of days in the month. It should be noted that cost distance is a relative measure and is therefore without units.

5.3.3. *Model fitting*

The LOTUS (Logistic Tree with Unbiased Selection) algorithim (Chan & Loh, 2004) was used to fit LRT models to the monthly data sets for adult bulls and family units. It is critically important for a classification tree or regression tree method to be free of bias when selecting split variables, otherwise misleading conclusions concerning the effects of predictor variables may result. LOTUS has the advantage of protecting the integrity of inferences drawn from the tree structure by using trend-adjusted chi-square tests to control bias in variable selection at the intermediate nodes.

LOTUS allows the user to choose one of three roles for each quantitative predictor variable. The variable can be restricted to act as a regressor in the fitting of the logistic models at the nodes, or be restricted to compete for split selection, or be allowed to serve both functions. In this analysis, the short-term rate of protein intake and cost distance from water were both set to participate in split selection during tree construction and also to serve as possible regressors in the logistic models at the nodes.

To keep the tree structure simple and to ensure non-trivial logistic models at the leaf nodes, the smallest number of cases permissible in a leaf node from each class of the dependent variable was set to 50. In other words, a node could not be split if at least one of its two classes contained fewer than 50 cases. The model trees were pruned to minimize a 10-fold cross-validation estimate of the predicted deviance, using a standard deviance setting of 1 (following Breiman et al., 1984).

To permit the estimated logistic function in each node to be visualized against a plot of the selected predictor, and to reduce the chance of encountering problems with complete or quasi-complete separation of the data, a best simple linear logistic regression model was fitted to the data in each node (Chan & Loh, 2004). In this method, the logistic models at each node have a single predictor, which is chosen as the variable that yields the smallest model deviance per degree of freedom.

5.3.4. *Model evaluation*

The LRT models were evaluated by calculating Cohen’s kappa (Cohen, 1960) and the area under the curve (AUC) of receiver operating characteristic (ROC) plots (Hanley & McNeil, 1982; Zweig & Campbell, 1993; Obuchowski, 2003) using the procedures of Systat 9 (SPSS, 1998).

Cohen’s kappa assesses the extent to which models correctly predict occurrence at rates that are better than chance expectation. The likelihood of occurrence predicted by the logistic regression models at the leaf nodes ranges from a possible low value of 0 to a possible high value of 1. Consequently, when calculating the kappa statistic, it is necessary to decide on a threshold for assigning predicted probabilities to either a presence or absence category. In this study, a threshold of 0.5 was used (following Franklin, 1998; Manel et al., 2001). Kappa values of 0.0 – 0.4 are considered to indicate slight to fair model performance, values of 0.4 – 0.6 moderate, 0.6 – 0.8 substantial, and 0.8 – 1.0 almost perfect (after Landis & Koch, 1977).

A problem with the kappa statistic is that it is reliant on a cut-off threshold, which introduces a potential source of bias (Liu et al., 2005). The ROC avoids this problem by evaluating the proportion of incorrectly and correctly classified predictions over a continuous range of probability cut-off levels (Zweig & Campbell, 1993; Obuchowski, 2003). To calculate a ROC curve, sensitivity and specificity are evaluated at different probability cut-off levels within the data to produce pairs of sensitivity/specificity values. Sensitivity is defined as the probability that a model yields a positive prediction where an animal actually occurs, whereas, specificity is the probability that a low score is predicted where no animal is observed. As the cut-off threshold is varied, different proportions of positive and negative cells are included. Plotting sensitivity as a function of (1 – specificity) for each threshold yields a ROC curve. The area under the ROC curve (AUC) can be used as an assessment of model performance (Cumming, 2000).

The ROC approach also has the advantage that it does not place restrictive assumptions on the distribution of response variables, with analyses based on the normal, logistic, negative exponential, chi-square, Poisson, and gamma distributions being possible. It is also possible to calculate ROC using a nonparametric model, which was the method employed in this study.

Good model performance is characterized by a curve that maximizes sensitivity for low values of (1 – specificity), in other words when the curve passes close to the upper left corner of the plot. High performance models are indicated by high AUC values. Usually, AUC values of 0.5 – 0.7 are taken to indicate low accuracy, values of 0.7 – 0.9 indicate useful applications, and values >0.9 indicate high accuracy (Swets, 1988).

5.3.5. *Spatial predictions of LRT models*

Maps depicting the probability of occurrence of adult bulls and family units were developed for each month of the study period by combining maps of the predictor variables according to the formulae of the LRT models using Idrisi Kilimanjaro GIS software (Eastman, 2003).

Several studies have shown sex related differences in habitat selection by elephants (Stokke, 1999; Stokke & du Toit, 2000; Stokke & du Toit, 2002; Shannon et al., 2006; Smit et al., 2007). Consequently, to determine whether sexual segregation was predicted by the monthly LRT models, maps depicting the degree of spatial segregation between adult bulls and family units were developed by subtracting the probability of occurrence of family units from that of adult bulls using the IMAGEDIFF module of Idrisi Kilimanjaro GIS software (Eastman, 2003). The pixels in the resulting images had scores ranging from a minimum of -1, indicating a high probability of occurrence by family units only, to a maximum of +1, indicating a high probability of occurrence by only adult bulls. A score of 0 indicated equal probability of occurrence by both adult bulls and family units.

5.4. Results

5.4.1. *Presence data*

The total number of positions recorded within the study area between 4 pm and 9 am was 9674 from the 3 collared bulls and 7561 from the 2 collared cows. The number and distribution of presence records from adult bulls and family units that were used in the LRT models are shown for each month of the study period in Figure 5.2 and Figure 5.3 respectively. The low number of positions recorded for adult bulls in June and December 2002, and January, February and March 2003 was due to emigration of the collared bulls from the study area during these months (Figure 5.4). In contrast, the family units only left the study area on a few occasions during the study period (Figure 5.5). The collar on one of the cows stopped working on the 6th of January 2003. Consequently, most of the positions for cows from January 2003, and all of the positions from February and March 2003 were from a single family unit.

5.4.2. *Total average rate of short-term protein intake*

There was considerable spatio-temporal variation in the average total rate of short-term protein intake for both adult bulls and cows (Figure 5.6 and Figure 5.7 respectively). The temporal trend for both sexes was a decrease in the average total rate of protein intake from the 12th of March to mid September 2002, followed by an increase up to the end of the study period on the 10th of March 2003.

Sex related differences in the average total rate of protein intake were small during the cool dry (March to July 2002) and wet (January to March 2003) seasons, and marked during the hot dry season (August to November 2002) when adult bulls achieved considerably higher protein intake rates relative to cows over a large portion of the study area (Figure 5.8). Differences were generally due to the ability of cows to achieve considerably higher rates of protein intake than bulls when feeding on green forbs, and the ability of bulls to achieve higher rates relative to cows when feeding on leaves, grass and bark. The markedly higher rate of protein intake achieved by adult bulls relative to cows during the hot dry season was largely due to curtailment of the total rate of protein intake by cows as a result of the scarcity of green forbs during this period, although differences in the rate of intake from other food types also contributed.

5.4.3. *Cost distance from water*

Presence of surface water was monitored at a total of 328 point sources (springs, pans and dams) and along 4 rivers. The spatio-temporal variation in cost distance from surface water during the study period is shown in Figure 5.9. The temporal change in the average cost distance from water over the study area was characterised by steep declines associated with rainfall events, and periods of gradual increase between rainfall events as surface water slowly dried up.

In general, the study area was well endowed with surface water, with the northern, western and southern parts being particularly well supplied relative to the south-eastern region.

5.4.4. *Logistic regression tree models*

Visual representations of the monthly LRT models are given for adult bulls in Figure 5.10 to Figure 5.13, and for family units in Figure 5.14 to Figure 5.16. Despite the models being simple (only 2 – 5 terminal nodes), model performance was high to very high for all months of the study period for both adult bulls ($0.794 \leq \text{Kappa} \leq 0.889$; $0.938 \leq \text{AUC} \leq 0.971$) and family units ($0.728 \leq \text{Kappa} \leq 0.838$;

$0.890 \leq AUC \leq 0.969$). The explanatory power of the models for adult bulls was generally higher than that for family units.

The high explanatory power of the models indicated that the distribution of elephants within the study area between 4 pm and 9 am was strongly influenced by the total rate of short-term protein intake and cost distance from water. In almost all cases, the response to the predictor variables in both the tree structure of the models and in the logistic regressions at the terminal nodes matched theoretical predictions (see chapter 1), with cost distance from water being negatively correlated and the total short-term rate of protein intake being positively correlated with the probability of occurrence. A notable exception to this rule occurred for adult bulls in April 2002, where probability of occurrence was negatively correlated with total short-term rate of protein intake for the logistic models at the leaf nodes.

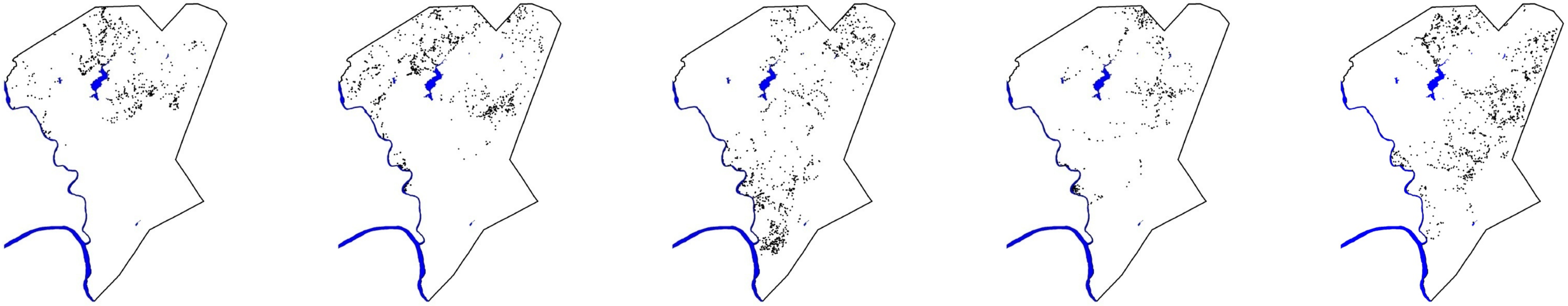
Trade-off between distance from water and rate of protein intake was evident during May, June, September, and October 2002 for adult bulls and June, August, September and November 2002 for family units. Trade-off was manifested as a willingness of elephants to travel far from water if returns in terms of protein intake were high but not if returns were low. However, this tendency could not be taken as a general rule because in some months it was not evident.

5.4.5. *Sex related differences in habitat selection*

Sex related differences in model structure were apparent. For adult bulls, cost distance from water was the dominant predictor variable used to partition data at the intermediate nodes during dry months (March, April, May, August, September and October 2002), while average total short-term rate of protein intake was the dominant split variable during wet months (June, July, November, and December 2002). In contrast, average total short-term rate of protein intake was the dominant split variable for family units for all months except January 2003, which was the wettest month modelled for cow herds.

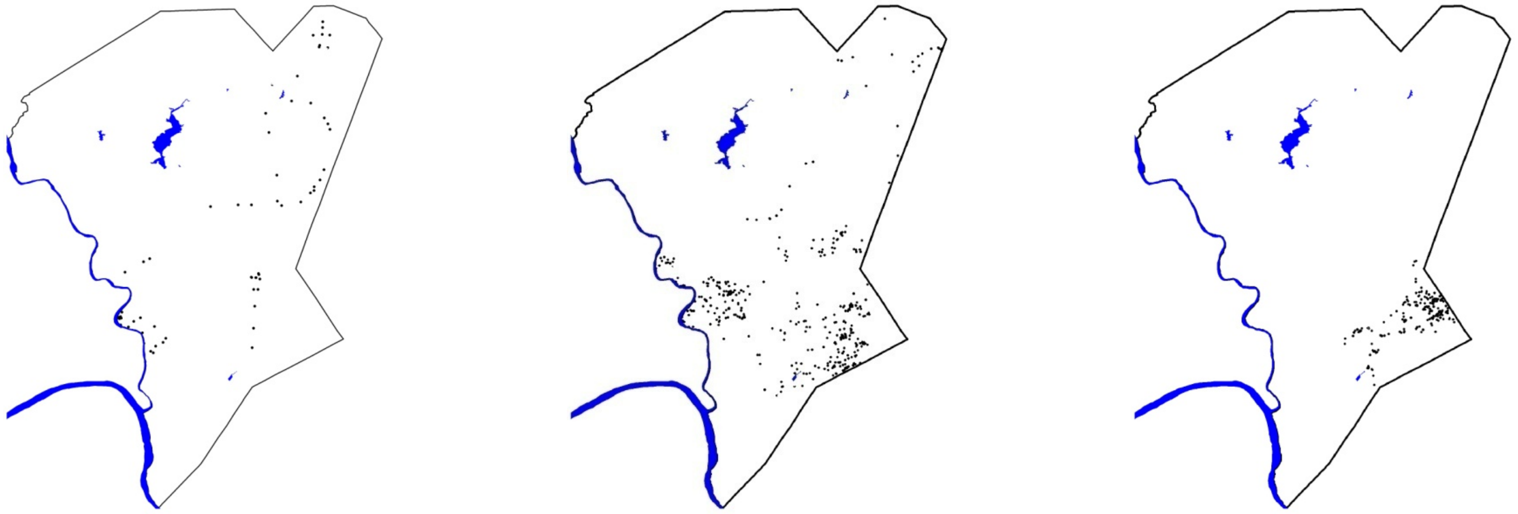
The sex related differences in choice of split variable reflected differences in the relative importance of the two predictors for determining the distribution of adult bulls and family units. For the greater part of the annual cycle, the distribution of adult bulls was more strongly influenced by cost distance from water than by average total short-term rate of protein intake. During the wet months, however, the roles of the predictor variables were reversed with average total rate of protein intake having the stronger influence. In contrast, the distribution of family units was most strongly influenced by average total rate of protein intake, with cost distance from water only becoming the dominant variable during the wettest month (January 2003). It should be made clear, however, that although seasonal changes in the relative importance of the two predictor variables were apparent, both variables were important predictors of elephant distribution throughout the year.

The monthly spatial pattern of habitat selection predicted by the LRT models is shown for adult bulls and family units in Figure 5.17 and Figure 5.18 respectively. Sexual segregation was predicted for all months (Figure 5.19), with the greatest spatial separation between adult bulls and family units being predicted during the cool and hot dry seasons (July, August, September, and October 2002) and during December 2002, which was characterised by a period of inter rainy season drought. Segregation was largely due to sex related differences in the spatial pattern of average total rate of short-term protein intake and differences in the relative importance of the two predictor variables in determining the probability of occurrence.



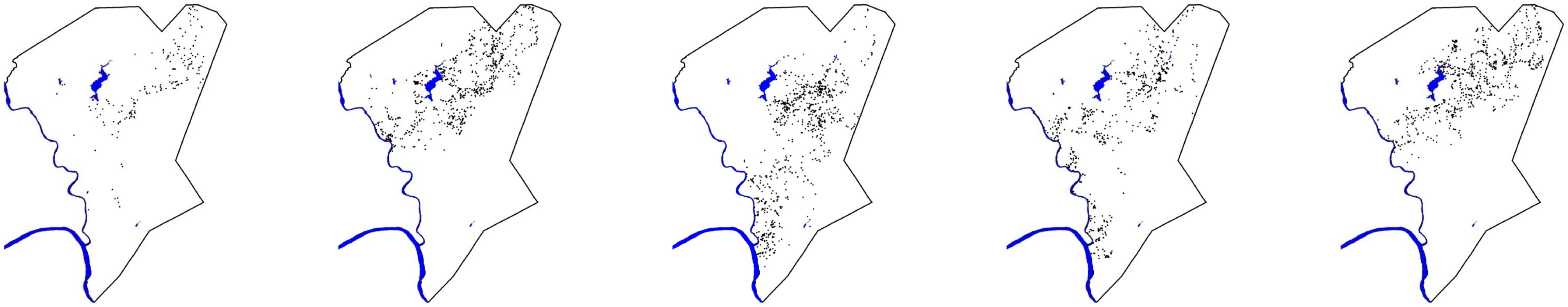
12th – 31st March 2002 (633) April 2002 (963) May 2002 (998) June 2002 (423) July 2002 (1109)

August 2002 (1100) September 2002 (1045) October 2002 (1123) November 2002 (1151) December 2002 (516)

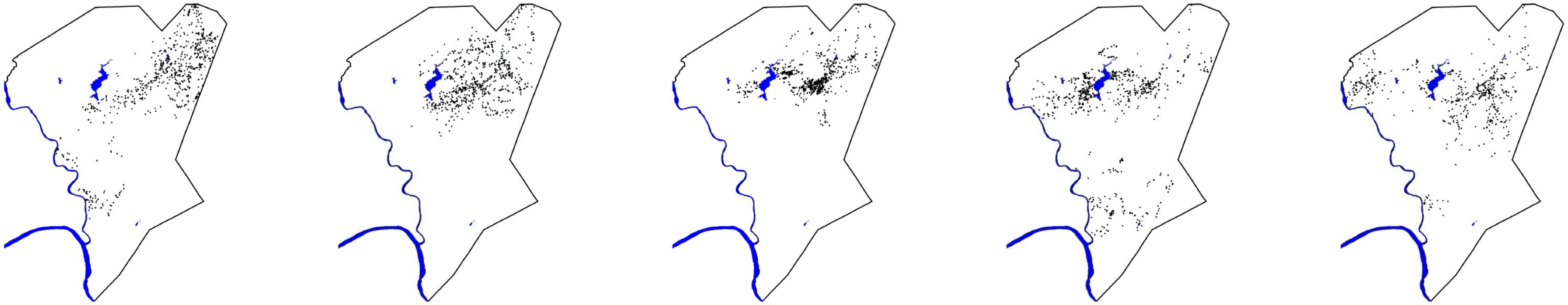


January 2003 (65) February 2003 (368) 1st – 10th March 2003 (180)

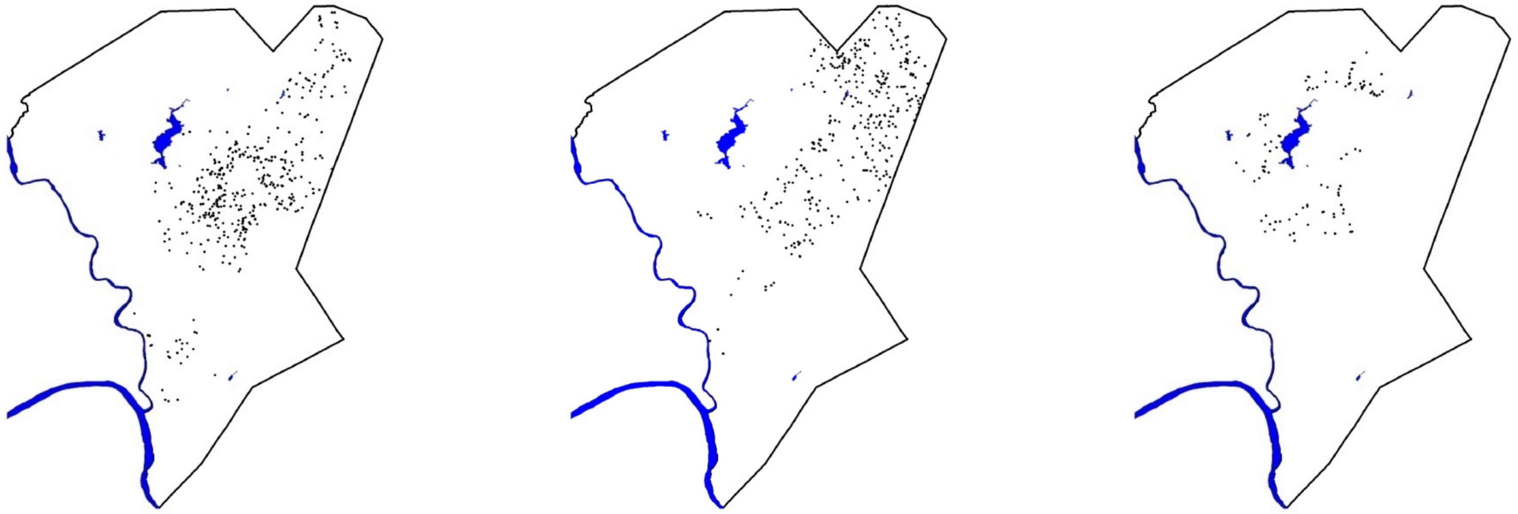
Figure 5.2 Monthly position data (•) collected in the study area between 4 pm and 9 am by GPS collars fitted to 3 adult bulls. The number of positions recorded for each month is given in parentheses below each image. The low number of positions recorded in June and December 2002, and January, February and March 2003 was due to emigration of the collared individuals from the study area.



12th – 31st March 2002 (180) **April 2002 (735)** **May 2002 (792)** **June 2002 (640)** **July 2002 (742)**

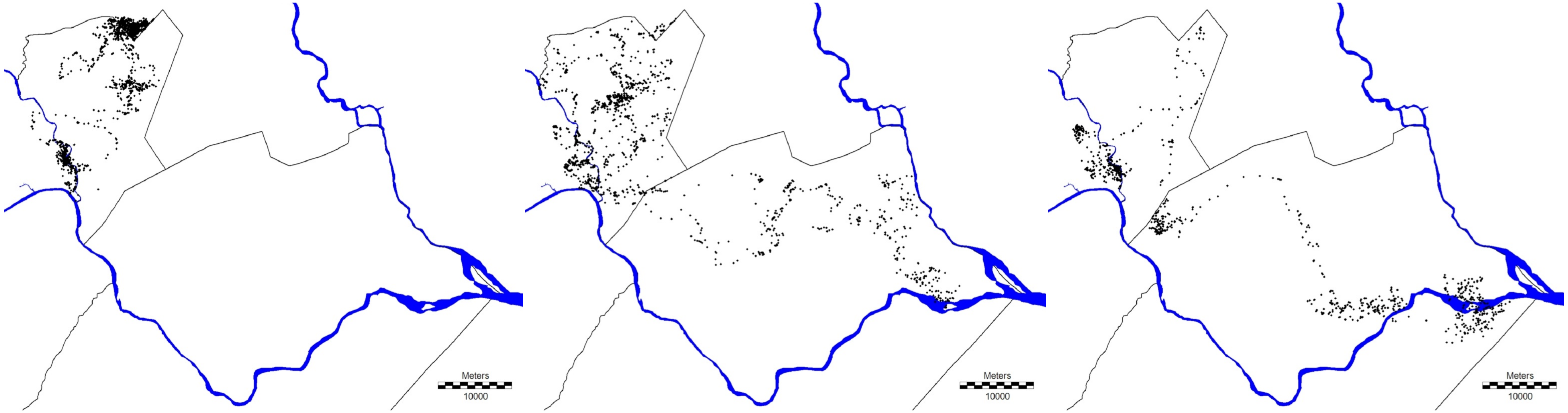


August 2002 (746) **September 2002 (760)** **October 2002 (750)** **November 2002 (710)** **December 2002 (582)**

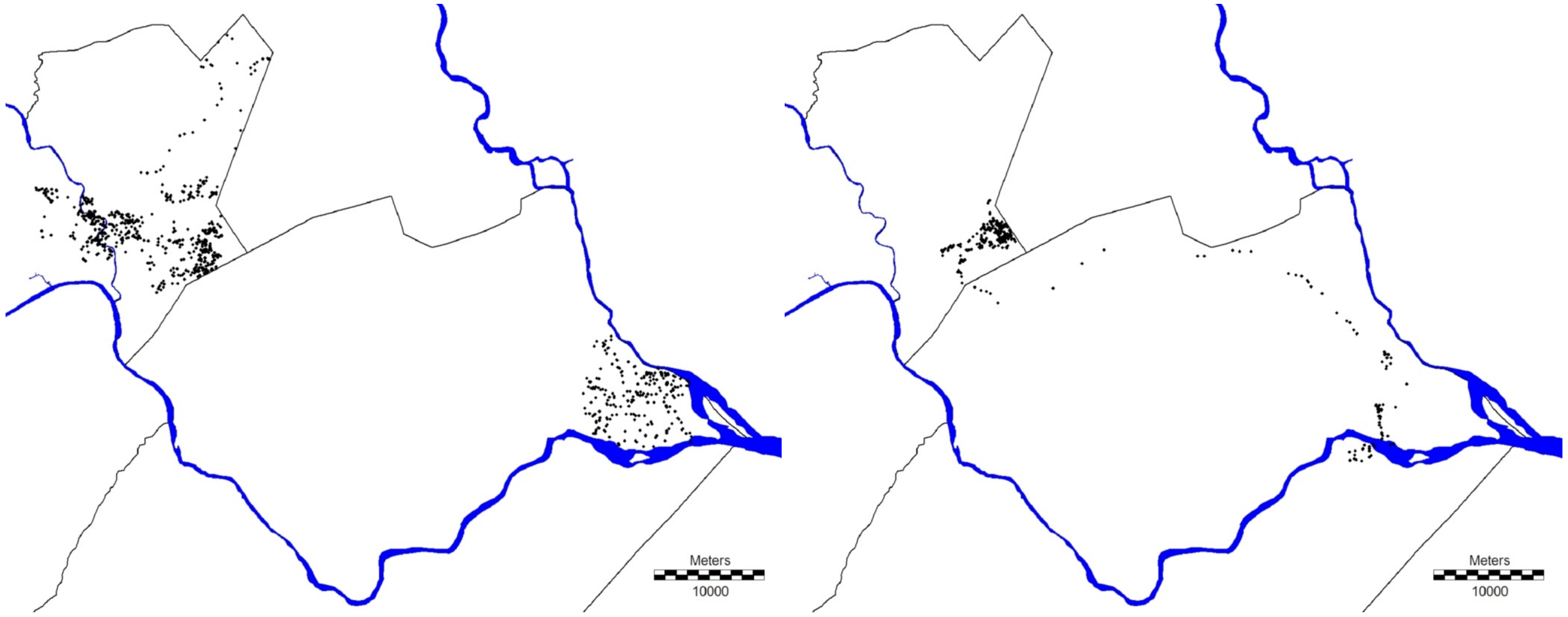


January 2003 (422) **February 2003 (396)** **1st – 10th March 2003 (106)**

Figure 5.3 Monthly position data (•) collected in the study area between 4 pm and 9 am by GPS collars fitted to 2 adult cows from separate family units. The number of positions recorded for each month is given in parentheses below each image. One of the collars stopped working on the 6th of January 2003. Consequently, most of the positions for January 2003, and all of the positions for February and March 2003 are from a single family unit.

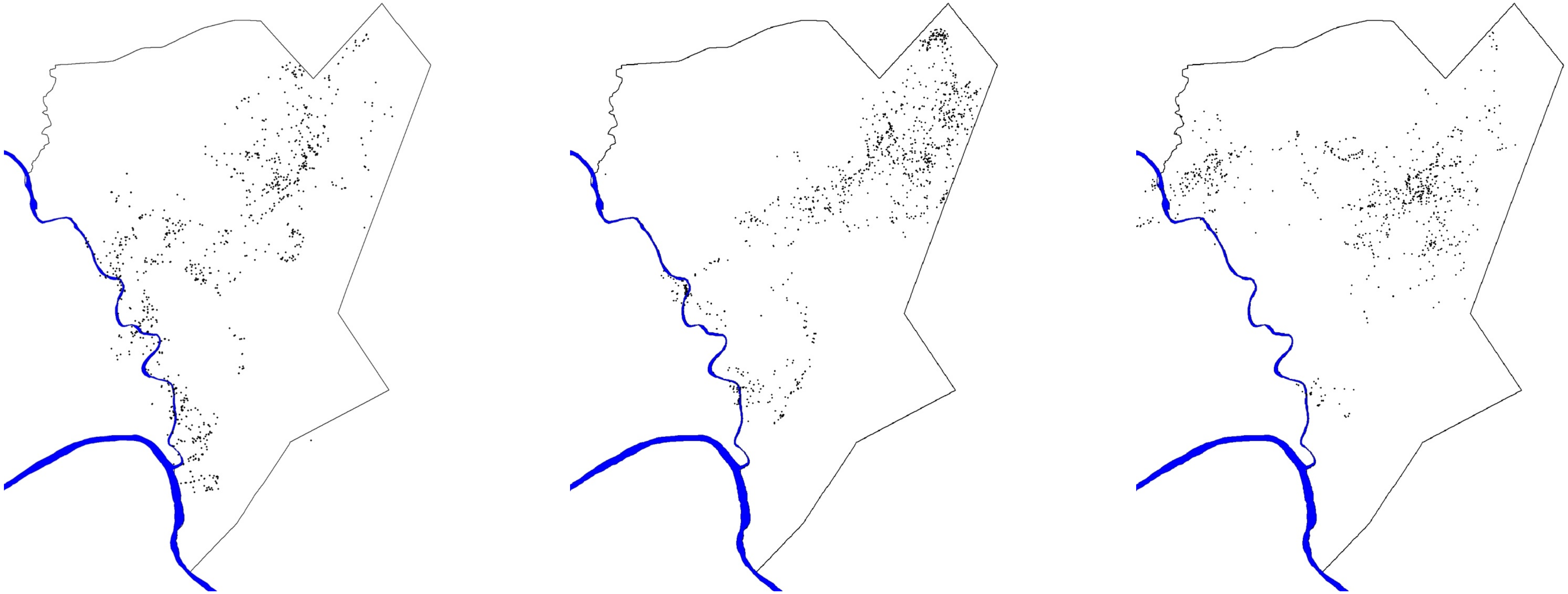


June 2002 December 2002 January 2003



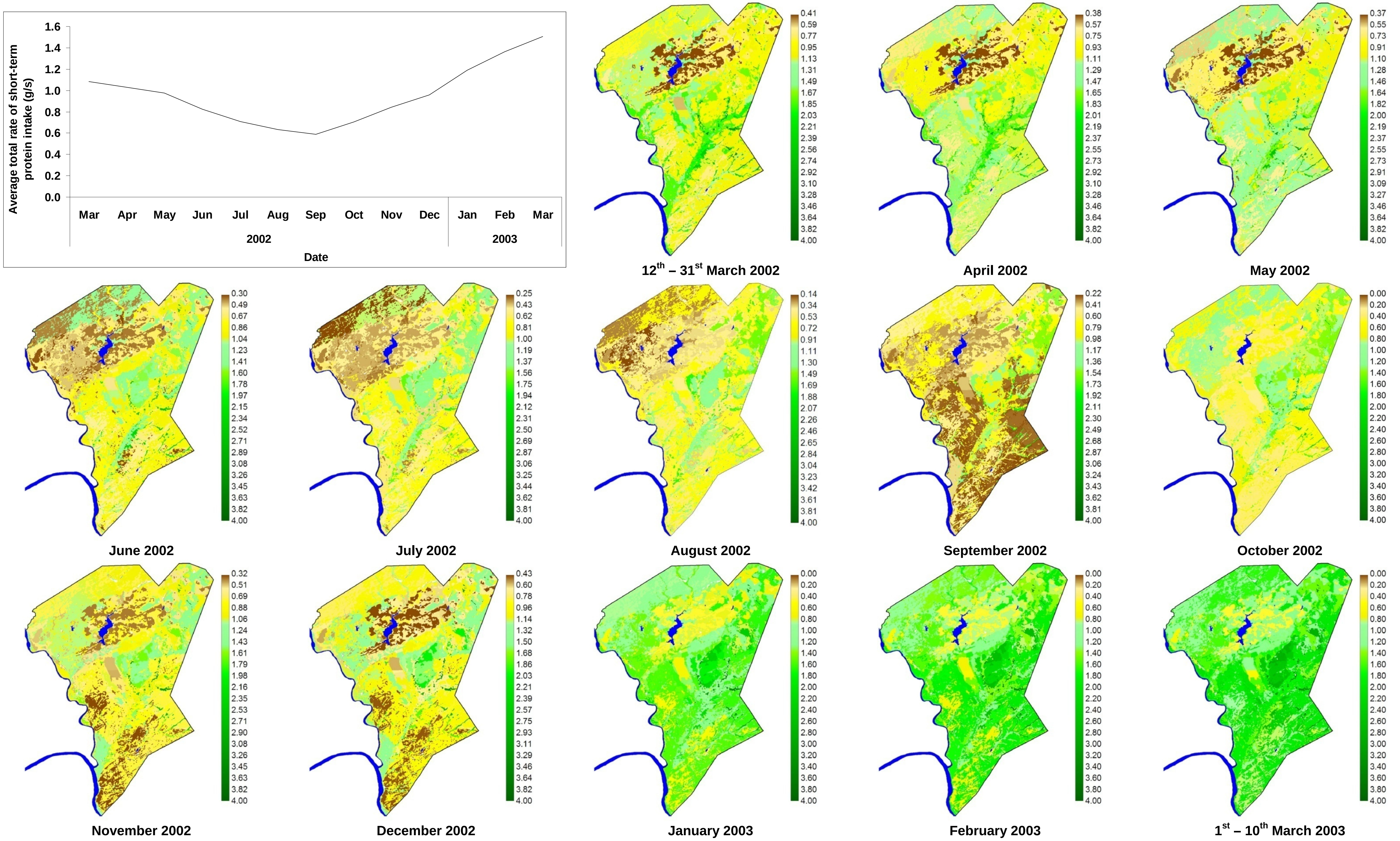
February 2003 March 2003

Figure 5.4 Maps showing GPS position data (•) from collared adult bulls for the months during which the collared individuals left the study area.



June 2002 August 2002 December 2002

Figure 5.5 Maps showing GPS position data (•) from collared adult cows for the months during which the collared individuals left the study area.



12th – 31st March 2002

April 2002

May 2002

June 2002

July 2002

August 2002

September 2002

October 2002

November 2002

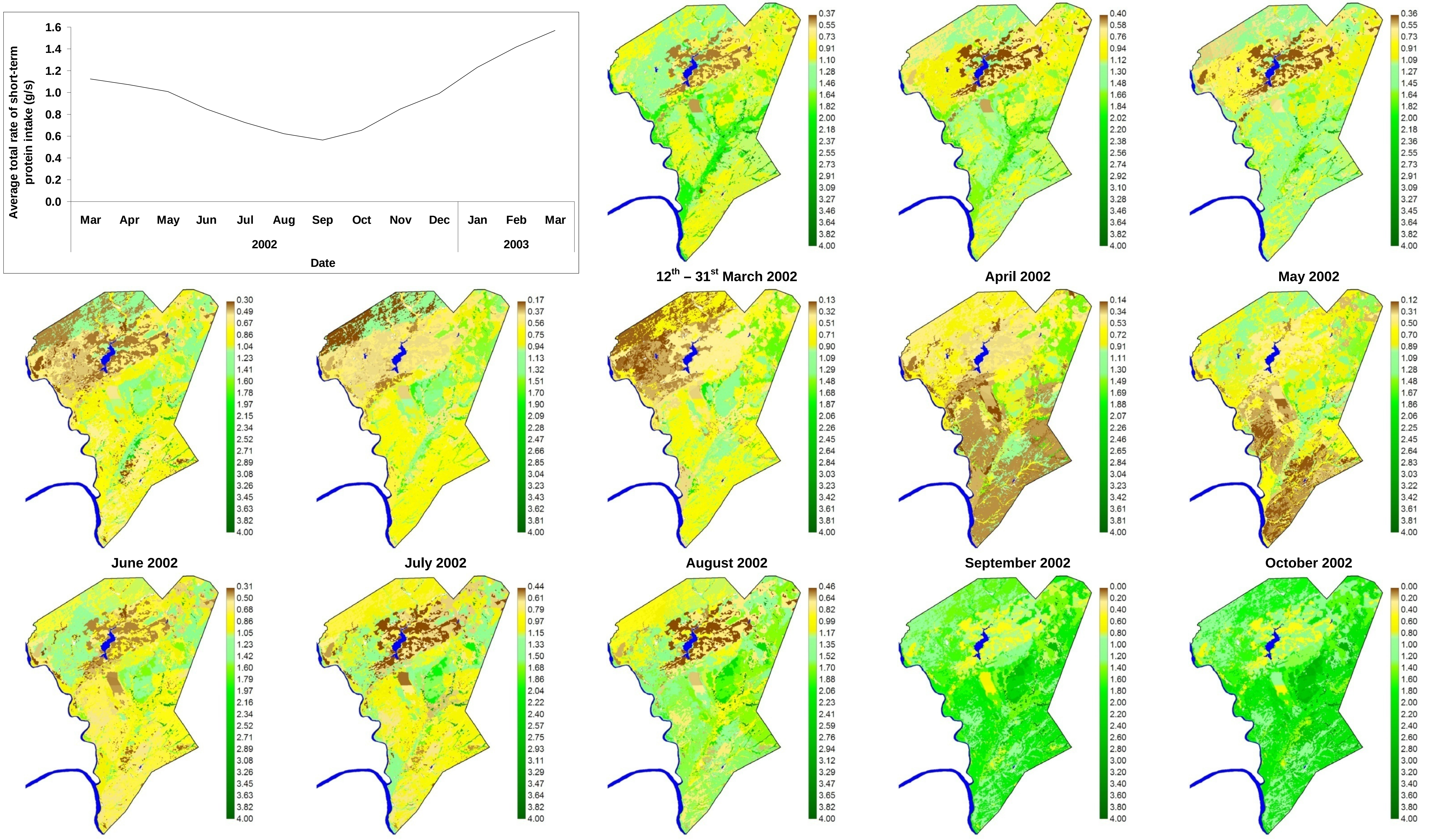
December 2002

January 2003

February 2003

1st – 10th March 2003

Figure 5.6 Chart depicting the temporal variation in the average total short-term rate of protein intake (g/s) for adult bulls over the study period, and maps showing the spatial variation in the average total short-term rate of protein intake (g/s) over the study area for adult bulls for each month of the study period.



12th – 31st March 2002

April 2002

May 2002

June 2002

July 2002

August 2002

September 2002

October 2002

November 2002

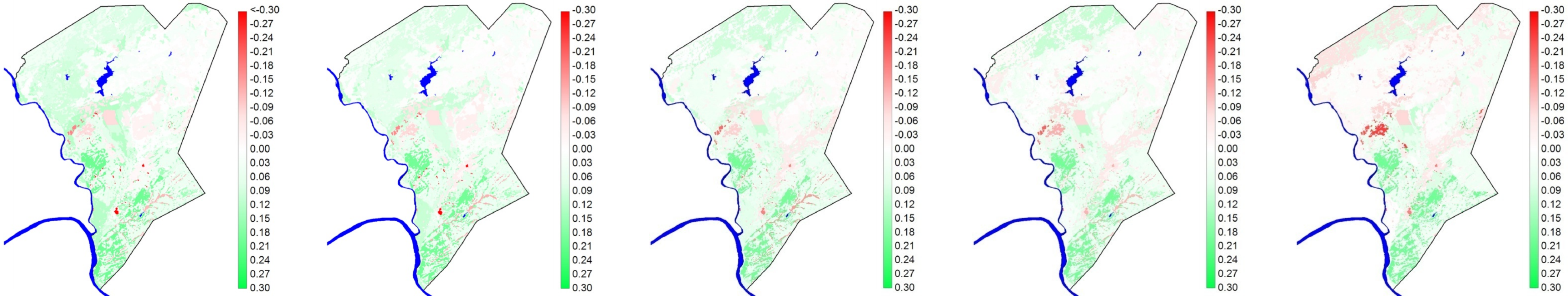
December 2002

January 2003

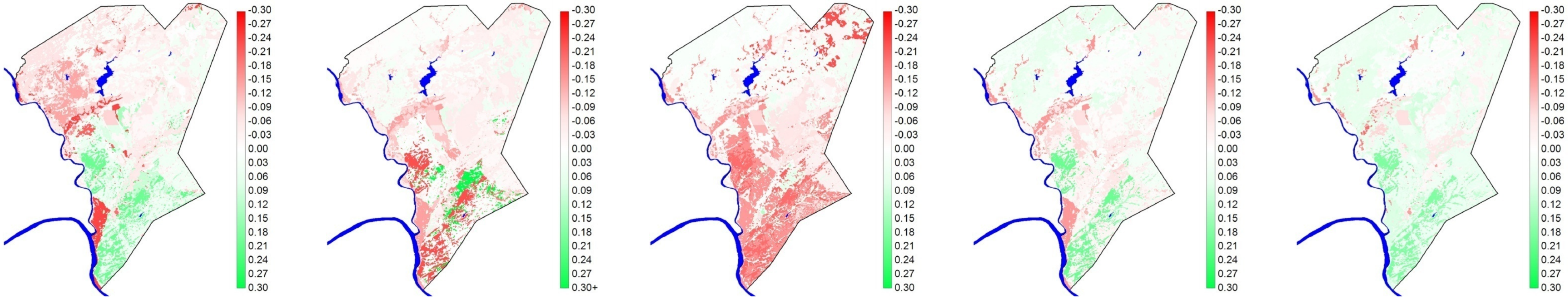
February 2003

1st – 10th March 2003

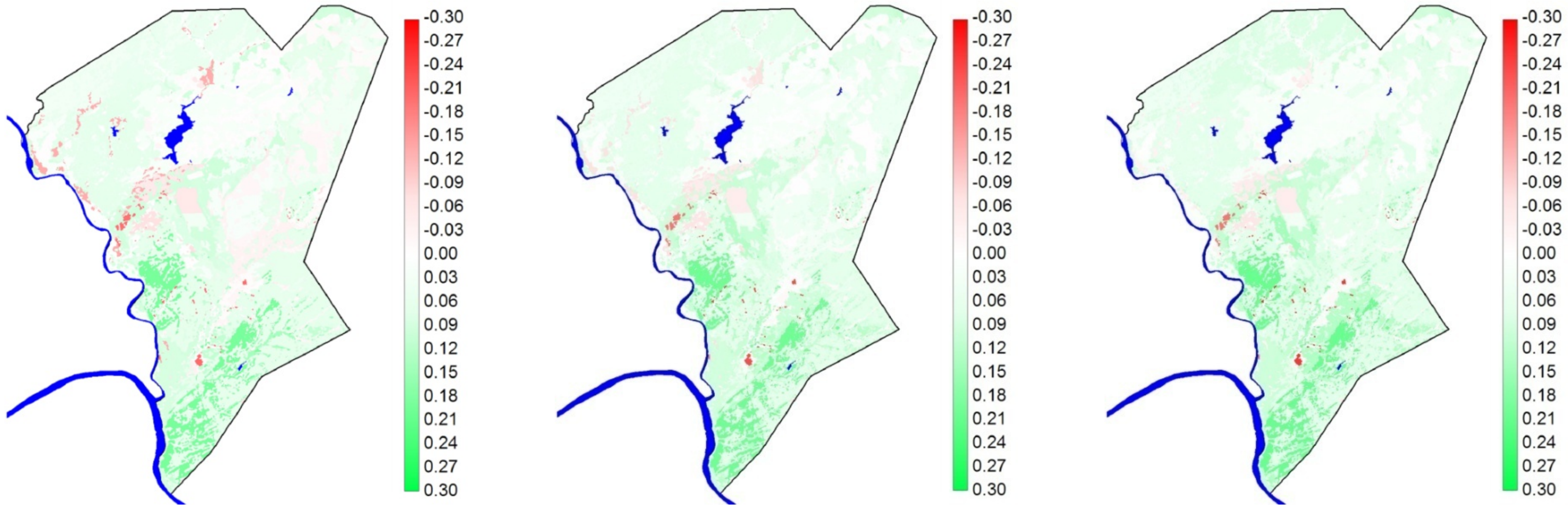
Figure 5.7 Chart depicting the temporal variation in the average total short-term rate of protein intake (g/s) for adult cows over the study period, and maps showing the spatial variation in the average total short-term rate of protein intake (g/s) over the study area for adult cows for each month of the study period.



12th – 31st March 2002 April 2002 May 2002 June 2002 July 2002

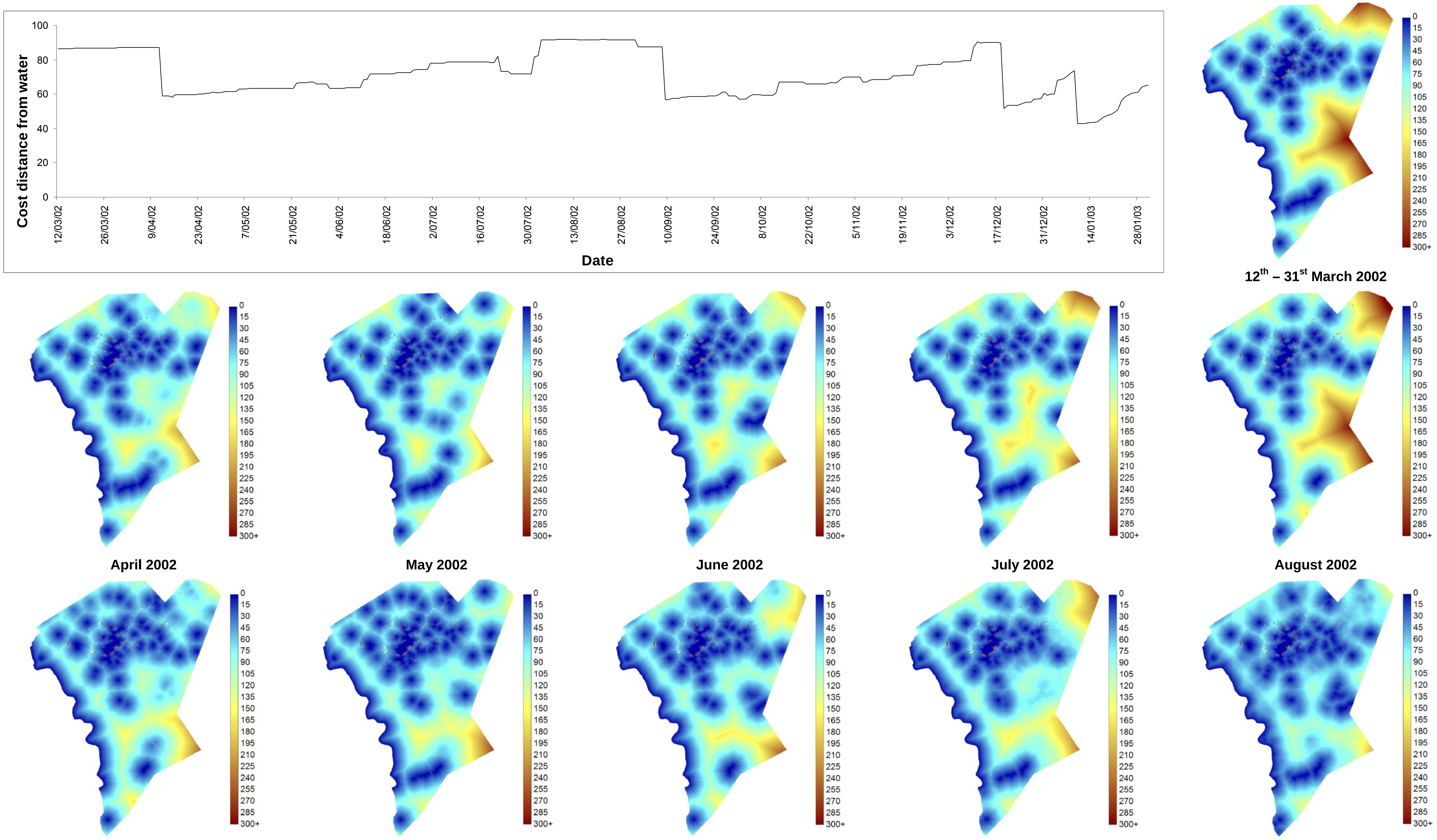


August 2002 September 2002 October 2002 November 2002 December 2002



January 2003 February 2003 1st – 10th March 2003

Figure 5.8 Maps depicting sex related differences in the average total short-term rate of protein intake (g/s) for each month of the study period. The maps were created by subtracting the average total rate of short-term protein intake (g/s) of bulls from that of cows. Negative values (red) signify higher rates of protein intake by bulls relative to cows, and positive values (green) signify the converse. Values close to zero (white) indicate little difference between the sexes.



12th – 31st March 2002

April 2002

May 2002

June 2002

July 2002

August 2002

September 2002

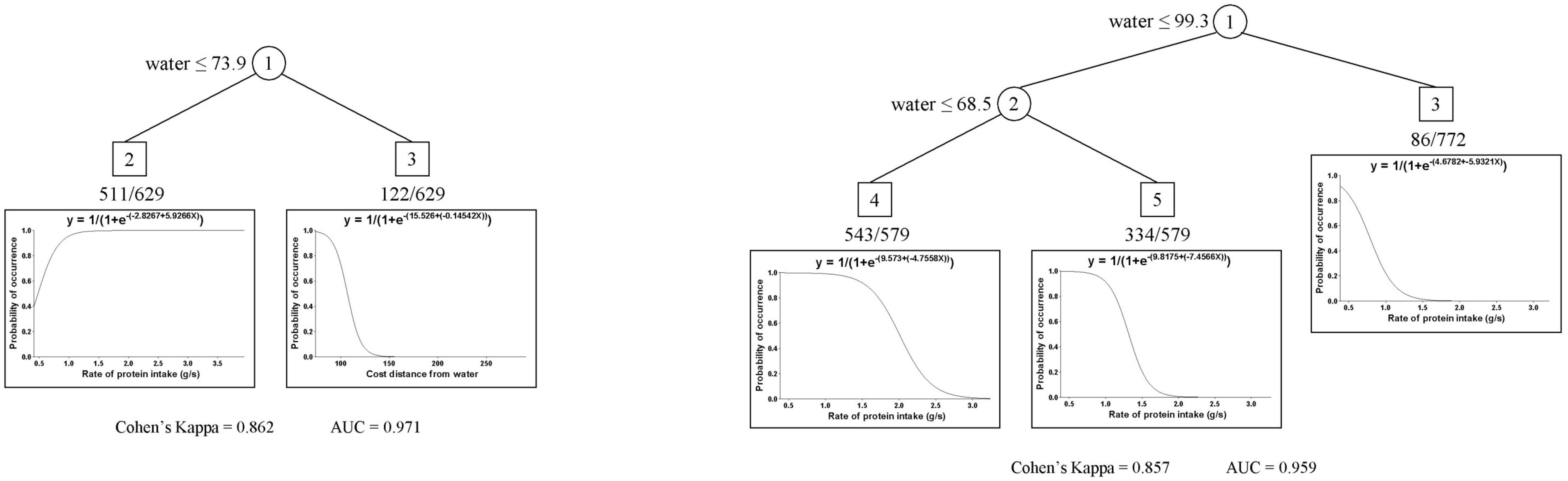
October 2002

November 2002

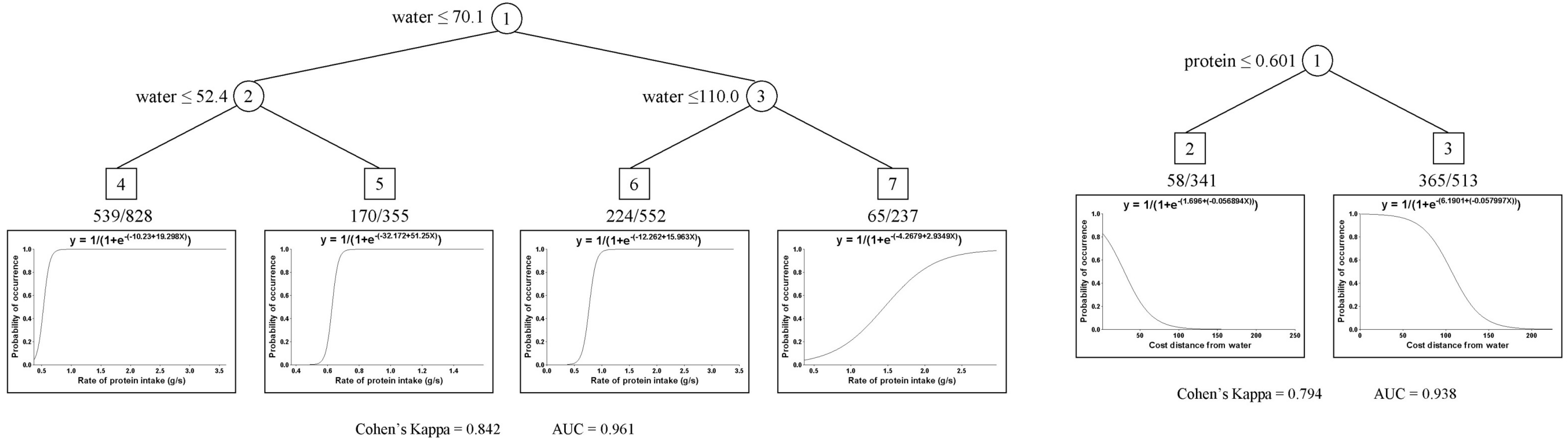
December 2002

January 2003

Figure 5.9 Chart depicting temporal variation in average cost distance from water over the study period, and maps showing the spatial variation in the average cost distance from water over the study area for each month of the study period. Distances were measured as the minimum amount of friction accumulated when moving from a given cell to the nearest source of drinking water. Cost distance from water is a relative measure and is therefore without units.

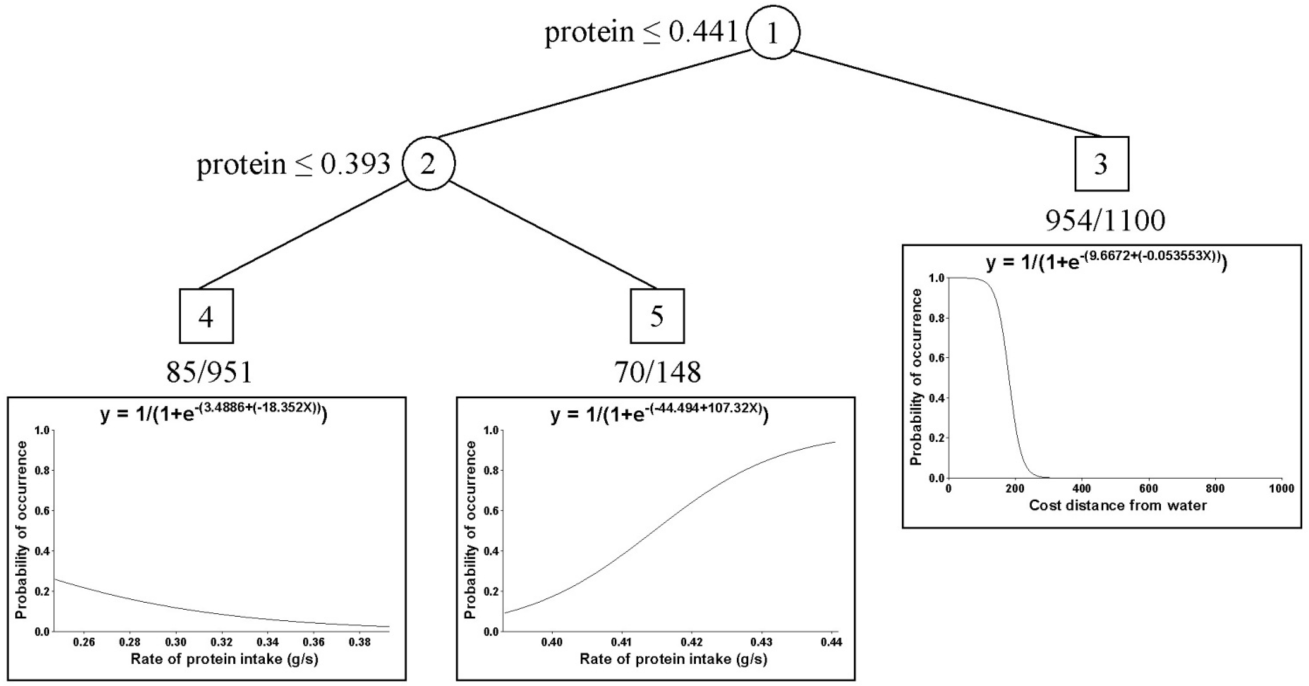


12th – 31st March 2002 **April 2002**



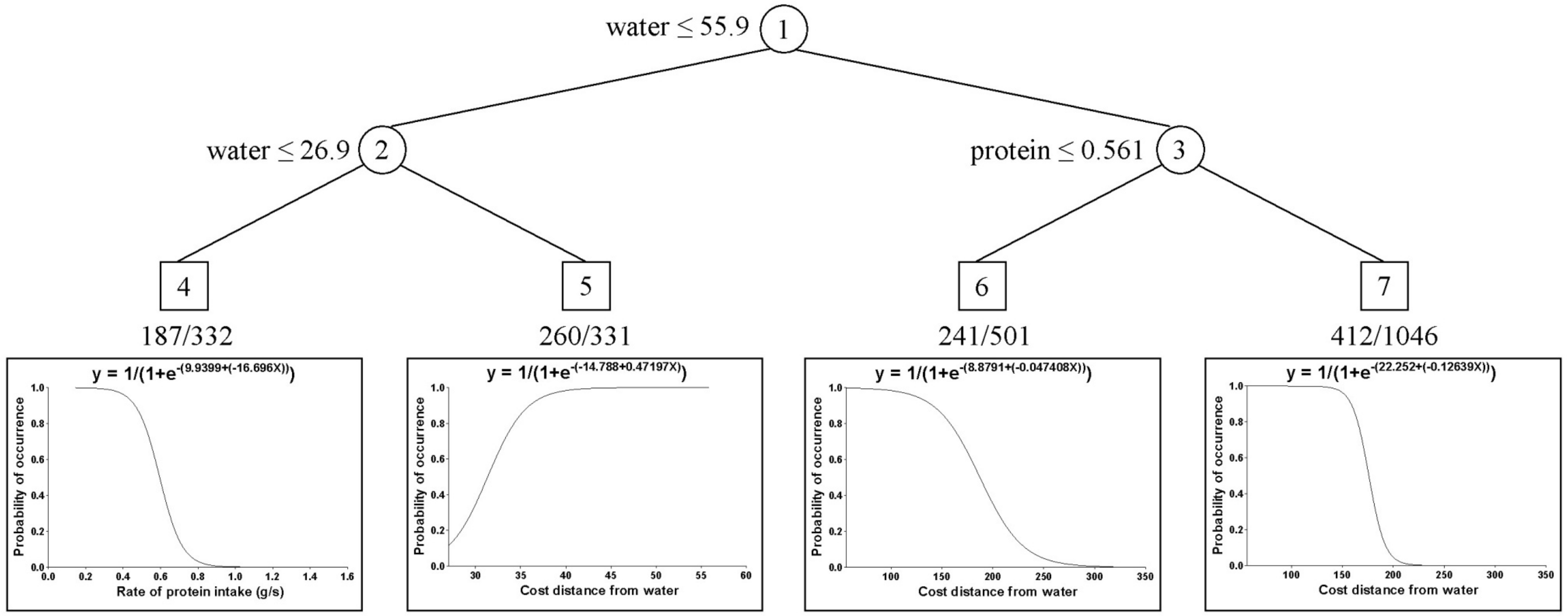
May 2002 **June 2002**

Figure 5.10 Logistic regression tree models of data from adult bulls for March, April and May 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule, it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.



Cohen’s Kappa = 0.875 AUC = 0.970

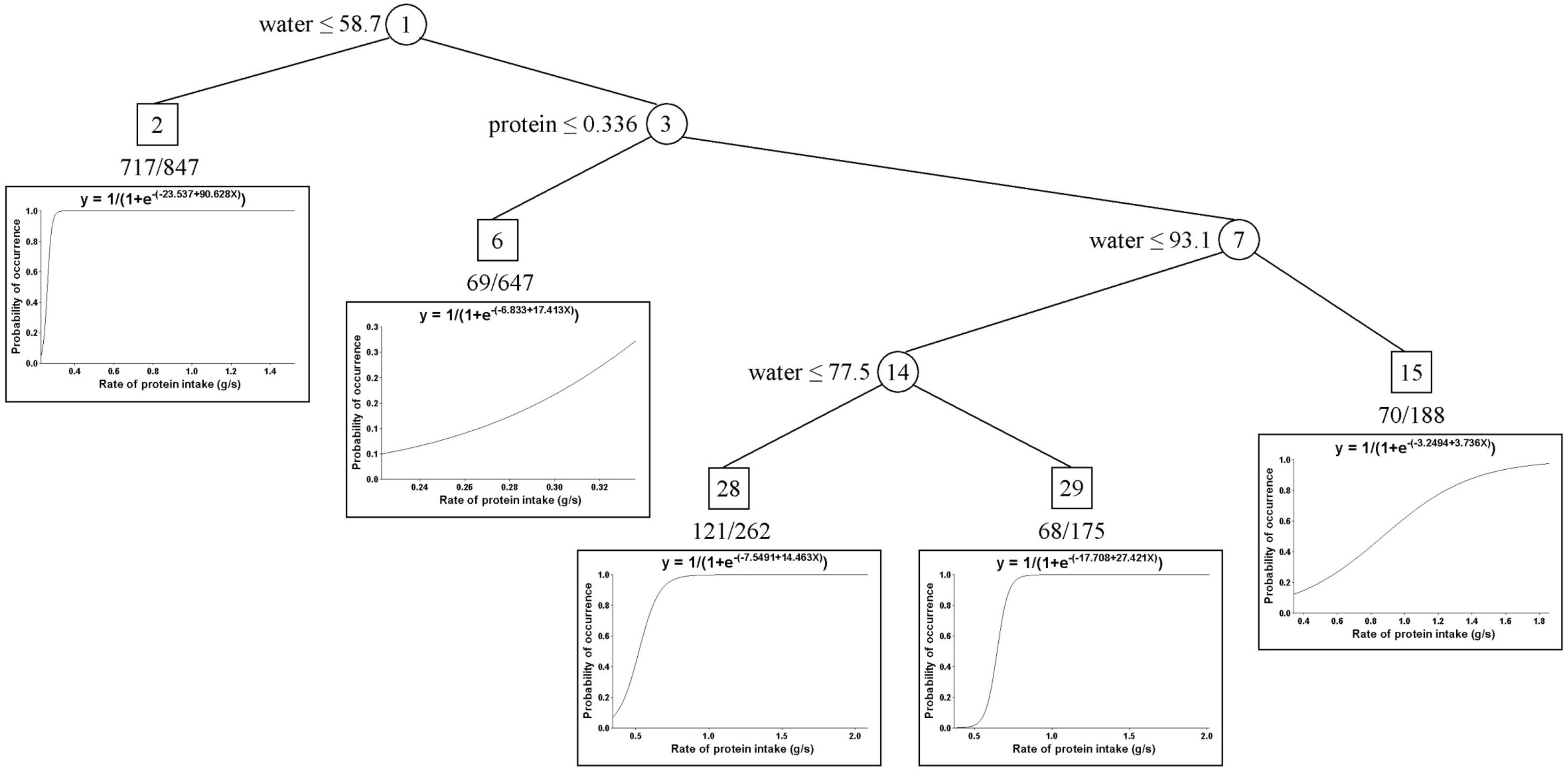
July 2002



Cohen’s Kappa = 0.889 AUC = 0.964

August 2002

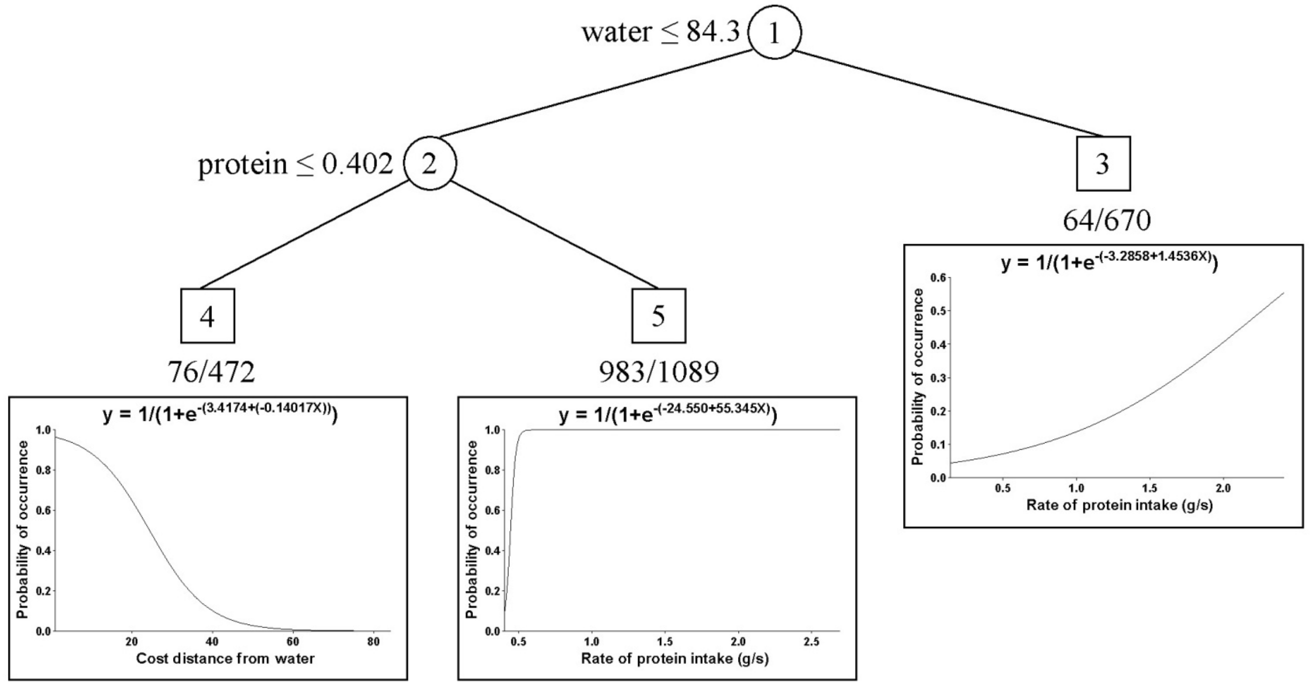
Figure 5.11 Logistic regression tree models of data from adult bulls for July, and August 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen’s Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.



Cohen's Kappa = 0.856 AUC = 0.949

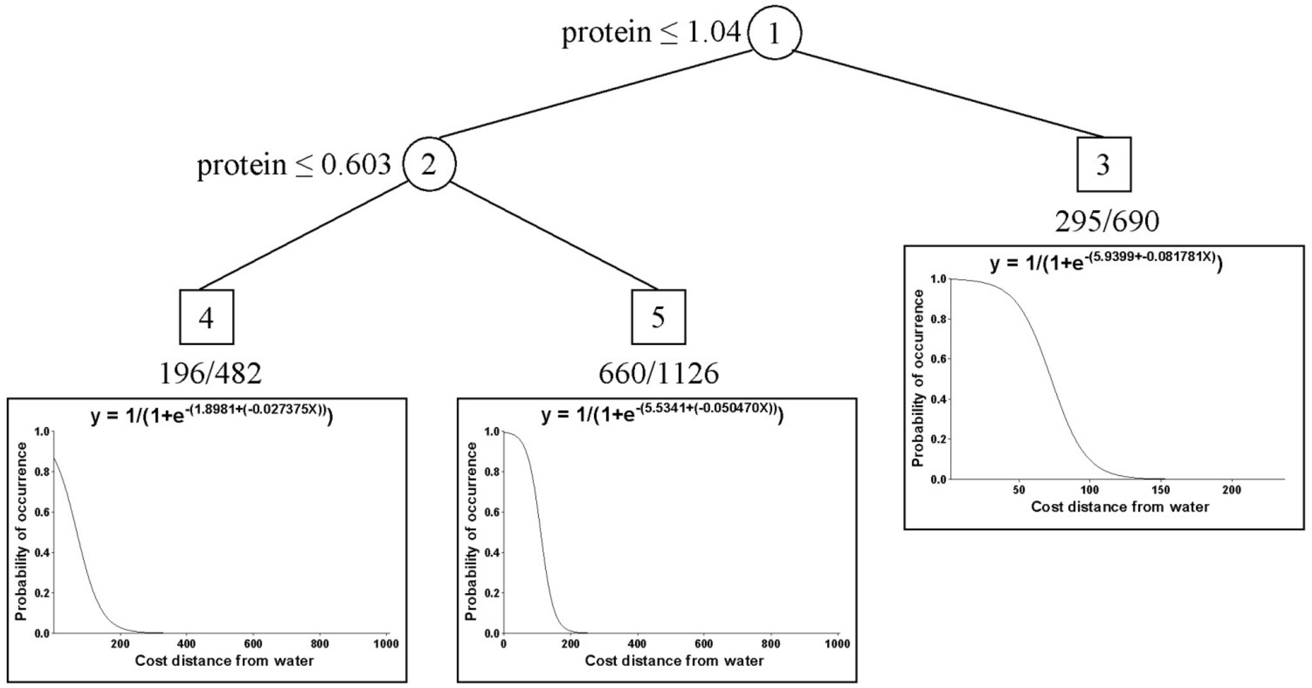
September 2002

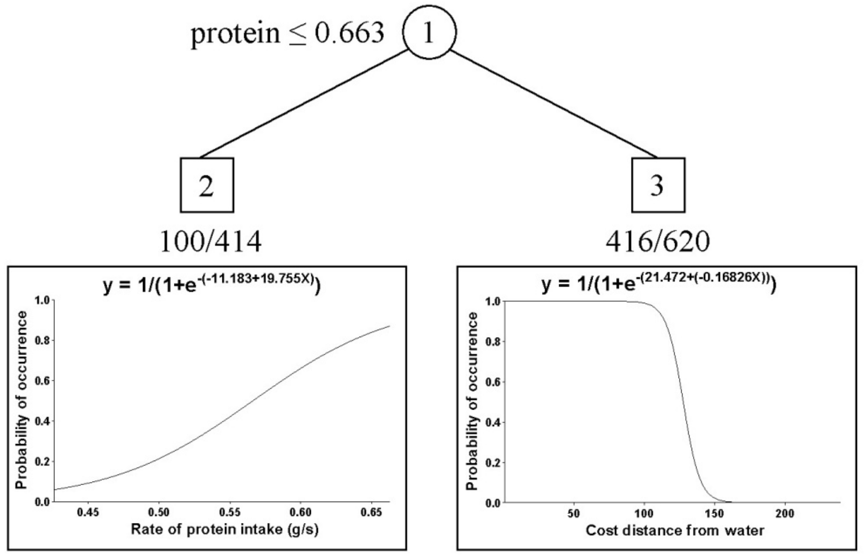
Figure 5.12 Logistic regression tree model of data from adult bulls for September 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.



Cohen's Kappa = 0.867 AUC = 0.971

October 2002





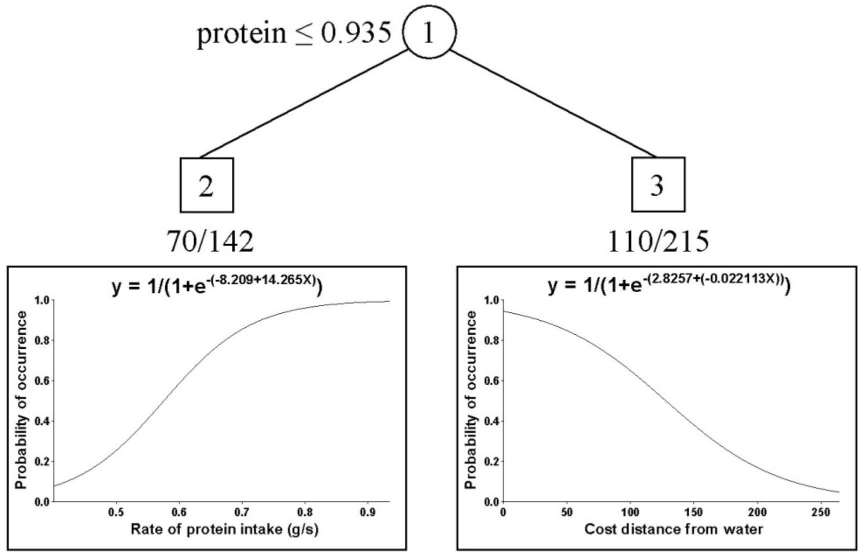
Cohen's Kappa = 0.849 AUC = 0.968

Cohen's Kappa = 0.834 AUC = 0.963

November 2002

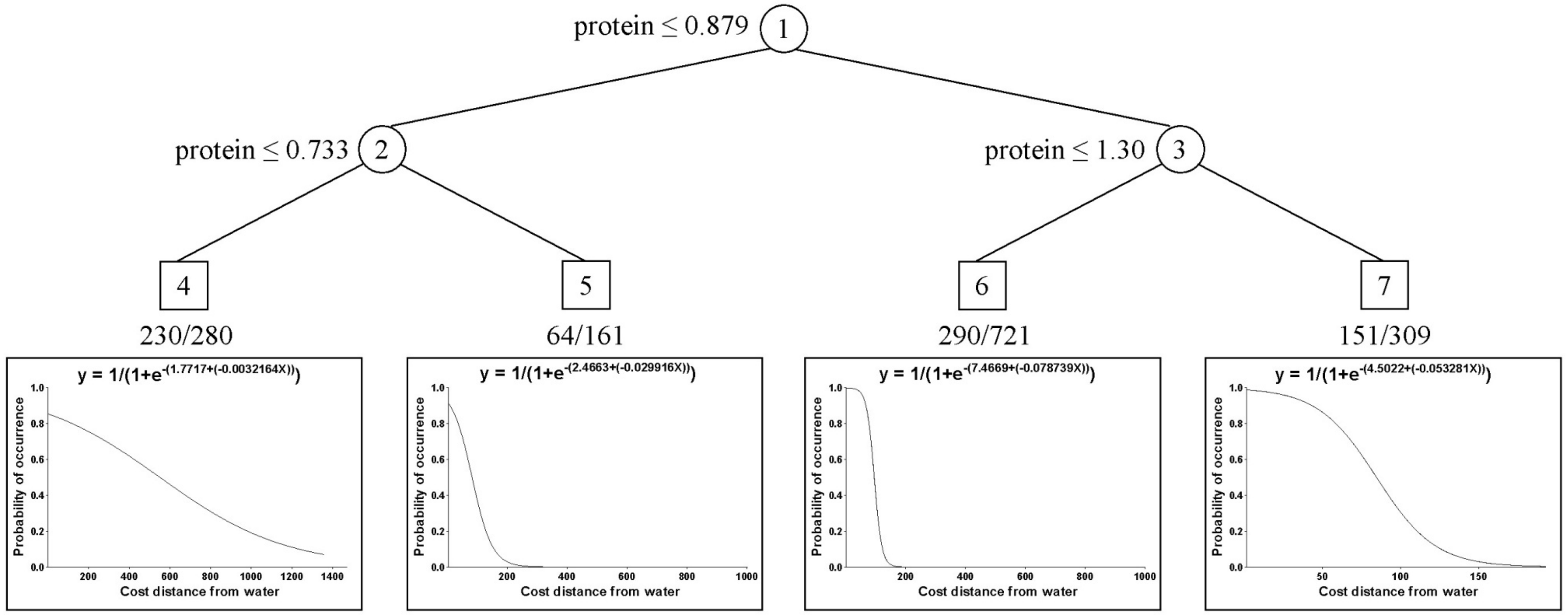
December 2002

Figure 5.13 Logistic regression tree models of data from adult bulls for October, November and December 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.



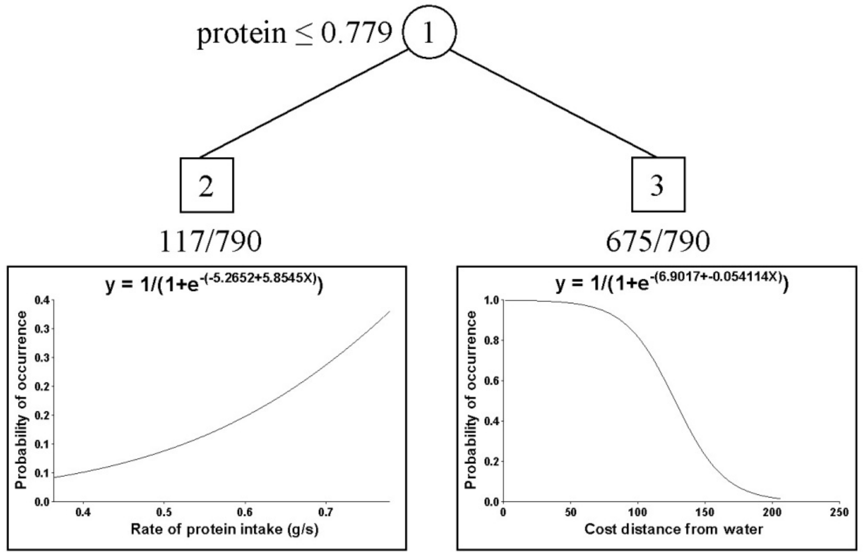
Cohen's Kappa = 0.753 AUC = 0.890

12th – 31st March 2002

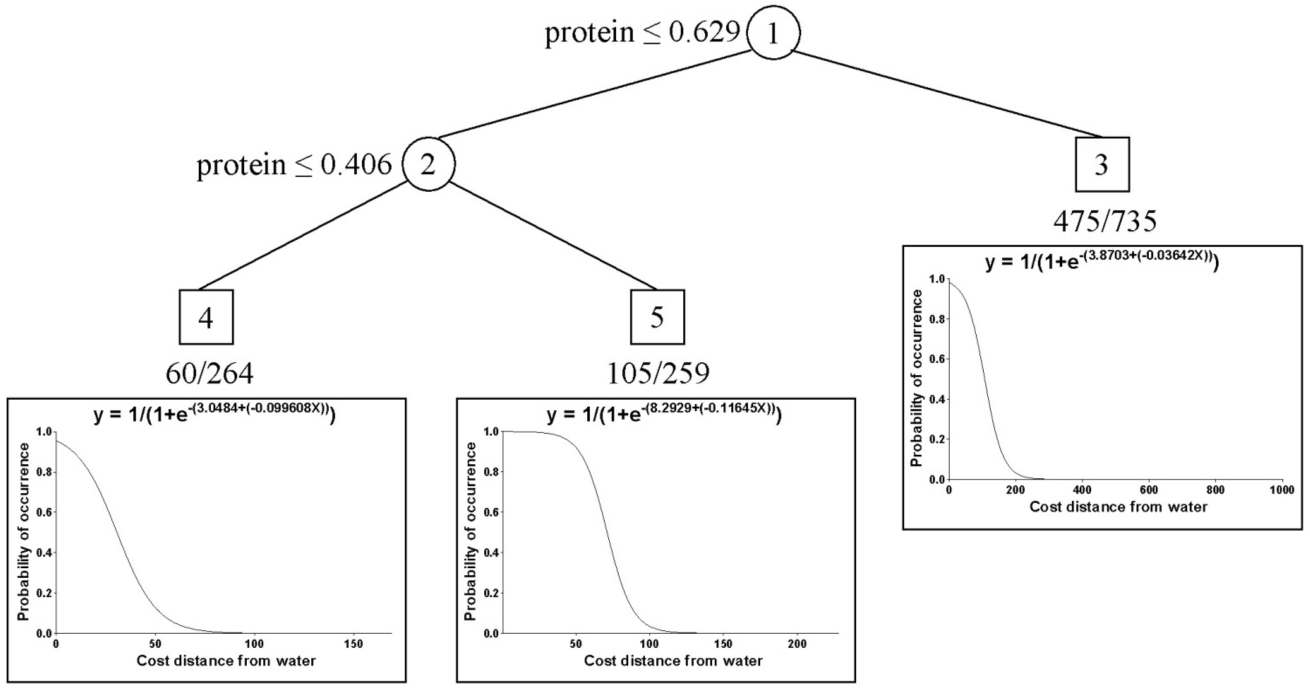


Cohen's Kappa = 0.781 AUC = 0.947

April 2002



Cohen's Kappa = 0.808 AUC = 0.931

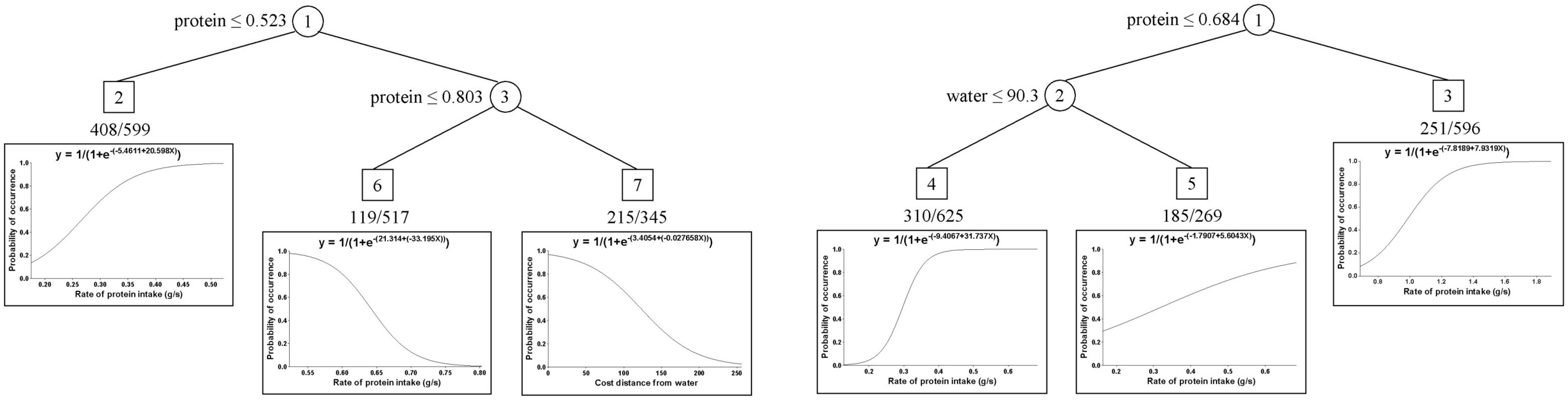


Cohen's Kappa = 0.798 AUC = 0.947

May 2002

June 2002

Figure 5.14 Logistic regression tree models of data from adult cows for March, April, May and June 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.

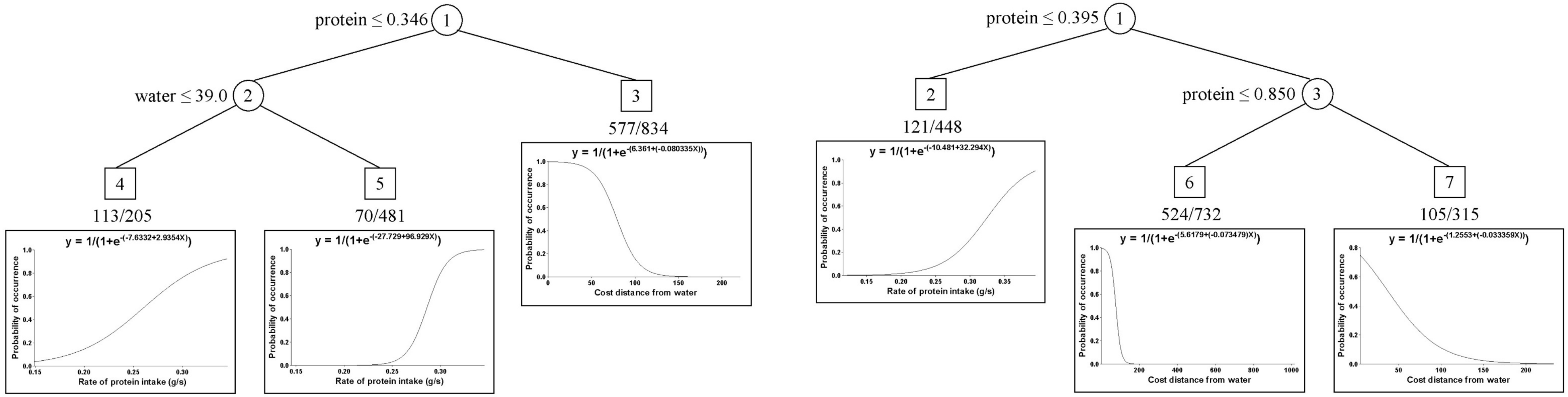


Cohen's Kappa = 0.775 AUC = 0.934

July 2002

Cohen's Kappa = 0.838 AUC = 0.933

August 2002



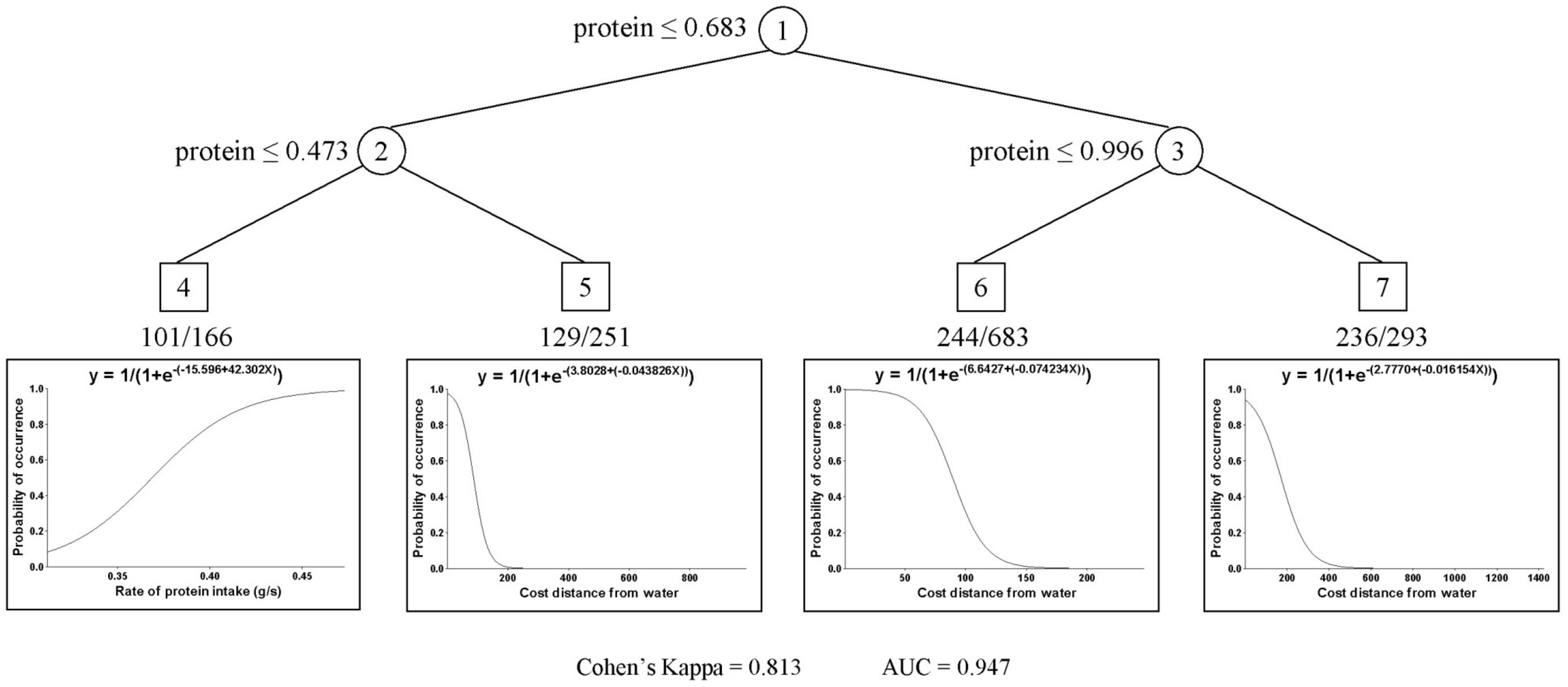
Cohen's Kappa = 0.805 AUC = 0.954

September 2002

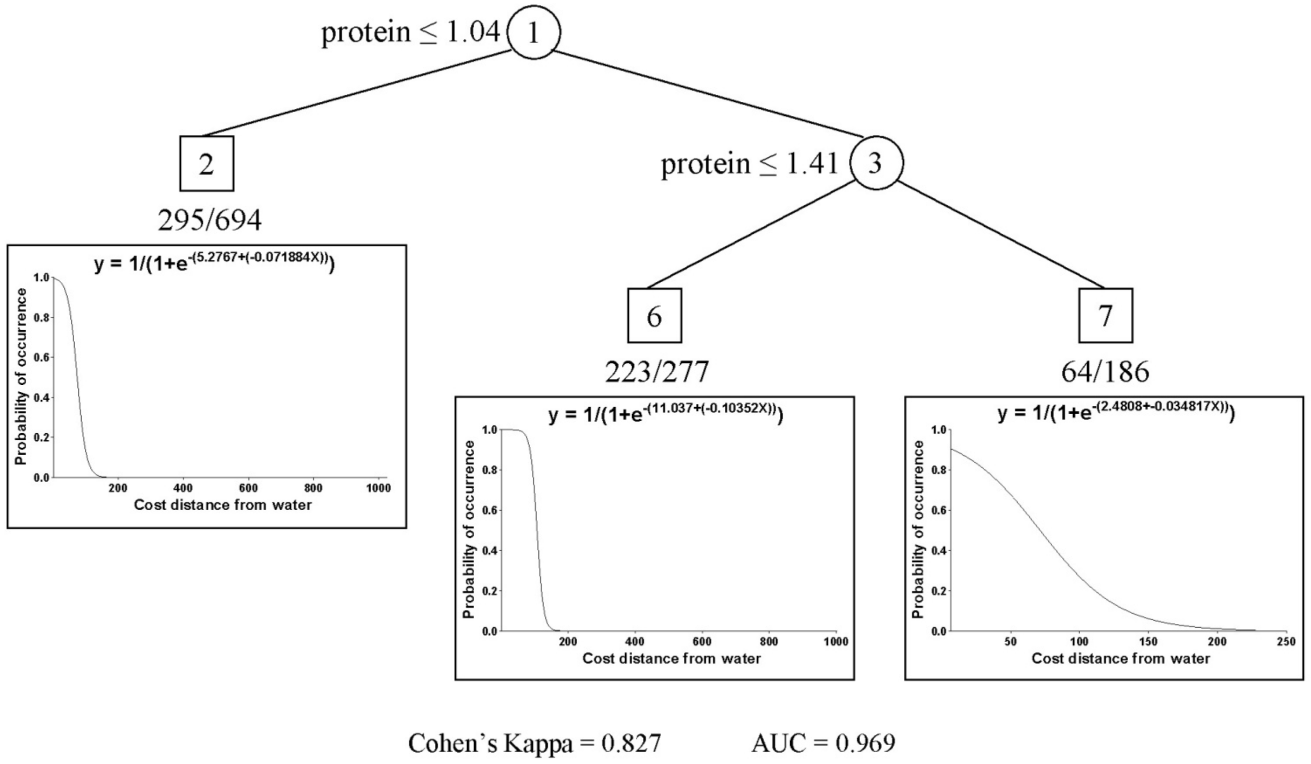
Cohen's Kappa = 0.728 AUC = 0.946

October 2002

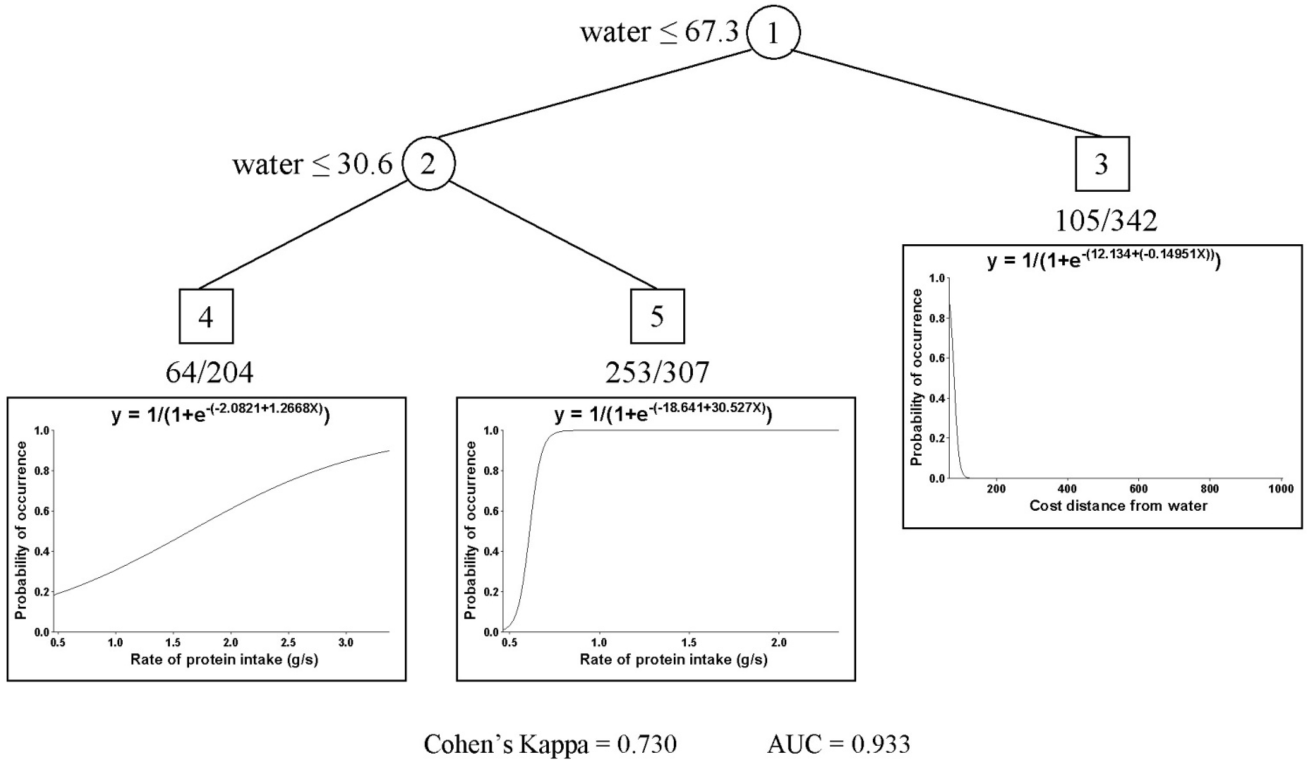
Figure 5.15 Logistic regression tree models of data from adult cows for July, August, September and October 2002. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.



November 2002

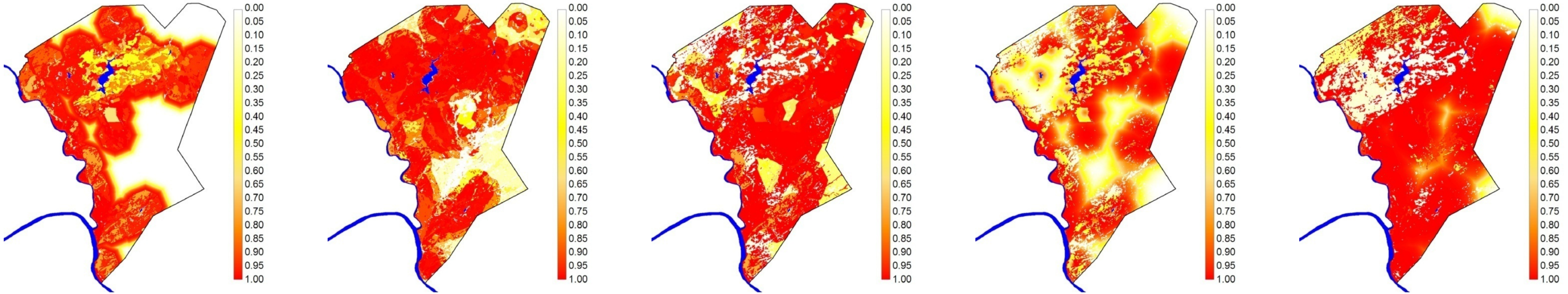


December 2002

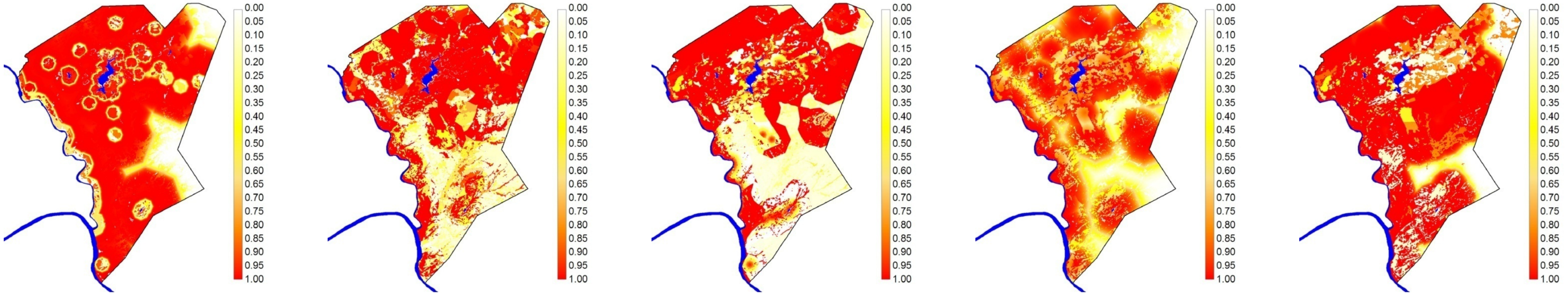


January 2003

Figure 5.16 Logistic regression tree models of data from adult cows for November 2002, December 2002, and January 2003. Intermediate and terminal nodes are represented by circles and squares respectively. The number inside a node is the node label. The splitting rule of an intermediate node is given beside it. If a case satisfies the rule it goes to the left child node; otherwise the right child node. The ratio of presence cases to the sample size and a plot of the best simple logistic regression model is given for the data in each terminal node. The value of Cohen's Kappa and the area under the receiver operating charatertistic (ROC) curve (AUC) is given below each model. Note that cost distance from water is a relative measure and is therefore without units.

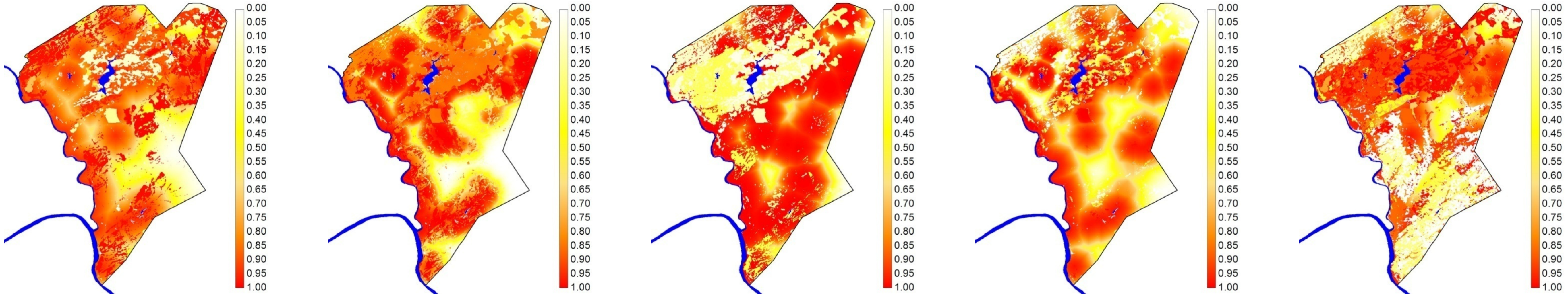


10th – 31st March 2002 **April 2002** **May 2002** **June 2002** **July 2002**



August 2002 **September 2002** **October 2002** **November 2002** **December 2002**

Figure 5.17 Maps showing the probability of occurrence of adult bulls predicted by the LRT models for each month of the study period.



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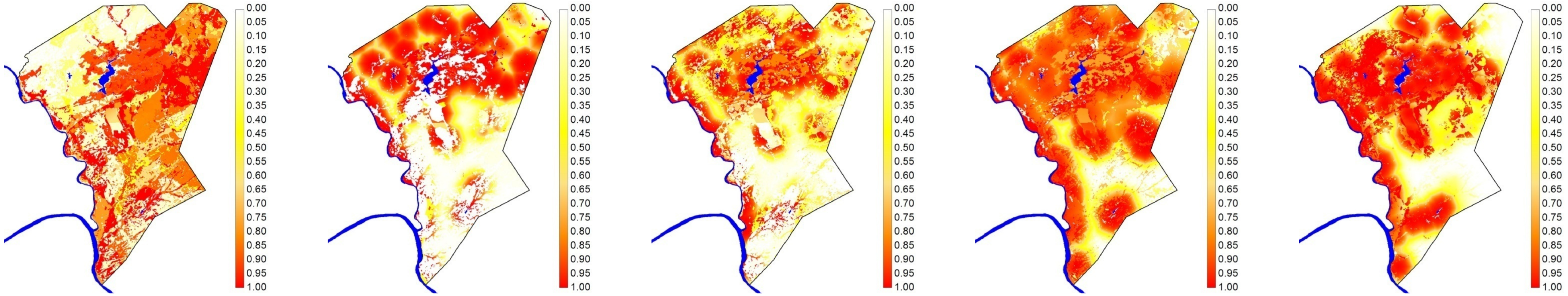
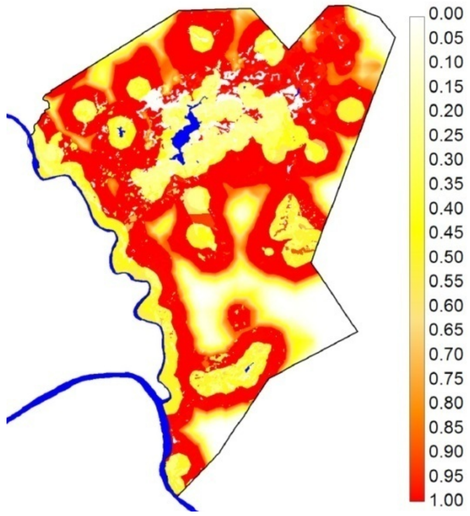
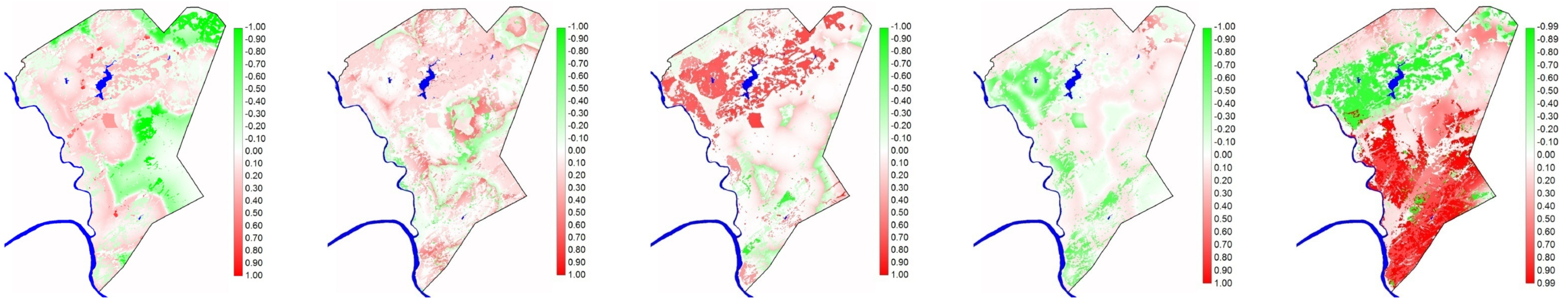


August 2002 September 2002 October 2002 November 2002 December 2002

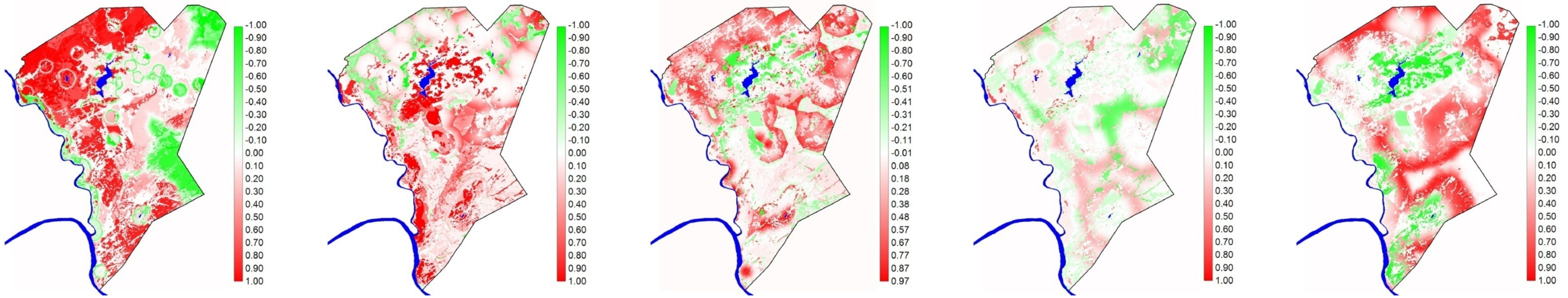


January 2003

Figure 5.18 Maps showing the probability of occurrence of family units predicted by the LRT models for each month of the study period.



March 2002 **April 2002** **May 2002** **June 2002** **July 2002**



August 2002 **September 2002** **October 2002** **November 2002** **December 2002**

Figure 5.19 Maps depicting the extent of sexual segregation predicted by the LRT models for each month of the study period. The maps were derived by subtracting the predicted probability of occurrence of family units from that for adult bulls using the IMAGEDIFF module of Idrisi Kilimanjaro GIS software (Eastman, 2003). The resulting index of segregation ranges from a minimum score of -1 (bright green), indicating occupance by family units only, to a maximum score of +1 (bright red) indicating occupance by adult bulls only. A value of 0 (white) indicates equal probability of occurrence for both family units and adult bulls.

5.5. Discussion

5.5.1. *Ecological insights*

Influence of short-term rate of intake

Given a short foraging time per unit nutrient, a low level of cell wall digestion, and an inability to recycle microbial protein, it was hypothesised that elephants take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time in order to meet their nutritional demands (see chapter 1). Accordingly, elephants were expected to optimise fitness by selecting habitats, from the available choice set, such that their rate of digestible energy and nutrient intake was maximised. However, because habitat selection by elephants is influenced by factors unrelated to food, such as safety (Buss, 1961; de Boer et al., 2000), distance from surface water (Young, 1970; Western, 1975; Stokke & du Toit, 2002; Conybeare, 2004; de Beer et al., 2006; Chamaillé-Jammes et al., 2007), and shade (Owen-Smith, 1988; Spinage, 1994), the distribution of elephants was expected to be governed by an interaction between the short-term rate of energy and nutrient intake and the non-dietary constraints to foraging. Furthermore, the nature of this interaction was expected to vary in response to sex related differences in foraging behaviour and the spatial distribution of suitable forage resources in relation to non-dietary requirements.

By controlling for shade (restricting presence data to positions saved between 4 pm and 9 am) and including cost distance from water as a second predictor variable in the model (safety was assumed not to be an issue within the study area) the LRT analyses clearly showed that both adult bulls and family units, within the constraints imposed by distance from water, tended to select habitats that had the potential to maximise their short-term rate of intake of digestible energy and nutrients (as measured by the protein intake proxy). In addition, the results were consitent with the prediction that the nature of the interaction between the short-term rate of protein intake proxy and distance from surface water would vary between sexes and over time in response to changes in the spatial position of suitable forage in relation to surface water.

Influence of distance from surface water

Although distance from water has already been established as an important factor influencing the distribution of elephants (Young, 1970; Western, 1975; Stokke & du Toit, 2002; Conybeare, 2004; de Beer et al., 2006; Chamaillé-Jammes et al., 2007), previous studies that investigated its influence were conducted over large tracts of land characterised by relatively long distance gradients from water. The results of this study bring new insight by showing that distance from water can have a strong influence on the distribution of elephants even in a relatively small reserve that is well supplied with surface water. This is an important finding because it points to manipulation of surface water as an important method of controlling elephant distribution even on small to medium sized reserves.

Distance from water was the primary determinant of the distribution of bulls during the dry season, with short-term rate of protein intake being of secondary importance. The converse was true for family units. This sex related difference in the relative importance of the two predictor variables can be explained in terms of the Jarman-Bell principle (Geist, 1974). This principle states that larger herbivores should be able to tolerate a lower minimum dietary quality than smaller ones because specific metabolic rate decreases with increasing body mass, while gut capacity remains a constant fraction of body mass. Consequently, because of a larger body size, the distribution of adult bull elephants should be less constrained by factors governing food quality than members of family units.

This finding has important implications for the management of elephant-woodland systems because it indicates that the feeding areas of adult bulls should be more easily manipulated by the sighting of artificial water points than that of family units. A recent study by Smit et al. (2007), conducted in the Kruger National Park, South Africa, provides support for this hypothesis. They found the density of adult bulls to be higher than expected close to artificial water, but the density of family units to be largely unaffected by artificial water points. It should be noted however, that this situation will only arise in landscapes where high quality forage is found in close association with natural water bodies (e.g. rivers), because family units will be more attracted to these water bodies on account of their proximity to high quality food. In systems where only artificial sources of water are available, the distribution of both bulls and family units will be influenced by distance from artificial water (see Chamaillé-Jammes et al., 2007) with the effect being stronger for bulls than family units.

Another important management implication of the difference in relative importance of distance from water and rate of protein intake in determining the distribution of adult bulls and family units is that travel distance between water and food should be more easily manipulated for family units than for adult bulls. Because of a strong dependency on high quality food, travel distance between food and water should be increased for family units by sighting artificial water points far from areas that provide high rates of protein intake. Increased travel distance between food and water may curtail growth of elephant populations by increasing age to first parturition, calving interval, and calf mortality (O'Connor et al., 2007). Travel distance should be less easily manipulated for adult bulls because they are not as dependent on high quality food.

Sexual segregation

Sexual segregation of habitat selection by elephants, and an increase in the degree of spatial separation between adult bulls and family units during the dry season has been reported previously (Stokke, 1999; Stokke & du Toit, 2000; Stokke & du Toit, 2002; Shannon et al., 2006; Smit et al., 2007). Several studies have tested hypotheses put forward to explain this phenomenon (Stokke & du Toit, 2000; Stokke & du Toit, 2002; Shannon et al., 2006), but a foraging mechanism capable of explaining sexual segregation in elephants has not previously been demonstrated within a modelling framework. The results of this study suggest that sex related differences in trunkload mass and handling time across food types (see Chapter 4) result in bulls and cows having different spatio-temporal patterns of the rate of energy and nutrient intake over the landscape, which may ultimately result in different patterns of habitat selection between the sexes. It should also be noted that, in this study, sexual segregation in habitat selection also appeared to be explained by the tendancy of the short-term rate of protein intake to be a more important explanatory variable than cost distance from water for the spatial distribution of family units, with the converse being true for the spatial distribution of bulls.

Importance of cross-scale linkages

Demonstration of how the response of a forager at the scale of the plant (trunkload mass and handling time) can strongly influence the response at larger spatial scales (habitat selection) was an important finding because it provided support for the idea that resource selection by herbivores is the integrated result of a number of choices made at different scales from components of plants, to plants, to plant communities, to landscapes and upwards (Johnson et al., 2004). Consequently, studies of resource selection by animals should not treat choices made at each scale as separate processes, but should rather aim to incorporate the cross-scale linkages inherent in the foraging process. The use of a submodel (the intake model) to create a functional predictor variable (short-term rate of protein intake) that was the integrated result of foraging decisions made at scales below the habitat, proved to be a simple way of incorporating the decisions made at small spatial scales into the habitat selection process. The technique also served to simplify the habitat models and, in so doing, made them easier to interpret.

Importance of a landscape level perspective

No generic model of habitat selection emerged. Despite use of the same predictor variables, the structure of the habitat models differed across months. The variability in model structure provides support for the hypothesis that short-term rate of protein intake and cost distance from water influence elephant distribution at the landscape level. In other words, the attractiveness of a habitat to elephants is not determined by the absolute measure of the factors for the habitat in question, but rather by a measure that is relative to the other habitats in the landscape. Development of a generic model to predict habitat selection by elephants throughout their range will only be achieved by using a technique that accounts for this conditionality of response.

The results of the study also highlight the importance of not only testing the congruence of predictor variables across multiple spatial scales, but also testing the predictive consistency of variables over time. In other words, a true landscape level approach is required for the study of habitat selection.

5.5.2. *Limitations and future improvements*

In this study, the potential profitability of the forage in each land unit was indexed as the sum of the potential protein intake rates of five food types. This was a simplification because, in reality, elephants utilised in excess of 10 different forage types. The existence of a strong relationship between short-term rate of protein intake and habitat selection justifies further study with a more complete set of available forage types.

The response of elephants was measured using only a few individuals (3 bulls and 2 cows) and, consequently, it was subject to the idiosyncrasies of the subject animals. A more reliable measure of the population response could have been obtained if a greater number of individuals had been used. This may explain why, for some months, the rate of protein intake was negatively correlated with the probability of occurrence of bulls.

Use of the rate of protein intake to predict habitat selection by elephants over large areas is limited by the fact that calculation of intake rate is highly data intensive. In this study, spatio-temporal change in the density of food patches was quantified using a ground-based approach that was both time consuming and labour intensive. The development of remote sensing techniques that reduce the effort required to quantify patch density of different food types should be the focus of future research.

The rate of protein intake does not provide a measure of the actual uptake of energy and nutrients from the ingested food. In other words, it does not take into account the constraints of digestion. A more realistic measure of the nutritional utility of habitats may be obtained by using the rate of protein uptake as a predictor variable.

In this study, the distance from water variable did not take into account the size of water bodies. Over the course of the study, it was evident that family units preferred larger water bodies over smaller ones because (1) the smaller water sources did not have enough water to satisfy the requirements of a large number of elephants, and (2) swimming could only take place in the larger dams. This may explain why habitat selection by family units was not modelled as well as that by bulls. The size of water bodies should be accounted for in future studies.

Chapter 6. Diet selection by elephants: the influence of short-term rate of protein intake

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6.1. Introduction

Choice of diet by elephants has a strong influence on their impact on woody vegetation. Impact is greatest when elephants feed on the stems, bark and roots of woody plants because harvesting of these food types invariably results in broken branches, pollarding or felling of trees, ring barking of main stems, and uprooting of whole plants. A diet composed largely of leaves results in less damage because elephants can often strip leaves from shrubs and trees without having to break branches. When diet is composed solely of grass and forbs, there is no damage to woody plants. Consequently, prediction of diet composition is a crucial first step towards forecasting elephant-induced changes in the composition and structure of woody vegetation.

Despite its importance for the management of elephant-woodland systems, little progress has been made towards predicting diet choice by elephants. This is because research into the foraging behaviour of elephants has largely been descriptive (Bax & Sheldrick, 1963; Field, 1971; Guy, 1976; Barnes, 1982; Bowland & Yeaton, 1997; de Boer et al., 2000; Cerling et al., 2004; Codron et al., 2006), with few explanatory studies being conducted. Consequently, possible mechanisms of diet selection need to be tested, and the important variables affecting choice identified before the necessary predictive models can be built.

Optimal foraging theory assumes that foraging behaviour and fitness are linked by a particular currency (Pyke, 1984). If elephants are able to rank potential food items according to their contribution to overall fitness and, on the basis of these rankings, select a diet from the available set of food choices that best meets their needs, what then is the currency that elephants use? In chapter 1, it was hypothesised that given a short foraging time per unit nutrient, a low level of cell wall digestion, and an inability to recycle microbial protein, elephants should take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time if they are to meet their nutritional demands. The objective of this chapter was to test this hypothesis by determining whether the short-term rate of intake of digestible energy and nutrients is an important factor influencing diet choice by elephants. Due to the difficulty of measuring the digestible energy content of forage for elephants, the short-term rate of protein intake was used a proxy for the rate of intake of digestible energy and nutrients (see Chapter 4 for an argument supporting the use of the rate of protein intake as a proxy).

6.2. Method

6.2.1. *Statistical model*

The influence of short-term rate of protein intake on diet choice by elephants was tested using a discrete choice model. Discrete choice analysis has its root in the social sciences where it has been used extensively to model how humans make choices from a constrained set of resources (Manski, 1981; Ben-Akiva & Lerman, 1985). Assuming choices made by humans are analogous to those made by animals, the technique has more recently found application in studies of resource selection by wildlife (Cooper & Millspaugh, 1999; McDonald et al., 2006; Balme et al., 2007; Cooper et al., 2007; Teo et al., 2007).

Discrete choice models assume that a consumer gains fitness from selecting a given resource, and that the level of fitness gained is a function of the attributes of the resource. When presented with a set of resources, known as the choice set, it is assumed that the consumer will select the alternative that maximises its level of fitness. This assumption provides the theoretical framework for the selection process in discrete choice models.

The level of satisfaction, or utility, provided by resource *i* to individual *j* (U_{ij}) is defined as:

$$U_{ij} = \beta' X_{ij} + e_{ij} = b_1 x_{1j} + b_2 x_{2j} + b_3 x_{3j} + \ldots b_m x_{mj} + e_{ij}$$

where X_{ij}, is a vector of length *m* of the attributes of resource *i* as perceived by individual *j*, and β' is a vector of length *m* of estimable parameters that determine each attribute's contribution to utility (which could be positive or negative). Given that information about each individual animal is incomplete, there are unobserved components of the utility function. For example, two animals of the same sex, age and size may choose different resources because of different past experiences or variability in taste that is peculiar to each individual. To account for these unobserved attributes, a random error term, $e_{ij,}$ is included in the utility function.

The concept of utility allows the profitability of a series of alternatives to be ranked. The primary implication of this ranking or ordering of alternatives is that there is no absolute reference or zero point for utility values. Thus, the only valuation that is important is the difference in utility between pairs of alternatives; particularly whether that difference is positive or negative. Any function that produces the same preference orderings can serve as a utility function and will give the same predictions of choice, regardless of the numerical values of the utilities assigned to individual alternatives. It also follows that utility functions which result in the same order among alternatives are equivalent.

The probability of individual *j* choosing resource *A* from the set of *i* potential resources can be written as:

$$P_j(A) = \Pr(\beta' X_{Aj} + e_{Aj} > \beta' X_{ij} + e_{ij} \forall i)$$

When the error terms in the above equation are distributed as Type I extreme values, the probability of individual *j* choosing resource *A* rather than any of the other *i* resources available can be rewritten as the multinominal logit discrete choice model (McFadden, 1973):

$$P_j(A) = \frac{\exp(\beta' X_{Aj})}{\sum_{\forall i} \exp(\beta' X_{ij})}$$

This form of the discrete choice model is commonly used to derive estimates of the parameters (*β,s*) for each attribute because it has a closed form solution in a maximum likelihood equation that includes all resources chosen and not chosen across all *j* individuals (Ben-Akiva & Lerman, 1985).

6.2.2. *Collection of data on diet choice*

Data on diet choice by elephants were collected over a one year period and across as many different land units as possible by following individual adult bull and adult cow elephants on foot and recording the number of trunkloads eaten of each food type. If the focal elephant crossed into a different land unit, the data collected in the new land unit were treated as a separate observation. The length and spatial position of the path followed during each observation were captured by saving a track on a GPS (see chapter 4 for a more detailed account of the observation and data recording methods).

6.2.3. *Defining the choice set*

In discrete choice analysis, the choice set is defined as the set of all possible resources available to an individual at a given time and place. In this study, five alternative food types namely, green forbs, green grass, mixed green and dry grass, green leaves from woody plants, and canopy bark from woody plants were considered available for all observations. Elephants were frequently observed eating trunkloads composed of both leaves and small branches from woody plants, but because the short-term rate of protein intake was not calculated for this food type, due to difficulties in estimating trunkload mass, this alternative was not included in the choice set. Although the choice set for each observation was composed of the same five food types, the utility of each food type, as measured by the rate of protein intake, varied across observations because observations were made at different points in space and time.

To fit within a classic discrete choice framework, the alternatives within the choice set must be mutually exclusive. In other words, choosing one alternative necessarily implies not choosing any of the other alternatives (Ben-Akiva & Lerman, 1985). As far as foraging by elephants is concerned, choice of alternative forage types is not mutually exclusive because often several different food types are consumed during a single bout of feeding. Consequently, in order to satisfy this requirement, the analysis was restricted to choice of primary food, with the primary food being defined as the alternative having the greatest number of trunkloads consumed during the period of observation.

To ensure reliable detection of the primary food type, only observations where the focal elephant stopped to feed at 3 or more stations and ate a total of at least 25 trunkloads were included in the final data set. A feeding station was defined as an individual shrub or tree for food types from woody plants, and, for herbaceous food types, as a site where the focal elephant took no more than 2 steps between trunkloads.

6.2.4. *Estimating the short-term rate of protein intake for each food type*

The short-term rate of protein intake achieved by elephants when feeding on each of the five alternative food types was obtained for the date and place of each observation by extracting average values for each GPS track from the appropriate daily maps of the rate of protein intake for each food type that were developed in chapter 4.

6.2.5. *Model fitting and hypothesis testing*

A maximum likelihood estimate of the parameter for the short-term rate of protein intake was obtained by fitting the multinominal logit form of the discrete choice model, with choice of primary food as the dependent variable and short-term rate of protein intake as the independent variable, to the data using Systat 9 (SPSS, 1998). The significance of the parameter estimate was tested using a t-test, and the change in the odds (odds ratio) of selecting the primary food type, given a 1 gs^{-1} increase in the short-term rate of protein intake, was calculated using the following equation:

$$\omega = \frac{p_{x+1}(1 - p_{x+1})}{p_x(1 - p_x)}$$

where ω is the odds ratio, and p_x is the probability of being chosen as the primary food type when the short-term rate of protein intake is x gs^{-1}.

6.3. Results

A total of 72 observations (62 from bulls and 10 from cows) were made across 24 land units (Figure 6.1). The temporal distribution of the observations were as follows: Apr 2002 = 2, May 2002 = 7, Jun 2002 = 3, Jul 2002 = 6, Aug 2002 = 7, Sep 2002 = 1, Oct 2002 = 8, Nov 2002 = 11, Dec 2002 = 8, Jan 2003 = 8, and Feb 2003 = 11. Fewer observations were obtained from cows than bulls because family units were more difficult to approach on foot. The mean (n = 72) number of feeding stations and trunkloads per observation was 15.9 and 81.0 respectively (Figure 6.2).

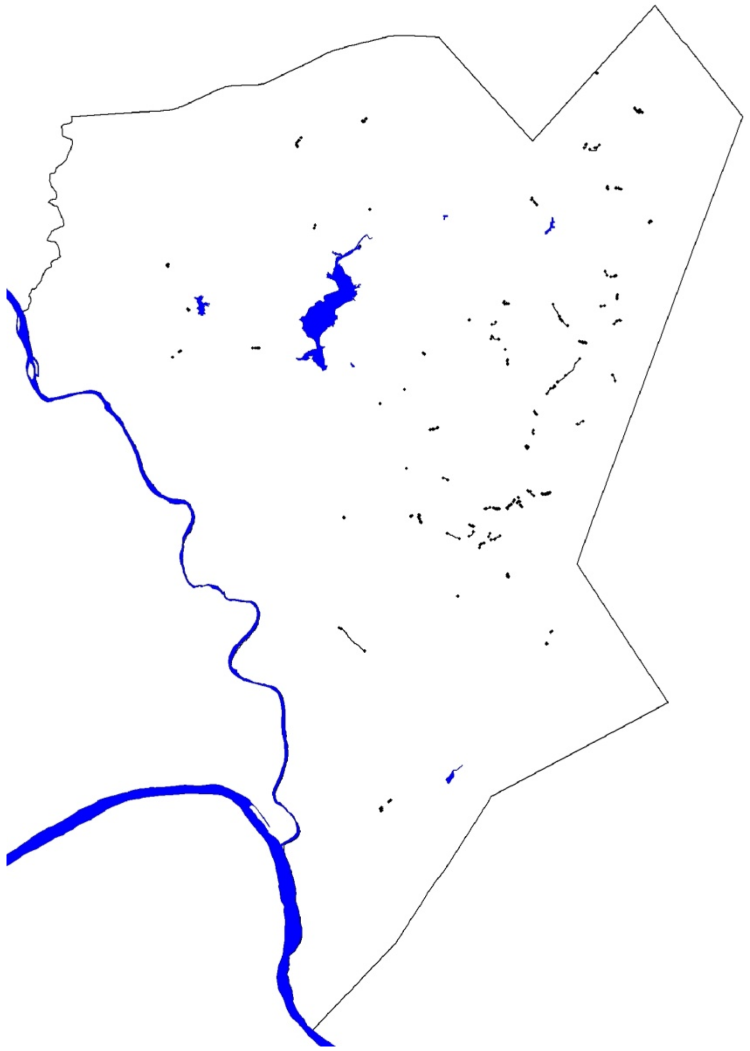

Figure 6.1 Map showing the spatial positions of the feeding observations used in the discrete choice analysis. The positions were recorded by saving a track on a GPS.

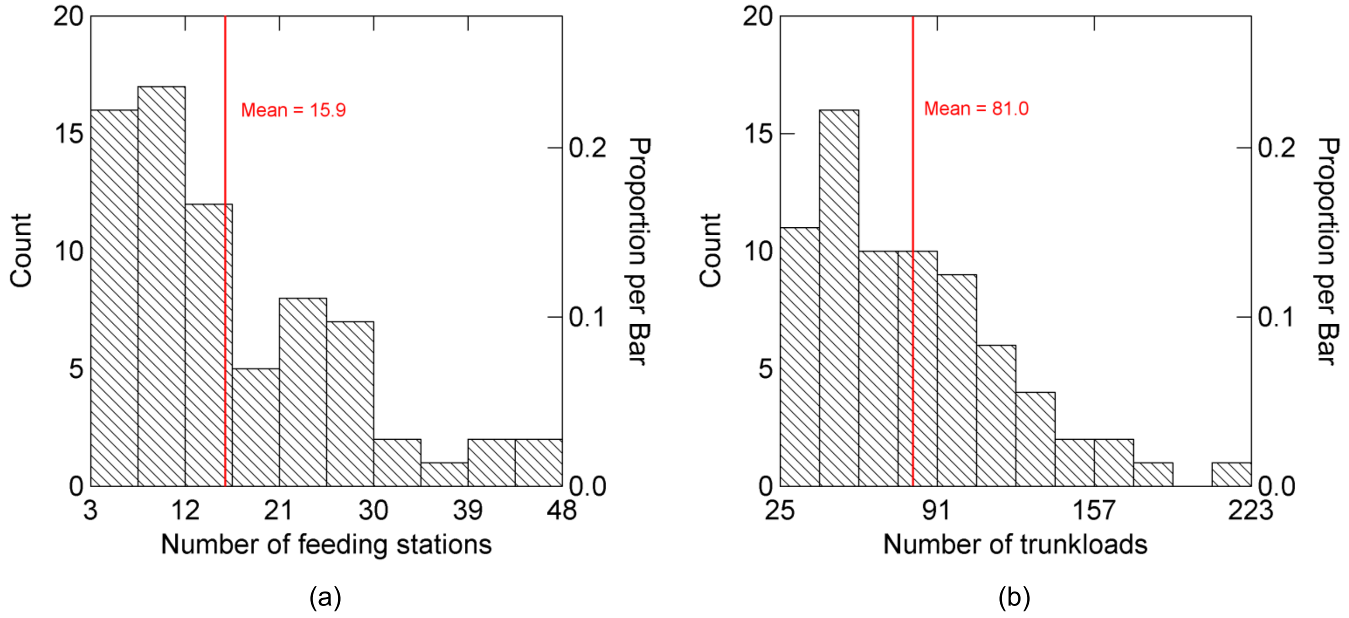

Figure 6.2 Histograms showing the frequency of (a) number of feeding stations and (b) number of trunkloads per observation (n = 72).

Elephants were recorded feeding from 101 plant species. However, this figure is an underestimate because for many trunkloads the plant species consumed could not be identified. Within each food type, certain plant species were eaten noticeably more often than others. These included: *Pupalea lappacea* (forb); *Panicum maximum* (green and mixed grass); *Urochloa mosambicensis* (green grass); *Grewia bicolor* (bark from canopy braches, green leaves, leaves and stems, and roots); *Colophospermum mopane* (green leaves, leaves and stems, bark from canopy branches, bark from main stem, and stems); *Acacia nigrescens* (green leaves, leaves and stems, and bark from roots); *Albizia petersiana* (green leaves); *Ehretia amoena* (green leaves); *Acacia tortilis* (leaves and stems, roots, and bark from main stem); *Dalbergia melanoxylon* (leaves and stems); *Dichrostachys cinerea* (leaves and stems); *Hippocratea indica* (leaves and stems); and *Gymnosporia pubescens* (leaves and stems) (Figure 6.3).

Green grass was chosen as the primary food most often (32 times), followed by green forbs (21 times) and green leaves (17 times). Both mixed grass and bark from canopy branches were only chosen as the primary food once.

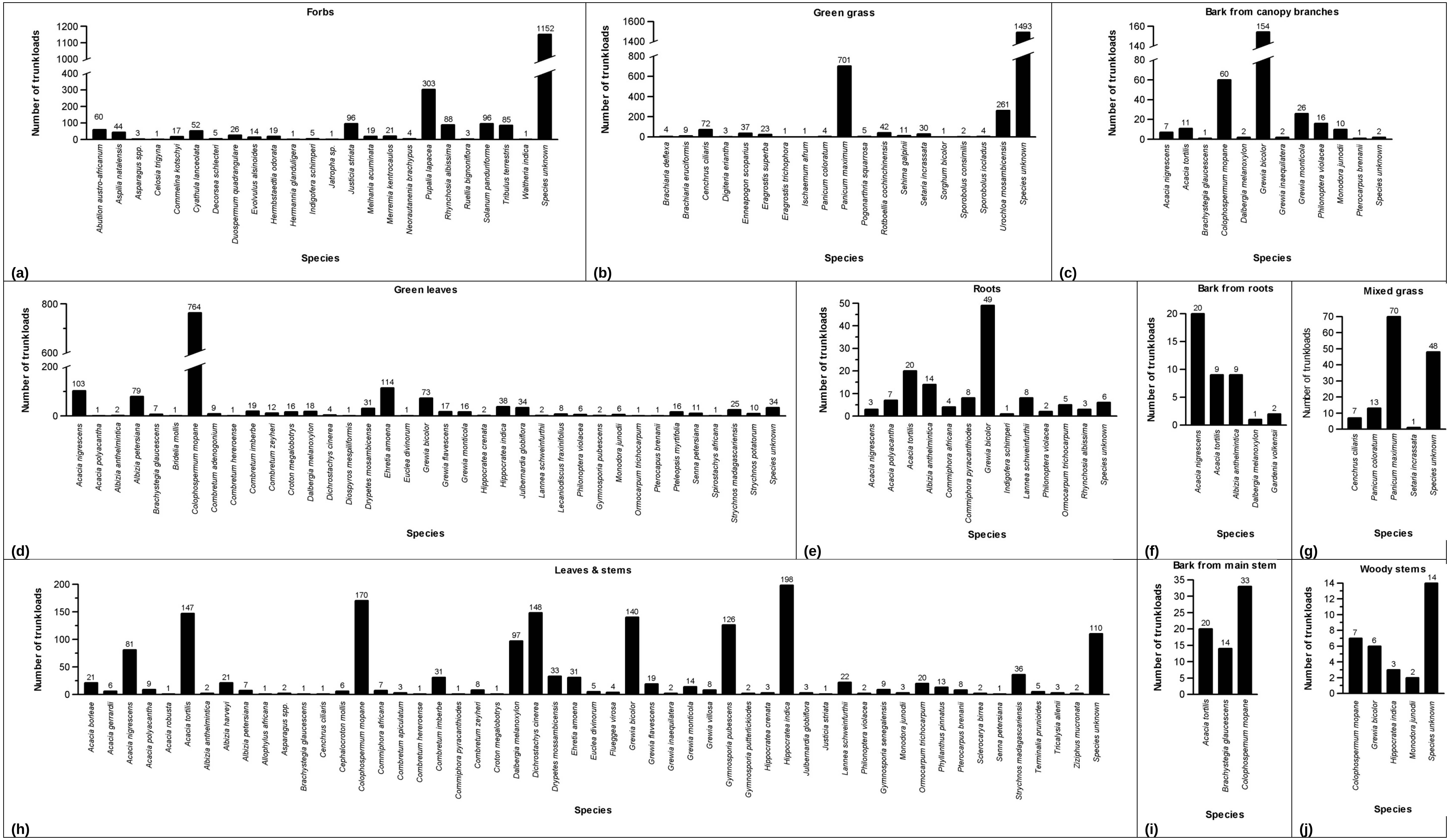

Figure 6.3 Charts showing the number of trunkloads consumed of each plant species for (a) forbs, (b) green grass, (c) canopy bark, (d) green leaves, (e) roots, (f) bark from roots, (g) mixed green and dry grass, (h) leaves and stems, (i) bark from main stem, and (i) woody stems.

The parameter estimate for the short-term rate of protein intake ($\beta = 2.27$, S.E. = 0.55) was highly significant (t-ratio = 4.16, P = 0.00003) indicating that the rate of protein intake had a strong positive influence on choice of the primary food type (Figure 6.4). The odds ratio was 9.68, with upper and lower 95 % confidence intervals of 28.19 and 3.33 respectively. This meant that an increase in the rate of protein intake of 1 gs^{-1} increased the odds of a food type being chosen as the primary food source by a multiplicative factor of 9.68. The effect was considered genuine because the lower bound of the confidence interval for the odds ratio was greater than 1.

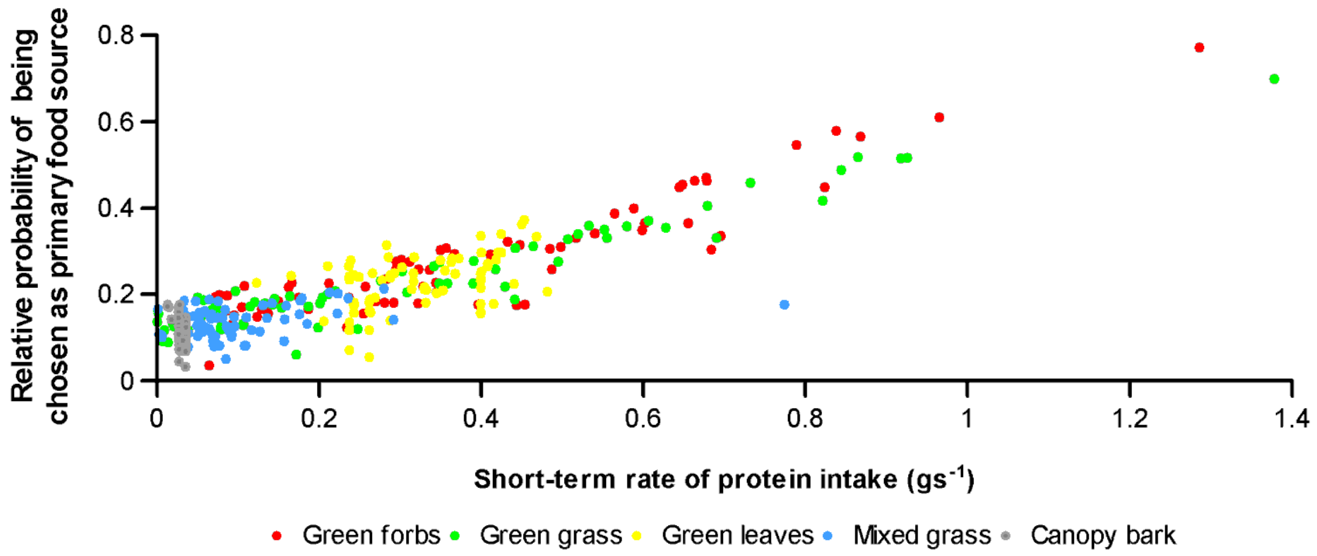

Figure 6.4 Chart showing the effect of varying levels of short-term rate of protein intake on the relative probability of a food type being chosen as the primary source of food. The relative probability was calculated using the estimated value of β (2.27) in the equation for the multinominal logit model given in section 6.2.1.

The highest rates of protein intake were achieved when feeding on green forbs and green grass, with green leaves, mixed grass and canopy bark supplying progressively lower rates (Figure 6.4). Because of the relationship between short-term rate of protein intake and relative probability of being chosen as the primary food type, the above ordering of food types was also reflected along the probability of choice gradient.

There was substantial variation in the probability of choosing canopy bark despite very little variation in its rate of protein intake. Consequently, choice of canopy bark may be influenced by factors other than rate of protein intake.

6.4. Discussion

6.4.1. *Ecological insights*

The results show the rate of protein intake to be a potentially important factor influencing diet choice by elephants and, in so doing, provide support for the hypothesis that elephants take advantage of a high passage rate of ingesta and process a large amount of food with cell solubles rich in energy and nutrients per unit time to meet their nutritional demands.

The seasonal change in the diet of elephants, which has been consistently reported by studies of elephant feeding behaviour (Buss, 1961; Bax & Sheldrick, 1963; Laws, 1970a; Field, 1971; Wyatt & Eltringham, 1974; Williamson, 1975; Field & Ross, 1976; Guy, 1976; Barnes, 1982; Owen-Smith, 1988; Kabigumila, 1993; de Boer et al., 2000; Osborn, 2004), is well explained by the influence of protein intake rate on diet choice. During the wet season, grass and forbs provide the highest rates of protein intake and, therefore, make up the bulk of the diet at this time. As the dry season progresses, the rate of protein intake from herbaceous food types declines below the level supplied by woody browse, which results in a switch from a diet predominantly composed of grass and forbs to a diet predominantly composed of leaves and stems from woody plants. Once woody plants have shed their leaves, elephants have no alternative other than to eat bark and roots, despite the very low rates of protein intake achieved when feeding on these food types.

It could be argued that preference for grass as opposed to browse during the rainy season is explained by the higher levels of chemical defence present in the latter (Shipley, 1999). However, this hypothesis is not supported by the fact that elephants consume large amounts of forbs during the rainy season, many of which are known to be chemically defended (e.g. *Acanthospermum* (Ali & Adam, 1978), *Tribulus* (Botha & Penrith, 2008), *Heliotropium* (Mohanraj et al., 1981; Asibal et al., 1989; Agarwal et al., 1995; Guntern et al., 2001), *Crotalaria* (Botha & Penrith, 2008), *Indigofera* (Garcez et al., 1989), *Sida* (Driemeier et al., 2000) and *Blumea* (Ahmad & Alam, 1996)). The consumption of forbs with high levels of secondary metabolites may adversely affect the health of elephants. For example, Flaccid Trunk Paralysis of elephants at Matusadona National Park in Zimbabwe (Kock et al., 1994) is thought to be caused by consumption of large quantities of *Heliotropium ovalifolium* and *Blumea gariepina* (Guntern, 2003).

Although the rate of protein intake proxy was able to explain choice of green forbs, green leaves, and mixed grass at both the coarse and fine scale, it was only able to explain choice of canopy bark at the coarse scale. This is possibly explained by a failure of the rate of protein intake to adequately represent the rate of intake of digestible energy by elephants when feeding on bark (i.e. the assumption that crude protein content and digestible energy are positively correlated is unlikely to hold for bark). However, it should be noted that in this study bark was never high on the preference hierarchy (relative probability of bark being chosen as the primary food choice did not exceed 0.2). This is possibly because the long handling time of bark makes it an unprofitable food type regardless of the potentially high levels of digestible energy it contains.

Dependency on an adequate rate of protein intake may provide an explanation for reports of coprophagy by elephants (Guy, 1977; Leggett, 2004) because when elephants eat their faeces they may be making use of undigested microbial protein contained therein. However coprophagy has been rarely recorded for elephants and therefore is unlikely to play a significant role in their nutrition.

Most published studies of resource selection by animals treat habitat and diet selection as separate processes because habitat selection occurs at the coarse scale whereas choice of diet occurs at the fine scale (Schaefer & Messier, 1995; Ginnett & Demment, 1997; Rolstad et al., 2000; Rettie & Messier, 2000; McLoughlin et al., 2002; Fortin et al., 2003; Martinez et al., 2003; Morin et al., 2005; Friar et al., 2005; Whittingham et al., 2005). In this thesis, the opposite stance was taken. It was postulated that the nutritional choices made by elephants at different spatial scales are directed towards achieving a common nutritional goal, and that the integrated effect of the nutritional choices made during habitat and diet selection can be represented in a statistical model by a single, functionally derived variable, namely the short-term rate of protein intake (see chapter 1). The results of this chapter, and those of chapter 5, show that the short-term rate of intake of digestible energy and nutrients (as indexed by the rate of protein intake) potentially has a strong influence on both habitat and diet selection by elephants and, in so doing, provide support for the idea that habitat and diet selection by animals should not be treated as separate processes but rather as interconnected processes that are driven by a common nutritional goal.

6.4.2. *Limitations and future improvements*

In this study, unlike most other studies of resource selection, the focal animals were not presented with each food type simultaneously because the choice set was delimited by the boundary of the relevant land unit as opposed to an area defined by a short radius around each feeding station. This approach rests on the assumption that the animal under study has prior knowledge of the potential availability of different food types in the land unit. This is because an animal may pass up an opportunity to feed on a particular food item in its path if it knows that there is a good chance it will encounter something better further on. In other words, each food type is still part of the choice set regardless of whether it is physically present when a decision is made about what or what not to eat. Prior knowledge of availability could be gained during previous bouts of foraging, and may improve with the number of days or years spent feeding in the land unit. Given that adult (> 15 years old) elephants were chosen as the focal animals, it is likely that the elephants under study had considerable knowledge of the availability of food types in each land unit and therefore the use of a discrete choice model without simultaneous presentation of each food type should not be inappropriate. Furthermore, patterns of diet selection that emerge from an analysis where each data point represents an accumulated set of feeding observations from within a land unit are likely to be more robust than those from a data set where each data point is a single observation from a feeding station. However, the effect of prior knowledge of food availability on diet choice requires further investigation.

In this study, the choice set was limited to five food alternatives whereas in reality elephants utilised in excess of 10 different forage types. The existence of a strong relationship between short-term rate of protein intake and diet choice justifies further study with a more comprehensive choice set.

The paucity of data from adult cows prevented an analysis of sex related differences in diet selection. An understanding of the differences in feeding behaviour between the sexes is important for the management of elephant-woodland systems because (1) adult bulls are more destructive feeders than cows (Barnes, 1982), and (2) density dependent effects that may act as natural controls on elephant populations are likely to be manifested when nutritional constraints are imposed on family units (O'Connor et al., 2007). For these reasons, future studies should focus on investigating whether the effect of the rate of intake of digestible energy and nutrients on diet choice differs between the sexes.

Use of the rate of protein intake to predict diet choice by elephants over large areas is limited by the fact that calculation of intake rate is highly data intensive. In this study, spatio-temporal change in the density of food patches was quantified using a ground-based approach. The development of remote sensing techniques that reduce the effort required to quantify patch density of different food types should be the focus of future research.

Chapter 7. Synopsis

7.1. Introduction

To predict resource selection by elephants, and its effect on vegetation structure and composition, an understanding of the processes that drive elephant feeding behaviour is required. For this reason, research into the foraging ecology of elephants should focus on uncovering functional relationships between the food resource and the feeding response. To this end, a functional hypothesis of the foraging strategy of elephants was developed and tested in this thesis. The principal tenet of the hypothesis was that if elephants are to meet their nutritional requirements they should adopt a foraging strategy that maximizes their rate of intake of highly digestible cell solubles. The hypothesis was supported empirically by data collected during the study and was consistent with the available literature.

In this chapter, the implications of the research methods and findings of the thesis are discussed with respect to the study of foraging ecology, and with respect to the dynamics and management of elephant – vegetation systems.

7.2. Foraging ecology

Feeding behaviour of large herbivores is notoriously difficult to study because, firstly, it is a complex process that is influenced by numerous factors and, secondly, many of its determinants vary spatially and temporally making them difficult to quantify over large areas and for long periods. For example, diet selection is influenced by seasonal and inter-annual variation in the phenology of plants, which results in a constantly changing array of available food types, each with its own chemical composition and set of constraints to harvesting, chewing and digestion. Choice of what and where to eat is further complicated by sex and age related differences in the ability to harvest, chew and digest food, and by non-dietary factors such as distance from surface water that constrain use of habitats. Study of foraging behaviour is especially difficult under natural conditions where the researcher has no control over the target animals or the environment in which they live. This is particularly true for elephants because they eat a wide variety of food types (10 were identified in this study) and forage over large areas, which exacerbates the already difficult task of quantifying the choice set.

Given the complexity of the foraging process, it is understandable why most research into elephant feeding behaviour has been limited to descriptions of easily observable features of foraging, such as seasonal variation in diet or sexual segregation in habitat selection, with little or no attempt to uncover the underlying causes of these phenomena. Although past research has described the characteristic features of elephant feeding behaviour, it has not uncovered the underlying principles and, therefore, little explanatory power has been gained.

To gain greater explanatory power, an attempt was made in this thesis to uncover the driving force behind the feeding response of elephants. This was done by firstly constructing a theoretical framework for the foraging strategy based on what is known about the body size, digestive physiology, and non-dietary requirements of elephants and, secondly, by testing the theory against actual landscape-level responses of elephants using a mechanistic foraging model. As far as the author is aware, this study represents the first attempt to investigate the foraging ecology of elephants using a true landscape-level approach.

The purpose of this section is (1) to highlight the theoretical and practical aspects of the study that were instrumental in its successful implementation, (2) to compare the approach used in this study with that employed in previous studies of herbivore foraging behaviour, and (3) to point out the new insights into the foraging ecology of elephants that were gained.

7.2.1. *A theoretical basis for resource selection*

Unlike most studies of resource selection, where the underlying ecological theory is implicit (Guisan & Zimmermann, 2000; Austin, 2002; Austin, 2007), this study began by constructing an explicit conceptual framework for the optimal foraging strategy of elephants that was based on the effects of body size, type of digestive system, and salient non-dietary factors. This was an important first step because (1) it identified a nutritional currency that could potentially be used to rank the profitability of habitats and food types for elephants, (2) it provided a theoretical foundation for the research that could be tested empirically, and (3) it integrated potential distal influences into a single proximal currency which served to reduce the complexity of the problem.

The theoretical analysis predicted that elephants should optimise their nutritional fitness by selecting habitats and diets that maximise their rate of intake of digestible energy and nutrients. The findings were consistent with this hypothesis and provided fresh insight into the foraging ecology of elephants. The benefit of integrating ecological theory with statistical modelling was also demonstrated.

7.2.2. *Detailed quantification of the pattern of resource availability at the landscape level*

The development of GPS and satellite collars has revolutionised the study of resource selection by free-ranging animals at both local and landscape scales (Douglas-Hamilton, 1998; Galanti et al., 2000a; Blake et al., 2001; Johnson et al., 2002a; Johnson et al., 2002b; Nielsen et al., 2003; Frair et al., 2005). However, meaningful interpretation of the fine-scale position data from these collars is only possible when spatial databases describing the environment of the landscape are available at an equally fine scale (Guisan & Zimmermann, 2000). It is the opinion of the author that the success of the landscape-level approach used in this study was largely due to the effort put towards accurately quantifying the spatio-temporal pattern of resource availability over the entire study landscape (see chapters 3 & 4). Considering that a true landscape-level response is driven by the relative profitability of the available habitats rather than by an absolute measure, a study that aims to uncover landscape-level influences must quantify resource availability simultaneously across the entire landscape. The species composition and phenological variation of the herbaceous and woody strata, the structure of the woody layer, the topo-edaphic variables that influence plant phenology, recent fire history, and the spatio-temporal pattern of salient non-dietary factors can be considered the minimum set of landscape-scale variables required to study the foraging ecology of mammalian herbivores at the landscape level.

It should be noted, however, that detailed quantification of resource availability at the landscape scale has only become practicable in recent times on account of manifold advancements in satellite and GIS technology. Despite these technological advancements, a large proportion of the required data still has to be collected using a ground-based approach, which is both time consuming and labour intensive. This makes studies that extend for longer than one season difficult because rapid changes in food availability between seasons are not easily quantified, especially when the vegetation resource is markedly heterogeneous. Future research should be aimed at developing remote sensing techniques that are capable of continuously collecting the necessary data over large areas.

7.2.3. *Functional representation of the plant/elephant interface*

Although variation in search time, handling time and bite mass across food types have long been recognised as important determinants of diet selection by herbivores (Cooper & Owen-Smith, 1986; Spalinger & Hobbs, 1992; Parsons et al., 1994; Farnsworth & Illius, 1996; Sauvant et al., 1996; Haschick & Kerley, 1997; Farnsworth & Illius, 1998; Pastor et al., 1999; Wilson & Kerley, 2003b; Baumont et al., 2004), attempts to explain the diet composition of elephants have to a large extent been based solely on analyses of the chemical composition of food types and plant species (Williamson, 1975; Osborn, 2004). In this study, a mechanistic ingestion model that functionally represented the plant/elephant interface showed that constraints to harvesting and chewing strongly influence diet selection by elephants (see chapter 4). In addition, by recognising that a high rate of food intake is made possible by simultaneous prehension and chewing of food, the mechanistic ingestion model revealed the important role played by the trunk in the nutritional ecology of elephants.

By functionally integrating the effects of seasonal variation in protein density, search time, handling time, and trunkload mass across food types, the mechanistic ingestion model provided a possible explaination for the seasonal change in the diet of elephants. Elephants may eat more grass during the rainy season because, at this time, the high patch density, short handling time and large trunkload mass of grass compensate for its low protein content to the extent that it has a higher rate of short-term protein intake relative to browse (Figure 4.62). With the onset of the dry season, grass begins to dry out and senesce. This has the effect of lowering the protein content, increasing search time, increasing handling time (because grass tufts must first be shaken to remove dry material before being ingested; see Table 4.2 and Table 4.3), and reducing the mass of a trunkload. The net result is a lower short-term rate of protein intake from grass relative to browse during the dry season, and hence the observed shift towards a diet largely composed of browse from woody plants.

Implementation of the ingestion model at the landscape scale also provided potential insight into why it should be necessary for some grazers to switch to a diet of browse at certain times, and why browsers rarely need to consume grass in large quantites (Clauss et al., 2003a). During the wet season, high quality grass is generally abundant in savannas and can be consumed at a higher rate than browse, making it a more profitable food source at this time (Figure 4.62). However, as the dry season progresses both the abundance and quality of the grass resource decline, which results in a lower rate of intake than when feeding on grass during the wet season. The potential for a nutritional deficit caused by the reduction in the rate of intake is further increased by a simultaneous decline in grass quality. As the dry season continues a point is eventually reached when, in most parts of the landscape, it is more profitable for grazers to feed on browse than grass. This is because the properties of the browse resource (quality, bite mass, search and handling times) are relatively constant and are not subject to marked seasonal fluctuations. Therefore, in order to meet their nutritional requirements during the dry season, grazers must either seek out the parts of the landscape where changes to the grass resource, relative to wet season conditions, have been negligible (e.g. swamps, flood plains or bottom lands with high levels of residual soil moisture), or they must begin to include larger portions of browse in their diets. Browsers, on the other hand, do not have to deal with a marked decline in profitability of their primary food source because savanna landscapes generally provide a relatively constant supply of browse over the annual cycle (Figure 4.62). This is because (1) woody plants are generally deeper rooted than herbaceous plants, and therefore have access to soil water for longer, and (2) variability in the timing of leaf drop and flush across woody plant species means that invariably there is some component of the woody layer with green leaf at any given time (see chapter 4).

Most studies of resource selection by herbivores have not attempted to include both top-down and bottom-up cross-scale interactions in their models of habitat and diet selection (Johnson et al., 2004). The use of a mechanistic intake model to create a functional predictor variable (short-term rate of protein intake) that was the integrated result of foraging decisions made at fine to coarse scales proved to be a simple way of incorporating the effects of cross-scale interactions in the selection process. The technique also served to simplify the habitat selection models and, in so doing, made them easier to interpret.

7.2.4. *Sex related differences in feeding behaviour*

Although sex related differences in diet and habitat selection by elephants have been recorded and potential explanations presented (Stokke, 1999; Stokke & du Toit, 2000; Stokke & du Toit, 2002; Shannon et al., 2006; Smit et al., 2007), a mechanistic justification for these phenomena based on sex related differences in handling time, trunkload mass and the relative importance of dietary and non-dietary factors has not been previously presented. This study showed that sex related differences in trunkload mass and handling time across food types (see Chapter 4) may cause bulls and cows to have different spatio-temporal patterns of the rate of energy and nutrient intake over the landscape and that this may ultimately result in different patterns of habitat and diet selection between the sexes. Sexual segregation in habitat selection may also be explained by the short-term rate of protein intake being a more important explanatory variable than cost distance from water for the spatial distribution of family units, and the converse being the case for the spatial distribution of bulls.

7.2.5. *Importance of a landscape level perspective*

The study showed that a true landscape-level approach is required to study habitat and diet selection by elephants. Short-term rate of protein intake and cost distance from water were shown to influence elephant distribution at the landscape level. In other words, the attractiveness of a habitat to elephants was not determined by the absolute measure of the factors for the habitat in question, but rather by a measure that is relative to the other habitats in the landscape. Development of a generic model to predict habitat selection by elephants throughout their range will only be achieved by using a technique that accounts for this conditionality of response.

The results of the study also highlighted the importance of not only testing the congruence of predictor variables across multiple spatial scales, but also testing the predictive consistency of variables over time.

7.3. Dynamics of elephant-woodland systems

In this section, problems associated with previously published explanations for the “elephant problem” are discussed and a new hypothesis that is based on the findings of this thesis is presented.

Three hypotheses have been put forward to explain the “elephant problem” namely: compression (Buechner & Dawkins, 1961; Lamprey et al., 1967; Laws & Parker, 1968; Watson & Bell, 1969; Field, 1971), intrinsic eruption (Laws, 1970b; Caughley, 1976) and stable limit cycle (Caughley, 1976). Note that the multiple stable state models of Pellew (1983) and Dublin et al. (1990) are discussed as extensions of the compression hypothesis and, therefore, are not listed separately.

7.3.1. *Compression hypothesis*

The compression hypothesis suggests that prior to the development of the “elephant problem” equilibrium prevailed between elephants and woodlands. The rapid growth of the human population in Africa during the early 1900’s caused human settlement to expand and encroach on resources, which forced elephants to take refuge in protected areas that constituted a fraction of their former range. This resulted in artificially high densities of elephants in the protected areas and, due to increased pressure of herbivory, the equilibrium point was displaced away from the woodland vegetation phase towards a shrubland or grassland phase. Pellew (1983) and Dublin et al. (1990) showed that once woodlands had been converted to shrubland or grassland, regeneration back to a woodland phase could be prevented by the combined effects of elephants, fire and other herbivores.

7.3.2. *Intrinsic eruption hypothesis*

The intrinsic eruption hypothesis (Laws, 1970b; Caughley, 1976) is similar to the compression hypothesis in that it assumes the existence of equilibrium between elephants and woodlands prior to the development of the “elephant problem”. However, it offers a different mechanism for the displacement of this equilibrium. The hypothesis asserts that the “elephant problem” was caused by a drastic change that happened sometime in the past and then manifested itself as a marked increase in elephant density several generations later. Laws (1970b) suggested that a drastic change of this sort could have been caused by control shooting measures, elimination of poaching without substituting rational cropping, direct change of habitat by forest management or burning, and compression. Caughley (1976) suggested that the rinderpest panzootic that swept Africa from 1889 to 1896 may have reduced the competitive effect of other animals to such an extent that an eruption in the elephant population ensued.

7.3.3. *Stable limit cycle hypothesis*

The stable limit cycle hypothesis was proposed by Caughley (1976). The principal axiom of the hypothesis is that there is no attainable natural equilibrium between elephants and woodlands. The relationship between elephants and woodlands is viewed as a stable limit cycle in which elephants increase while thinning the woodland and then decline again when the trees become too sparse. When elephant populations decline to low densities the trees are able to regenerate and this in turn triggers an increase in elephants and the cycle repeats.

7.3.4. *Problems associated with the hypotheses*

The compression and intrinsic eruption hypotheses are based on the assumption that equilibrium existed between elephants and woodlands prior to the development of the “elephant problem”. However, they do not provide a mechanistic basis for this equilibrium and, as a result, leave half the problem unanswered. Elephant populations continue to increase at healthy rates despite being compressed (Blanc et al., 2005). What then prevented elephant populations from reaching compressed densities, with associated impacts to woodlands, prior to the emergence of the “elephant problem”?

The stable limit cycle hypothesis assumes that elephant populations peak at the woodland vegetation phase and decline as woodlands are converted to shrubland. This is contrary to the findings of this thesis. When feeding, elephants favour shrubland over woodland or forest (Guy, 1976; Jachmann & Bell, 1985) because shrubs offer higher rates of food intake than trees on account of shorter prehension times of the more easily accessible browse (trees often have to be felled before browse can be harvested from them (see chapter 4)). This is most obvious in forest habitats where elephants favour the young regeneration patches over areas with mature trees (Laws, 1970a). Elephants, through their foraging behaviour, tend to convert woodlands into shrublands and, in so doing, change the vegetation to better suit their needs (Jachmann & Bell, 1985; Smallie & O'Connor, 2000). For this reason, conversion of woodland to shrubland should lead to an increase in elephant populations and not a decline. This is indeed what appears to happen in reality. Elephant populations across Africa, and in particular southern Africa, have continued to increase despite conversion of woodlands to shrublands (Cumming, 2005; Blanc et al., 2005). However, elephant populations cannot increase indefinitely because further habitat modification will drive the shrubland phase to a grassland phase, and the population will begin to decline (see Laws & Parker, 1968). This is because members of family units can only maintain high rates of protein intake when feeding on green grass (Figure 4.62), which is scarce in most grasslands during the dry season. Consequently, when green grass or forbs are unavailable cows require a source of browse if they are to maintain reproductive output (see chapter 4). The decline in elephant numbers will, in turn, allow the vegetation to recover back to a shrubland phase and the elephant population will then begin to increase again. Clearly, if the largest population of elephants is sustained at the shrubland phase and not at the woodland phase, and if a stable limit cycle is the correct representation of the dynamics of the system, then there is no place for woodlands at all in the elephant-vegetation relationship. How then did woodlands exist prior to the development of the “elephant problem”?

It has been suggested that the wholesale slaughter of elephants for ivory that continued for at least 4000 years (Spinage, 1994) reduced the elephant population to such an extent that woodlands were able to develop where they could not before (Gillson & Lindsay, 2003). Although the reduction in elephant numbers may have promoted the development of woodlands, there is paleoecological evidence that extensive areas of woodland existed in Africa prior to the ivory trade (Adams & Faure, 1997; Olago, 2001; Jacobs, 2004). This suggests that over the course of time woodlands have been a natural component of the African landscape and are not merely an anthropogenic artefact.

In the following section, an alternative hypothesis to explain the “elephant problem” that is based on the findings of this thesis is presented along with supporting evidence from the literature.

7.3.5. *Alternative hypothesis*

The alternative hypothesis explains the upsurge in woodland loss is in terms of (1) a man-induced shift in the diet of elephants, and (2) a breakdown of the natural controls of elephant populations.

Diet shift

The underlying basis of the diet shift component of the hypothesis is that elephants are primarily grazers that will browse only when grass of sufficient quality and quantity is unavailable (see chapter 6). The widespread destruction of woodlands is explained in terms of a shift from a primarily herbaceous diet to a diet largely composed of browse. This notion contrasts with the previously published hypotheses that explain woodland destruction in terms of an increase in elephant density (Caughley, 1976). It is argued that elephants, and in particular bulls, are best suited to eating green grass because it provides the highest rate of protein intake relative to other food types, and that elephants have been forced to shift their diet by a man-induced reduction in the availability and accessibility of suitable grass resources. It should be stressed that woodlands can develop and persist only when elephants have access to "key" grass resources and not simply any type of grass resource. This is because not all grass species provide elephants with food of a superior quantity and quality to that provided by other food types. Elephants prefer green material from soft, broad-leafed grasses (e.g. *Panicum*, *Urochloa*) with a high ratio of cell contents to structural material. They seldom eat senescent (dry) grass material. A key grass resource area for elephants may be defined as one that supplies green grass of adequate quality during the dry season. These areas may occur in fixed points in the landscape (e.g. swamps, dambos, floodplains, shorelines of lakes), or at variable positions depending on the spatial pattern of rainfall. It is proposed that in the past elephants, and in particular bulls, fed primarily from key grass resources and, as a result, woodlands were able to develop and persist. In contrast, the diet of modern elephants is primarily composed of browse (Cerling et al., 1999).

In Africa, significant impact by man on elephant populations began with the ivory trade. There is evidence that humans have hunted proboscideans since prehistoric times (Surovell et al., 2005) but whether prehistoric man had a significant impact on populations of proboscideans or not is still a subject of much debate (Grayson & Meltzer, 2003; Wroe et al., 2004; Grayson & Meltzer, 2004; Haynes, 2007). The effect of the ivory trade on the elephant populations of Africa has been documented (Spinage, 1994) and explored using models (Milner-Gulland & Beddington, 1993). However, the effect of this long period of hunting on elephant behaviour and, in particular, habitat and diet selection has received little attention. It is argued that hunting not only reduced elephant numbers but also caused a departure from the ideal free distribution that would result if elephants were allowed to roam unmolested. In other words, elephants could no longer forage optimally because safety became a more important habitat selection criterion than food quality and quantity. Elephants generally respond to hunting pressure by selecting closed habitats that provide concealment, such as forest or thickets, in preference to open habitats such as savanna or grassland. This response is expected to be associated with an increase in the proportion of browse in the diet because grass is less abundant in heavily wooded areas. During his hunting expeditions, Buss (1961) noted that members of breeding herds in the North Bunyoro region of Uganda appeared nervous when feeding in the open but would noticeably relax and move more slowly when they encountered stands of tall, mature grass or woodlands. He suggested that this behaviour probably affected the proportions of mature and young grass that the elephants ate. De Boer et al. (2000) compared the diet and distribution of elephants in Maputo Elephant Reserve before and after the civil war in Mozambique. Prior to the civil war, when poaching levels were low, elephants preferred open grass plains. In contrast, elephants selected dense forest patches, when poaching levels were high after the civil war. It was concluded that the change in habitat preference was a reaction to poaching and that it was probably the cause of the increased browse content in the post civil war diet of elephants. Selous (1881) recorded that by 1870, elephants, in what is now Zimbabwe, had retreated into the districts infested with tsetse flies in response to hunting pressure. The tsetse fly afforded some protection to elephants because they prevented hunting from horseback. To hunt elephants on foot was considered by many to be "too fatiguing a pursuit to be followed with much chance of success by Europeans" (Selous, 1881). In the 1870's, tsetse flies were restricted to the hot, low-lying, semi-arid regions of Zimbabwe. Availability of green grass in these regions is highly variable because of frequent droughts (Dye & Spear, 1982), but browse production is relatively stable (Kelly & Walker, 1976). Therefore, it is logical to assume that the retreat of elephants into areas infested with tsetse flies was associated with an increased utilisation of browse.

Change in habitat selection by elephants in response to hunting during the period of the ivory trade provides a possible mechanism for a shift towards a diet composed primarily of browse. However, the effect of this change in diet was only manifested after the trade in ivory collapsed, when laws controlling elephant hunting were put in place, and elephant populations began to recover.

When large-scale hunting of elephants in east and southern Africa ended at the turn of the 19th century (Spinage, 1994), elephants were actively prevented from recolonising their former range because much of it had been set aside for commercial agricultural development by the ruling colonial governments (Neumann, 2002). Instead, areas within the bounds of the compressed elephant range, that were least suitable for agriculture, were set aside as game reserves (Davison, 1967; Attwell & Cotterill, 2000). These were invariably the forested areas that required considerable effort to clear for agriculture or the areas that were either deficient in rainfall or infested with tsetse flies and, therefore, unsuitable for cattle ranching or crop production. Some game reserves were set up in areas with extensive grasslands (e.g. Murchiston Falls and Queen Elizabeth National Parks in Uganda, Serengeti National Park in Tanzania and Masai Mara National Park in Kenya) but the grasslands of these high rainfall areas were apparently of inappropriate composition for offering adequate nutrition to members of family units as is evident by the fact that cow elephants within Murchiston Falls National Park showed symptoms of poor nutrition (Laws & Parker, 1968).

It is argued that because the prevailing (i.e. compressed) elephant distribution as opposed to the historic distribution was used as a benchmark for elephant habitat, most protected areas did not provide elephants with grass of a satisfactory quantity and quality during the dry season and, therefore, elephants were essentially locked into a diet primarily composed of browse. As elephant populations began to increase under the protection afforded by the reserves, the effect of the enforced shift in diet was manifested in the destruction of woodlands. In addition, on account of the dry conditions, browse leaf fall occurs early in many protected areas, and elephants are forced to consume bark and roots for an extended part of the dry season. It is argued that this is a compounding influence on impact to woodlands. It should be noted that elephant populations have been able to increase despite the enforced shift in diet because the nutrition of cows has possibly been less affected and than that of bulls (members of family units are better adapted to eating browse than bulls (see chapter 4)). In fact, conversion of woodlands to shrublands may well have improved feeding conditions for cows and calves (Jachmann & Bell, 1985; Smallie & O'Connor, 2000).

Because man has continued to impinge on the key grass resources available to elephants the situation has become worse over time. In many countries, it is no longer feasible for elephants to leave protected areas in search of green grass produced by rainfall outside reserve boundaries and, in many cases, dispersal routes to flood plains or swamps have been cut off (Spinage, 1994). Instead, the drive to seek out high quality grass resources has been satisfied by crop raiding, which has become a widespread problem (Bhima, 1998; Smith & Kasiki, 2000; Hoare, 2000; O'Connell-Rodwell et al., 2000; Wambwa et al., 2001; Hoare, 2002; Omondi et al., 2004). Many key grass resources have been put under the plough or have become degraded as a result of heavy use by domestic stock (Roberts, 1988; Kairu, 2001; Jenkins et al., 2003; Schuyt, 2005; Mtahiko et al., 2006). The hydrology of rivers has been disrupted through the degradation of catchments and the construction of dams. This has altered the flood regimes of many rivers (Hughes, 1988; Nilsson & Berggren, 2000; Snoussi et al., 2007) and created more xeric conditions on their banks and flood plains, which has reduced the availability of green grass during the dry season (Jarman, 1971; Jarman, 1972; de Longh et al., 2004). The proliferation of artificial water points has increased populations of water dependent species such as buffalo and zebra within reserves and cattle outside of reserves, and has lead to degradation of herbaceous vegetation (Thrash, 1998; Parker & Witkowski, 1999). It is argued that this has increased the level of competition between elephants and other grazers for key grass resources during the dry season. In addition, large portions of protected areas are burnt annually. This reduces grass availability at the critical time of the year and forces elephants to feed on browse.

In summary, it is argued that man has disrupted the historic foraging pattern of elephants by preventing them from ranging freely in search of the best patches of food. In the past, elephants were free to roam over very large areas. It is argued that this increased the probability of encountering food types high on their preference hierarchy and, therefore, prolonged the consumption of food types such as green grass that result in little impact to woodlands. For the past 100 years, elephants have become increasingly confined to areas where their preferred food types are only available for a short period during the growing season. For the remaining part of the year, elephants have had to make do with what is available in situ and, therefore, have been forced to feed on food types that result in higher levels of damage to woodlands.

Breakdown of natural controls of elephant populations

Although a man-induced shift in diet provides a possible explanation for the upsurge in woodland loss, it cannot explain why historically elephant populations did not continue to increase until they were forced to feed on woody browse because the large population size could no longer be sustained by key grass resources alone. This section describes how in the past elephant populations may have been controlled by natural processes and how anthropogenic influences have either directly or indirectly caused a breakdown of these natural controls.

The number of elephants that can be supported in an area is potentially determined by the amount of food available within daily walking distance from water (O'Connor et al., 2007). When elephant numbers increase food resources within reach of water begin to decline and density-dependant effects manifest as an increased age to first breeding, a longer inter-calving period, and increased juvenile mortality (Buss & Savidge, 1966). These effects are exacerbated by drought (Dudley et al., 2001) and potentially act as natural controls on elephant populations.

Although the relationship between elephant population size and the amount of food available within daily walking distance from water was not investigated directly by this study, it was shown that habitat selection by elephants is potentially strongly determined by an interaction between food availability and distance from water, with prime habitat being characterised by an abundant supply of high quality food in close proximity to water (see chapter 5). It is argued that the widespread practice of artificially supplying water to previously waterless areas has increased the availability of prime habitat and resulted in an increase in the number of elephants that can be supported in a given area. Historically elephants would have had to subsist on the food available in the vicinity of far fewer water points (water would have been restricted to natural sites only) and this may have limited elephant populations to lower levels.

Reduction in the extent of sexual segregation in habitat selection during the dry season, due to a shift in the diet of bulls, may also have caused a break down of natural population regulation. When adult bulls and family units occupy the same feeding areas, adult bulls tend to improve availability of browse for members of family units by felling trees whose canopies could not otherwise be accessed by cows and calves. During the hot dry season, it is a relatively common sight to see members of family units rush to browse on the canopy of a tree that has just been pushed over by an adult bull (pers. obs.). The increased level of browse available to family units as a result of the feeding actions of adult bulls during the critical time of the year may provide an additional explanation for the rapid growth of elephant populations despite compression.

It is important to note that given the two parts to the hypothesis it is possible to have a scenario whereby woodland loss takes place despite the elephant population being stable at low density. In other words, because of the shift in diet development and persistence of woodlands may not be achieved by only controlling elephant numbers.

Evidence in support of the hypothesis

There is evidence that elephants will graze in both the wet and dry seasons if green grass is available. Elephants have been recorded feeding on grass or sedges in swamp, marsh, or floodplain habitats during the dry season in Amboseli National Park, Kenya (Western & Lindsay, 1984); Lake Albert Marsh, Uganda (Buss, 1961); Gorongosa National Park, Mozambique (Tinley, 1977); Logone floodplain, Cameroon (de Longh et al., 2004); Maputo Elephant Reserve, Mozambique (de Boer et al., 2000); and Mweru Marsh, Zambia (Bulpin, 1987). Between June 1984 and May 1985, elephants in Ngorongoro Crater, Tanzania, grazed on the sedge *Cyperus immensus*, which remained green during the dry season and was particularly abundant in the crater at that time (Kabigumila, 1993). In Ruwenzori National Park, Uganda, elephants were able to graze year round by utilising green grass found on the periphery of thickets during the dry season. Elephants pushed back the branches of thickets with their tusks to get at the verdant growth (Wyatt & Eltringham, 1974). Tinley (1977) records that when extensive areas of the grass stratum of the Rift Valley of Gorongosa National Park, Mozambique, were burnt by dry season fires, excessive damage to woodland in other habitats by elephants was buffered by the availability of green pastures in marsh areas. In the north Bunyoro region of Uganda, grass comprised 88 % of the total food material in the stomachs of 71 African elephants collected during the dry season of 1958-59 (Buss, 1961). Although elephants spent considerable time in woodlands, only 10 % of the food material utilized by the 71 elephants consisted of leaves, twigs and fruits of trees and shrubs. In 1980 and 1981, elephants in Lake Manyara National Park, Tanzania, spent most of their diurnal feeding time grazing grass on the lakeshore (Kalemera, 1989). The level of Lake Manyara fluctuates so when rainfall is high for a period, the grasslands on the shore are flooded and elephants are forced to browse in the surrounding woodlands, but in dry periods the lakeshore is exposed and grazing increases.

Strong evidence in favour of the hypothesis comes from the impact of the construction of Magda dam on habitat selection by elephants in Waza National Park in northern Cameroon (de Longh et al., 2004). After the construction of the dam in 1979, the perennial grass vegetation of the downstream floodplains was replaced by annual grass cover (de Longh et al., 2001). This caused a change in habitat selection by elephants during the dry season, with significantly more time being spent in the surrounding savanna woodlands than in the floodplain. This, in turn, resulted in increased impact to the woodlands. In 1994, approximately 30 % of the original natural floodplain was restored by initiating an artificial flooding regime. The partial restoration of the floodplain induced a shift in habitat selection back to that which prevailed prior to the construction of the dam, with elephants spending more time in the floodplain and less in the surrounding woodlands. The shift in habitat selection was attributed to the increase in perennial grass cover in the floodplain that occurred between 1994 and 1997. The change in habitat use had the positive effect of releasing the woodlands from excessive pressure of exploitation.

Another line of evidence in favour of the hypothesis comes from an analysis of the stable isotope record of modern and fossil proboscideans carried out by Cerling et al. (1999). In tropical Africa, most trees and shrubs use the C_3 photosynthetic pathway and have $\delta^{13}C$ values between –22 and –35 (averaging about –27), whereas most tropical grasses use the C_4 photosynthetic pathway and have $\delta^{13}C$ values between –10 and –15. The differences in photosynthetic pathway allow a *post hoc* determination of the diet of herbivorous mammals because the $\delta^{13}C$ of tooth enamel, which is resistant to isotopic exchange, preserves a record of diet. Cerling et al. (1999) analysed $\delta^{13}C$ of tooth enamel from 43 savanna elephants from Kenya, and 27 forest elephants from Kenya and the Republic of Congo. The results, along with other published data for modern elephants in Africa, showed that modern elephants are primarily browsers. Cerling et al. (1999) also analysed the $\delta^{13}C$ of tooth enamel for fossil *Loxodonta* and *Elephas* in Africa between 5-1 million years ago and found a predominantly grazing (C_4) diet. The results clearly showed that there has been a shift from a historical diet composed primarily of grass to a modern diet largely composed of browse. However, the point in time at which the shift took place is yet to be determined.

Future research

A test of the diet shift component of the hypothesis could be conducted by examining the extent of damage to woody vegetation in protected areas with varying abundance of green grass during the dry season. Less elephant-induced damage would be expected in reserves with an abundant supply of suitable grass than in reserves where green grass is scarce for a large portion of the annual cycle. A test could also be conducted in a single reserve by determining whether annual woodland loss is negatively related to inter-annual variation in the availability of green grass, or opportunistically by determining whether increased access to key grass resources has a mitigating effect on impact to woodlands.

Tests of the population regulation component of the hypothesis could be conducted by comparing the growth rates of elephant populations across reserves with varying amounts of artificial surface water, or by determining whether closure of artificial water points has the effect of reducing the size of elephant populations.

7.4. Implications for management

7.4.1. *Restoration of historic diet by increasing access to key grass resources*

A number of authors have suggested the creation of mega-parks as a potential solution to the “elephant problem” (Gillson & Lindsay, 2003; van Aarde & Jackson, 2007b). It is argued here that the size of protected areas, although important, is not the main problem, but rather the quality and abundance of resources contained within their boundaries.

The study showed that (1) elephants attempt to maximize their rate of intake of cell solubles rich in energy and nutrients, and (2) that rates of energy and nutrient intake (as measured by a protein intake proxy) are highest when elephants feed on green grass and forbs (see chapters 4 & 6). This implies that, as optimal foragers, elephants are driven to seek out areas with an abundant supply of these food types. However, they will only achieve this goal if green grass and forbs are available in the area in which they are free to roam. For this reason, management should aim to increase availability of suitable herbaceous forage during the dry season by configuring the boundaries of protected areas to include key grass resource areas such as swamps and floodplains. By prolonging the availability of suitable herbaceous forage over the annual cycle, increased access to key grass resources may help to restore the historic diet of elephants and, in so doing, may curtail elephant-induced woodland loss.

Although there is a better chance of isolated rainfall events and therefore patches of green herbaceous vegetation occurring within the bounds of a large reserve than a small one, rainfall is considered too variable to reliably provide green grass during the dry season. Consequently, inclusion of permanent swamps or floodplains within protected areas is considered to be a more reliable means of increasing the availability of green herbaceous forage than increasing reserve size.

Restoration of the historic diet of elephants through increased access to key grass resources should also promote sexual segregation of habitat selection during the dry season. When sexual segregation is pronounced, members of family units will no longer benefit from increased availability of browse caused by bulls felling trees. The reduction in the amount of food available to members of family units during the critical time of the year may strengthen density-dependent effects and ultimately limit the growth of elephant populations.

7.4.2. *Conservation of key grass resources*

A key grass resource area may be defined as that which supplies elephants with an abundant supply of green herbaceous forage during the dry season (see Illius & O'Connor, 1999; Illius & O'Connor, 2000). Note that elephants seldom eat senescent (dry) grass material. Examples of key grass resource areas include swamps, marshes, floodplains and dambos. It is argued that, by supplying elephants with a source of green herbaceous forage, these areas buffer woodlands against excessive impact by elephants during the dry season. However, the ecology of these important components of the landscape is often disrupted by degradation of catchments, the construction of dams, and by abstraction of water for agriculture or industry. This ultimately results in more xeric conditions and loss of function. If woodlands are to develop and persist, it is imperative that management actions be carried out to lessen the negative impacts of these hydrological disruptions. A classic example is the management of the Logone floodplain in northern Cameroon (de Longh et al., 2001; de Longh et al., 2004). By partially restoring the flood regime, which had been disrupted by the construction of Magda dam, management were able to restore the natural ecology of a portion of the floodplain. This had the knock-on effect of shifting the dry season attentions of the local elephant population away from the surrounding woodlands and back to the perennial grasses of the floodplain, thereby reducing the level of impact on the woodlands.

7.4.3. *Artificial surface water*

Manipulation of artificial surface water has long been recognised as a potential tool for controlling both the spatial distribution and the number of elephants that can be sustained in a given landscape (Davison, 1967; Owen-Smith, 1996; O'Connor et al., 2007; Chamaillé-Jammes et al., 2007). The findings of this thesis provide further insight into its potential use as a management tool.

Distance from water had a strong influence on the spatial distribution of both adult bulls and family units (see chapter 5). In many instances, the probability of encountering elephants declined markedly with only relatively short distance from water. This finding supports the idea that the spatial distribution of artificial water can be manipulated to create partial refugia from elephants (O'Connor et al., 2007) and shows that this can be achieved even in medium- to small-sized reserves.

The study also showed that the effects of manipulating surface water on the distribution of elephants can only be predicted when water distribution is considered in conjunction with the spatio-temporal pattern of the rate of protein intake. Surface water will exert a stronger attractive force when it is situated in areas where elephants can achieve a higher rate of protein intake than in areas where rates of protein intake are lower.

Distance from water was the primary determinant of the distribution of bulls during the dry season, with short-term rate of protein intake being of secondary importance. The converse was true for family units (see chapter 5). This finding has important implications for management because it indicates that the feeding areas of adult bulls should be more easily manipulated through the configuration of artificial water points than those of family units.

By contrast, the difference in relative importance of distance from water and rate of protein intake in determining the distribution of adult bulls and family units indicates that travel distance between water and food should be more easily manipulated for family units than for adult bulls. Due to a strong dependency on high quality food, travel distance between food and water should be increased for family units by sighting artificial water points far from areas that provide high rates of protein intake. Increased travel distance between food and water may curtail growth of elephant populations by increasing age to first parturition, calving interval, and calf mortality (O'Connor et al., 2007). Travel distance should be less easily manipulated for adult bulls because they are not as dependent on high quality food.

7.5. Conclusion

In this thesis, a functional hypothesis for the foraging strategy of elephants was developed and tested. The hypothesis was found to be consistent with empirical data collected in a medium-sized reserve in a semi-arid savanna environment. However, to determine if the hypothesis has widespread relevance, further testing is required in large reserves and across a range of environmental conditions. Future research should strive to identify contradictions and make improvements where necessary.

An alternative explanation for the “elephant problem” is presented, with associated implications for the management of elephant-woodland systems. Where possible, restoration of the historic diet and natural controls of elephant populations through (1) increased access to key grass resources, (2) conservation of existing key grass areas, and (3) limiting surface water to historic sites, is seen as an alternative to the conventional management practice of actively controlling elephant numbers.

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