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Diversity in 198 Ethiopian linseed (*Linum usitatissimum*) accessions based on morphological characterization and seed oil characteristics

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Abstract

Morphological and molecular characterization of germplasm is important for the sustainable exploitation of crops. Linseed or flax (*Linum usitatissimum* L.) is a multipurpose crop grown in many environments for food, feed, fibre and industry. In Ethiopia, a centre of diversity for linseed, it is valued for food and export. Here, we aimed to develop and use a set of morphological descriptors to determine levels and patterns of diversity in Ethiopian germplasm from the tropical highlands (3-15°N, >2000 m a.s.l.) in 198 Ethiopian traditional varieties. The Ethiopian traditional varieties included plants with both fibre and oil-seed stem-branching morphotypes, although most were relatively small-seeded. Traditional variety oil quality was assessed; oil content was as low as 30% compared to 47% reported elsewhere. Days-to-flowering and days-to-maturity varied widely and were highly heritable. Ethiopian linseed had dominant and recessive yellow seed genotypes; some had a recessive twinned or conjoined-seed character. The descriptors developed here will be useful for genetic mapping and

selection of breeding lines. The results show the range of characters which can be exploited in breeding lines appropriate for smallholder and commercial farmers in Ethiopia, producing a sustainable, secure, high-value crop meeting agricultural, economic and cultural needs.

Key words: biodiversity, descriptors, Ethiopia, flax, landraces, varieties

Introduction

Linseed or flax (*Linum usitatissimum* L.) is an important crop for seed oil, stem fibre, and, to a lesser extent, flour. Linseed oil is used for paints, inks, varnish and other wood treatments, soap, linoleum, putty and pharmaceuticals. The fibre from flax is a widely used and valuable raw material for textiles, thread/rope and packaging materials; the straw and short fibre for pulp to produce special papers: for cigarettes, currency notes and artwork; and the wooden part serves as biomass energy or litter in cattle farming (Mackiewicz-Talarczyk et al. 2008; Rowland 1998). The strength, non-elasticity, repeated flexibility, and its recyclable nature, with a low density, was very attractive for use as a rope and thread; interest in its use is increasing (Jhala and Hall 2010) after many years of decline. Flax is a bast fibre consisting of the stem phloem, contrasting with fibres such as cotton that are from fibre cells. Linseed oil comprises five fatty acids: alpha linolenic acid (ALA), an omega-3 fatty acid, represents up to 61% of the whole fatty acid composition. It hardens in air (oxidizes), contrasting with other solvents for paints or putties which evaporate. Linseed meal and seed oil has many reported health benefits (Ayad et al. 2013). Although formerly a dual-purpose crop, most varieties are now specialized. Linseed grows in temperate, subtropical regions and tropical highlands.

L. usitatissimum, the only cultivated species from the genus *Linum,* has been cultivated for oil from the start of agriculture (Zohary and Hopf 2000) 8000 years ago, and slightly later for fibre. The whole genome sequence (Wang et al. 2012) is enabling more detailed study of the genes and diversity in commercially important accessions. Allaby et al. (2005) suggest that the cultivated species arose from a single domestication event from *L. bienne,* and the first domestication characters involved selection for annual habit, non-shattering of capsules and more efficient self-fertilization (Fu 2011; Durrant 1976; Hammer 1984). Currently the fibre type is the third largest textile fibre crop, and the oil-type is fifth oil crop in the world (Ottai et al. 2011), although with a magnitude lower production than the major fibres (cotton and jute) or other oil crops (maize, soybean, palm and *Brassica*). Of the 2,000,000 t annual world production, China, the Russian Federation and Canada account for more than half; Kazakhstan, USA, India and Ethiopia produce 120,000 to 160,000 t each.

Linseed is well utilized and valued for food in Ethiopia, the focus of the current work: for cooking oil; to make a beverage especially during fasting periods and visiting friends and relatives for cultural occasions; for stew or "Wot" substituting pluses (Geleta et al. 2002; Vaisey-Genser and Morris 2003; Worku et al. 2012); for export (women at family level use it as a cash crop); and medicine. However, its use for fibre in Ethiopia is hardly known (Engels and Hawkes 1991; Vavilov 1951; FAOstat 2014). Westphal (1975) suggests linseed has been cultivated for 3000 years by the Agaw in Ethiopia (Abyssinia), although this is not supported by archaeobotanical finds of *Linum* from Axum before 500 BC (Boardman 1999). Edwards (1991) reported that *L. strictum* L., *L. keniense* Fries, *L. holstii* Engl. (may also be *L. volkenssii* Engl.) and *L. trigynum* L. var. *sieberi* (Planch.) Cuf. are found in Ethiopia; Vavilov (1951) and Harlan (1969) have proposed Ethiopia as one of the origins and centres of diversity of linseed. In Ethiopia, linseed is part of a crop rotation of five to seven years with cereals and maize as good preceding crops (Worku et al. 2012; Rowland 1998; Seegeler 1983). Under intensive conditions, linseed seed yield ranges up to 3000kg/ha, compared to a world average of 1000kg/ha, similar to average yields in Ethiopia. It is cultivated by small holders only, both for home consumption and as a cash crop, and linseed is the second oil crop, next to Noug (niger, *Guizotia abyssinica* Cass., Asteraceae; Geleta and Ortiz 2013), being cultivated in areas where Noug and safflower are not cultivated (Seegeler 1983).

Low productivity of the crop, sensitivity to fungal diseases, damage by pests, poor response to chemical fertilizers and competition with weeds are major constraints on cultivation of the linseed crop in Ethiopia (Worku et al. 2012; Belayneh et al. 1990; Seegeler 1983). Plant genetic resources are represented by cultivars and wild relatives which breeders can exploit to improve agricultural production (Heslop-Harrison and Schwarzacher 2012; Diederichsen and Fu 2008). In world germplasm collections, there are 46,513 linseed/flax accessions reported (with perhaps 10,000-15,000 unique accessions; Lund et al. 2013), of which only 1% are from wild species (Diederichsen 2007). There is some evidence that fibre flax is over-represented compared to seed-oil collections (Diederichsen 2007). The Ethiopian Institute of Biodiversity Conservation (IBC/ETH; formerly The Plant Genetic Resources Centre Ethiopia, PGRC/E) was established in 1976 to promote collection, evaluation, documentation and scientific

studies; preserve and provide germplasm for researchers; and repatriate and introduce new germplasm into Ethiopia (Worede 1991) and has 3,433 linseed accessions (no wild species).

Describing the characteristics of a crop species based on standard descriptors is effective for better utilization and conservation of germplasm (Diederichsen and Richards 2003; Bioversity International 2007). Descriptors used in genetic resources documentation can be morphological or molecular molecular, and may also include contain passport, management, environment and site, characterisation and evaluation descriptions. Different researchers and gene bank curators characterized their linseed holdings using nationally developed guidelines (UPOV TG/57/7 2011; Maggioni et al. 2002). Descriptors, including those used for gene mapping and heritability studies, and understanding influence of environment on characters, are well developed for crops such as maize (*Zea mays*) (IBPGR 1991), sesame (*Sesamum indicum*) (IPGRI and NBPGR 2004), Brassica (*Brassica* spp.) (IBPGR 1990) and tea (*Camellia sinensis*) (IPGRI 1997), but linseed has variable descriptors, not all appropriate for the full range of diversity in cultivated and wild accessions. Robust descriptors are required for defining 'Distinctness, Uniformity and Stability' (DUS) of a variety (UPOV TG/57/7 2011).

In the present work, we aimed to generate a list of descriptors and identify benchmark genotypes for some morphological characters; to characterise Ethiopian linseed accessions, and determine the levels and patterns of morphological diversity; and survey agronomic characters of the linseed crop and the status of germplasm collection in Ethiopia.

Materials and methods

Plant materials

Two hundred linseed accessions (including a small number of segregating traditional varieties which were divided during the study) were used: 130 from the Institute of Biodiversity Conservation-Ethiopia (IBC/ETH); 21 accessions ("lines") from Ethiopian Agricultural Research Centres; and 49 collections from local farmers on-farm holdings. Selection of accessions acquired from IBC/ETH took into consideration their spatial distributions to represent the different parts of the country and agro-ecosystems as

well as the times of collections. The altitude, longitude and latitude ranges were from 1410 to 3440m, 05°17' to 14°38'N, and 34°57' to 42°40'E directions, lying in different former administrative regional divisions of Ethiopia (Fig. 1A). Samples collected from local farmers were also from different parts of the country.

Sites for field studies

Two environmentally different research field sites were used to grow the linseed crop: the University of Gondar campus located at 12°35′07″N 37°26′08″E and 2108 m a.s.l.; and Amhara National Regional State Agricultural Research Centre Gondar branch Dabat site located at 12°57′53″N 37°44′58″E and 2593 m a.s.l. Annual average rainfall, relative humidity and monthly average temperature of Gondar site are 1216 mm, 49.28% and 20.42 °C, respectively. A plastic house was used to study seedling characteristics, with some other laboratory-based germination tests.

Field trials

Field studies were conducted in five cropping seasons from 2009 to 2012 to characterize the germplasm and to study their agro-morphological characters and diversity under both rainfed and irrigated conditions. The 200 accessions were grown from July to December in 2009 in the main cropping season at both sites using a randomized complete block design (RCBD) field layout. Qualitative and quantitative characteristics were scored for 44 traits adopted from UPOV TG/57/7 (2011) and Maggioni et al. (2002) (IFDB). For spatial diversity analysis altitude information grouped into eight classes using Agarwal (1996) formula: —; where I is class width; L is the largest and S is the smallest values from altitude records, respectively; K is number of classes obtained from ; and n is total number of observations, which is 130.

Cotyledon leaf, boll and seed sizes were measured using Photoshop software from pictures scanned on a scaled computer flat-bed scanner (mean of five measurements). Seed coat colours were scored by comparison with standards by multiple observers. Boll dehiscence status from hybrid plants was measured by heating matured and dry bolls from 22°C to 80 °C for 40 min on an electrically heated clay disc ("Mitad") and then kept at room temperature for 15 min before scoring the degree of dehiscence. Oil content was measured from oven-dried and intact seed by continuous-wave nuclear magnetic

resonance spectroscopy (NMR; Newport 4000NMR Analyzer, Oxford Analytical Instruments, UK) as an average of three readings from three samples. Fatty acids compositions from intact seed samples were analyzed by using NIR System model 5000 (Foss NIRsystem Inc., MD, USA) in the reflectance mode at 1108 to 2492 nm with an 8 nm step. Each sample was scanned five times and the mean composition of each fatty acid in a sample seeds determined. Fifty seeds from each of 198 accessions were planted on compressed and levelled bed soil with two centimetres depth furrows in plastic house. The soil was kept wet constantly. Germination time (days), germination percentage, cotyledon leaf size, seedling stem colour, length of hypocotyl, and primary branch development were determined as seedling characteristics and vigour. Germination time (GT) was determined using: GT = $\frac{}{}$ where: N_n = number of seedlings emerged at the prescribed time (day); and T_n= the prescribed time (day) used to score germinated seeds. Germination percentage (GP) = $\frac{}{}$.

From the 198 sample germplasm accessions grown for characterization and diversity studies, 44 accessions were selected as core samples to conduct tests for DUS in the next growing season and then to develop descriptors. Quantitative and qualitative characters were examined using measurements from a single plant or its part (MS), or from groups of plants or their parts (MG); visual assessments from single plant or its part (VS), or from groups of plants or their parts (VG) depend on the element used to characterize the accession. Mean values with standard deviations were used to describe characters from accessions with a heterogeneous plant population. The Royal Horticultural Society (RHS) colour chart was used in natural daylight to determine colour. Most scores of characters were grouped into classes between 1 and 9. Where use of a 9 point scale was not appropriate, some of the numbers were omitted to fit the number of classes. Seeds from plants of an accession showing different expressions for subclasses of a trait were harvested separately and grown on separate plots for further characterization for uniformity and stability. These characters were scored in three generations both at the same and different field sites from June 2009 to December 2012,

with rows typically 20 cm apart with 10 cm distance between plants, with three replications.

Descriptive statistics, correlation, principal component analysis and analysis of variances were conducted on different groups of genotypes by using SAS Version 9.1. and PAST Version 1.18.

Results

Descriptors for linseed germplasm

Table 1 details the nature and range of agronomic and morphological descriptors and classifiers that we defined for the linseed germplasm grown in field plots (Fig. 1). Ranges reported below refer to the 198 accessions of Ethiopian material except where noted.

Seedling characters: For *germination time (GT),* only two accessions (1%) took 7 days or more for germination. For *germination percentage (GP),* the total number of seedlings emerging from 19,800 seeds was 18,878 (overall germination 95%): in two samples seed quality was notably lower than others, with c. 30% of seed having either a concave, slightly shrivelled testa, or uneven matt coloration. In seedlings, *cotyledon leaf size (CL)* was variable in surface area (Fig. 2). Many accessions (132 or 67%) had seedlings with heterogeneous sizes of cotyledons. The timing of *basal branch development (BD)* was scored as a measure of seedling vigour at 17 days old (Table 1; Fig. 3); 79 accessions were heterogeneous (fast+medium: 27; fast+medium+late: 6; medium+late: 46), although, whether this was a consequence of genetic heterogeneity or environment is not clear. As a general characteristic, linseed plants showed the development of lateral shoots on the epigeal stem when the first shoot including the cotyledon leaves was removed by the researchers or by rabbits in the field. When the lower part of a mature plant stem is damaged and approaches the ground, adventitious roots developed on the upper and healed part of the stem.

Plant characters: Days to flowering (DF) showed continuous variation from 37 to 86 days. *Days to maturity (DM)* ranged continuously from 88 to 159 days, in a selection from the tallest line. The *flowering to maturity period (FM*; the length of the time between 50% of the plants flowering and 90% of the bolls maturing period) ranged from

36 to 89 days. *Plant natural height (NH)* was measured in 5,940 individual plants and ranged from 27 cm to 112 cm in the first generation (Fig. 4). Averages for accessions (measured in 30 plants and excluding two heteromorphic lines discussed below) ranged from 29±1 cm to 82±5 cm. Only two accessions were described as very short, also characterized by early maturity and twinned seeds (Figs 6, 7). *Systemic/technical stem height (SH),* a discriminator of the branched oilseed-type varieties and strong, long-stemmed fibre types divided the Ethiopian germplasm between the two categories. *Growth habit and leaf colour (GH, LC)* were also measured (Table 1).

One group of plants segregating from a heteromorphic accession, PGRC/E13610, was characterized by early maturity, large boll size, more productivity, fewer tillers, and a thick and erect stem. The second group was characterized by very late maturity, small boll size, less productivity, more tillers and a weak and thin stem. From accession PGRC/E13535 the two groups of plants developed into two different groups: one very tall and late; and the second tall and medium maturing type. They were differentiated only in these characters. In the fourth generation all groups of plants from the two accessions became uniform and stable.

*Flower and boll characters***:** Floral characters were highly polymorphic and provided a useful group of five descriptors. *Crown stage petal colour (CP)* were well differentiated among white and pink, although more crown colours like pale-blue and yellowish-white from blue-violet, blue and white flower origin plants were observed during the development of the advanced generations (Fig. 5). *Corolla/petal colour (CC),* scored in fully opened flowers (Fig. 5), did not entirely match crown colour in the 'blue' group; white and pink crown colours developed to white and pink petal/corollas. Open-flower petal colour showed higher polymorphism than crown colour. *Petal aestivation (PA)* (Fig. 5), describing overlapping of petals, ranged from twisted to valvate flowers. *Flower shape (FS;* not scored in Table 1) included disk shaped, funnel shaped and four accessions with star shaped flowers. *Anther colour (AC)* (Fig. 5) showed a continuous range of colour variation between yellowish through pink to blue. About a third of accessions showed polymorphism for anther colour. *Filament/stamen colour (FC)* had a narrower range of colour than anthers and petals (Fig. 5). *Colour of style (CS)* is shown in Fig. 5. *Corolla or flower diameter (CD)* was measured from fully opened flowers. All

white petal flower accessions had a large corolla diameter. More than half of the studied accessions were characterized by medium size corolla.

Boll size/diameter (BS) is associated with seed size, itself associated with yield. Boll size/diameter is used as a trait to distinguish one genotype from others since it is not much affected by environmental factors.

Seed characters: Seed size - length and width (SL, SW), were generally proportional to each other; there was little difference in seed shape (Fig. 6; some variation was seen in having blunt to sharp points). Scanning seeds to measure their thickness was difficult so that seed size was measured from the two dimensions; although not scored formally, no genotype with conspicuously thick (a flattened ovoid to spherical, giving a tendency to roll on glass or out-of-focus edges when scanned) or thin seeds were noted during measurement. *Thousand-seed weight (TW),* an important yield character, varied extensively from 2.30g (11 accessions less than 3g) to 7.54g. *Seed colour (SC),* was classified into yellow, light brown, medium brown and dark brown. 'Yellow' was variable, with a distinct bright variant in PGRC/E237001. Fifteen accessions were dimorphic with segregation of two different seed colours and 183 accessions were monomorphic in seed colour.

Twinning of seeds (TS) was seen in PGRC/E13538 and PRGC/E13700 (Fig. 6). These genotypes were also very early maturing, and had a very short plant height, very low oil content and a spreading growth habit. Twinned seeds resulted from much reduced false septa plants (Fig. 7) so the two seeds are conjoined. The twin seed character is not well-known by farmers.

Oil content (OC) was measured in two different seasons but was quite stable, varying from 30.5% up to 43.57%, placing Ethiopian linseed in a low to medium position compared to international varieties. *Linolenic fatty acid (LnF*: 18:3 carbon chain:double bonds) content ranged from 50% to 60%, categorizing them as medium genotypes (Table 1). In the second growing period the number of samples scored as greater than 60% LnF increased from 1 to 7 accessions. *Linoleic fatty acid (LF*: 18:2) content ranged from 13.81% to 15.65%. Three other fatty acids (16:0, 18:0 and 18:1) were also measured (Table 1).

Biodiversity and component analysis

The descriptors were analysed by both administrative region-origin (Table S3 and Fig. 1A) and altitude of collection (Table S4 with ANOVA in Table S5). Variability of characters within regions was high for nearly all descriptors and (while sometimes reflecting number of accessions or perhaps collection strategy) also showed differences in environment or reflected agronomic practices in the regions. The non-geographic accessions acquired from ARC showed the highest mean values for some characters (NH, SH, BD, CD, SL, SW, and OC), suggesting these were selected. Excluding the ARC samples, the 14 accessions from Wollo had many characters with the highest mean values (TW, BD, SL, SW, GT and OF). Descriptor averages among groups with altitude information (Table S4) showed half of the characters with the lowest means (NH, SH, SN, DF, DM, CD, SL, OC and SF) were from altitude class one (1410-1664 m a.s.l.) and 57% of the characters with the highest means (NH, SH, TW, BD, CD, SL, SW, GT, OC, PF and SF) were from altitude class eight (3195-3449 m a.s.l.) and, except for DF, also showed variation with regional origin. The characters BN, GP, GT and PF showed no significant variation with region or altitude; SF and OF showed only regional variation. Accessions from low altitiude

A principal component analysis (Table 2, with correlations and factor analysis in Table S2) showed a quarter of the total variance was accounted for in the first axis, and 19% in the second, confirming the independence of some characters. For other characters, both positive (eg NH and SH, 0.970**; SL and SW 0.838**; SB and BN 0.818**) and negative (OF and LnF, -0.936**; SN and TW, -0.764**; SF and LnF, -0.718**) associations were found.

Discussion

Agronomic and phenotypic characters of linseed

A range of descriptors was elaborated for Ethiopian linseed, and these have uses for both the characterization of germplasm and its evaluation for use by farmers and breeders. The Ethiopian linseed accessions were shown to be diverse, with a continuous range of variation; comparison with the international varieties included in the measurements suggests that, as for many other species of tropical and sub-tropical origin, 1) much of the genetic variability present is underutilized (eg *Phaseolus*: Singh 2001; Meza et al. 2013); and 2) there is considerable potential for genetic improvement of local

varieties. Engels and Hawkes (1991) considered that there was limited diversity in Ethiopian linseed and concluded that serious genetic erosion had occurred. The germplasm from throughout the country studied here (Fig. 1) was clearly diverse, but perhaps sampling distortion lead to reports of lower diversity as noted for diploid wheats (Moghaddam et al. 2000).

Some additional descriptors were considered and measured during the first field season. However, many of these proved difficult to score, or varied within lines or between years. Primary branching, for example, is an important agronomic character, but in small-scale trials was very dependent on plant density: it would need to be assessed in additional trials that included planting at multiple densities (seeding rate). Characters where there is likely to be a strong genetic basis and that can be evaluated on the small-plot scale were emphasized. A few characters showed minimal variation: these were retained in the table since some were used in other studies, and they may show variation to other *Linum* species. Seed characters were partitioned to as many traits as possible to assist with future genetic analysis. It was notable that the character with the highest variability (CV = 31.82%) was 1000-seed weight (TW), a key component of yield. Most of the accessions evaluated were below the values from international or reference varieties, suggesting that TW is a key target for improvement. Despite the correlations noted between some factors scored here (Tables 2 & S4), some deviations (for example between oil content and 1000-seed weight) will be very important for breeders and geneticists to identify lines with novel and important combinations of characters.

A high rate of quick and uniform germination after storage are key early characters for domestication (Hammer 1984; Vaughan et al. 2007; Fu 2011; Heslop-Harrison and Schwarzacher 2012), where crop seeds often differ from their closet wild ancestors: seed samples from wild species may show germination over several years or require special conditions (vernalization, light wavelengths, imbibition rounds, or even smoke). The results here suggest that the accessions carry the desirable traits regarding germination: Lu et al. (2004) reported that linseed seed has 97% germination percentage, similar to that found here.

Ethiopian linseed traditional varieties have high variation in seedling vigour, some but not all or which may be from heterogeneity (Mezghani et al. *20*14). Plant

establishment is an increasingly seen as an important character for crops: rapid establishment exploits available soil moisture efficiently, and prevents soil loss through run-off or wind. The range of cotyledon sizes was notable here and the impact on crop establishment should be investigated. Seedling basal branch development (BD, Figs 2 & 3) from axillary meristems, leading to variation in apical dominance (Darwin 1880), was also highly variable, and the basis of this will be interesting to study since it is likely to be caused by mutations in auxin production or receptors. Two other characters noted here, twin-seeds (Figs 6 & 7) and sprouting in the stem when the seedling is decapitated below the cotyledons will also be amenable to further study with functional genetics and hormonal studies: Ishikawa et al. (1997, reviewing also Adams 1924), reported that most plants die when their seedlings are cut below the cotyledons.

The accessions varied widely in both time to flowering (DF) and time to maturity (DM): indeed, the longest flowering to maturity FM period, 89 days, equalled the total lifespan of the fastest accessions from seedling to maturity. These characters are of adaptive significance. Yield (not measured here) has a relationship to length of the developmental stages allowing accumulation of biological products. Development times must also be matched to growth season conditions to ensure efficient use of moisture, and the time to maturity must be appropriate for the crop cycles, including perhaps future multiple crops per year. In Punjab, India, much of the area is now double-cropped each year, meaning shorter life cycles are required. Changes in linseed agronomy, for better water conservation or multiple cropping seasons each year may change genetic requirements, and the variation found here will be able to meet these challenges.

Flax fibre-types of plants have a higher systemic to natural stem height ratio (S/N) compared to oilseed varieties, a ratio that is also reflected in absolute values of SH and NH. Despite mostly being used for oil, many of the Ethiopian accessions had a high S/N ratio. Some of the varieties are segregating for height, and one selected line of 143cm was obtained (outside the 17cm to 130cm range reported by Diederichsen et al. 2013). As with the bud development, study of the genes involved in phytohormone effects (production, transport and receptors) on height will be important to study.

Seed size, which has direct relationship with endosperm amount, can also contribute for seedling vigour by providing enough nutrients to the growing embryo

(although in domesticated crops where seeds are produced, seeds are normally selected to be larger than the wild relatives). Seed weight is a complex genetic trait and one of the most important indicators used to rate linseed cultivars. SSR (simple sequence repeated) - based clustering of linseed germplasm showed correlation with thousand seed weight (Wiesnerova and Wiesner 2004).

Although showing less diversity than other characters, there were some differences between lines in content of the various oil types (LnF, a product of desaturation of LF derived from OF, and also SF and PF, each with different carbon chain lengths and double bonds, Table 1). Time between the beginning of flowering (starting synthesizing LF) and boll maturity (accumulation of LnF) thus influences oil type ratios (Rao et al. 2008), and there is a positive association between DM and LnF percentage. Breeders have variation available and can selected complex inherited traits (Jain 2011) based on oil needs from the crop.

All the floral structures had different subclasses of colour as colour trait characters (Figs 5 & 6). The number and type of petal colour reported by Hayes and Immer (1942) are similar to petal colour scored in the present study: Flax Council of Canada (1995) and Hayes and Immer (1942) reported linseed anther only as blue and yellow, different from the range of anther colours found here, although we did not find the yellow and lavender (26%) colour petals scored from world core collections (Diederichsen 2007). Diederichsen and Fu (2008) reported three anther colours: white, blue and yellow. Results from the present study indicate that several genes interact in the control of anther, stamen and petal colours: Hayes and Immer (1942) were able to find eight interacting genes. Although *Linum* flowers are rarely visited by insectsoccasional cross-pollination is important for gene-flow, small flowers can exclude pollinators while insects can slip past anthers and stigmas without pollinating large flowers (Armbruster 2014). Ethiopian linseed germplasm has diversified genetic structure regarding genes controlling floral and seed coat colours (see also Yurkevich et al. 2013). This shows the presence of wide range of genotypes for these scored characters. Worku et al. (2012) reported 17 varieties identified by local farmers although some of them were duplication as a matter of differences in language from different ethnic groups.

The existing diversity of linseed in Ethiopia reflects regional and altitudinal (Fig. 1; Tables S3 & S4) variation (including edaphoclimatic parameters), as well as the agroecological systems, the cultural history of the people and farmers knowledge (Engels and Hawkes 1991). Bekele (1996) reported high diversity in the Ethiopian crop tef (*Eragrostis tef*), with some association between regions where farmers have migrated. When DNA genotyping arrays or appropriate sequencing technologies become available based on genomic sequences (Wang et al. 2012), it will be important to analyse linseed germplasm and hybrid populations for signatures of selection involving loss of heterozygosity, fixation of alleles, and linkage disequilibrium or segregation distortion as has been shown in many minor crops such as carrot (*Daucus carota*) (Grzebelus et al. 2014).

The association between high altitude, tall plants, and long times to flowering and maturity could be due to the cooler and wetter growing season. In the oil crop *Guizotia abyssinica*, Geleta and Ortiz (2013) have considered late maturity and factors leading to increases in oil content. Here, there was some association between higher altitude and oil, presumably a result of longer maturity times whereas faster maturity lowers oil content. Positive correlations between commercially important characters are rare and this is one of the problems of selection for breeding (Kearsey and Pooni 1996): any outliers where there is less correlation will be important to identify and follow.

In conclusion, there is substantial morphological variation within the linseed germplasm pool in Ethiopia, and reflecting both regional and altitude differences. It is important to ensure that the full diversity present in the country has been assessed and collected for preservation and use, perhaps emphasizing lower and higher altitude extremes, and also the minor linseed producing regions like Sidamo, Illubabor and Kefa. Measurements of morphological variation will be helpful in the selection of suitable parents for breeding programs, while knowing the population structure of crop genotypes from morphological and DNA markers will be helpful for association studies through linkage disequilibrium in populations for identifying particular alleles associated with a given phenotype (Anhalt et al. 2008). Breeding aims regarding oil, linen fibre or dual use need to be considered, and integrated with the regional ways that the crop is used, including as animal feed-meal and bedding, or whole-seed and flour use as human food.

It will be an ongoing challenge to develop improved varieties and disseminate these as appropriate to smallholders, at the same time aiming to conserve all diversity in traditional varieties: morphological, genetic and marker based studies will assist in reaching these aims.

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Legends to tables

Table 1. Agronomic and morphological descriptors, descriptor scales or states, and frequency distribution for linseed accessions.

Table 2. Principal component (PC) analysis of 198 linseed accessions for 22 morphological variables/characters from Table 1.

Supplementary material

Table S1. List of germplasm accessions analysed and their geographical origin. NK: not known

Table S2. Mean values for each descriptor and Coefficient of Variation (CV) of linseed germplasm grouped by administrative-region.

Table S3. Mean values for each descriptor and Coefficient of Variation (CV) grouped by altitude of collection.

Table S4. Descriptor averages among groups with altitude information showing characters with the lowest means (NH, SH, SN, DF, DM, CD, SL, OC and SF)

Legends to figures

Fig. 1. Ethiopian linseed collections sites and diversity between accessions. A) Former administrative regions (1-13) of Ethiopia with locations of collections (symbols), overlaid with topographic map (green < 250 m a.s.l. through brown to white > 3000 m). Numbers of on-farm collections are show in a light box while those from ARC are shown in light boxes. B) Plots (1.5 m x 1.5 m) show extensive variation in characters that were measured including plant height, growth habit, branching, colour (on-line version) and flowering date (days to flowering).

Fig. 2. Characters in linseed seedlings showing uniformity within accessions and variation between accessions in vigour and cotyledon size. A) 2-day old germinating seedlings (three rows each, separated by grey lines); b) Variation in size of 5-day old cotyledons (bar =10 mm); c) 7-day and d) 17-day old seedlings.

Fig. 3. Linseed seedlings at 17 days old showing variation between accessions in height and basal branch (axillary bud) development (descriptor *BD*, Table 1). (A, B) are tall with suppressed buds (descriptor class 2). (C) is short with bud development (class 3). (D) is an intermediate height and has developed buds (class 3). (E) is short without buds (class 4). (F) is tall and has strong axillary bud development (class 1). Scale bar: 30 mm.

Fig. 4. Variation in height (from 30 cm to 75 cm), systemic/technical stem height, and branching as seen in four Ethiopian linseed accessions.

Fig. 5. Biodiversity in linseed flower structures and colours.

Fig. 6. Biodiversity in linseed seed size and colour. Lower panel, centre right shows twinned seeds; cf Fig. 7. (Bar: 10 mm)

Fig. 7. Cross-section of bolls of linseed with A) normal; and B) twin-seeds (bar = 3 mm), showing the difference in development with much reduced false septum resulting in conjoined (paired) seeds (cf Fig. 6) or twinning.

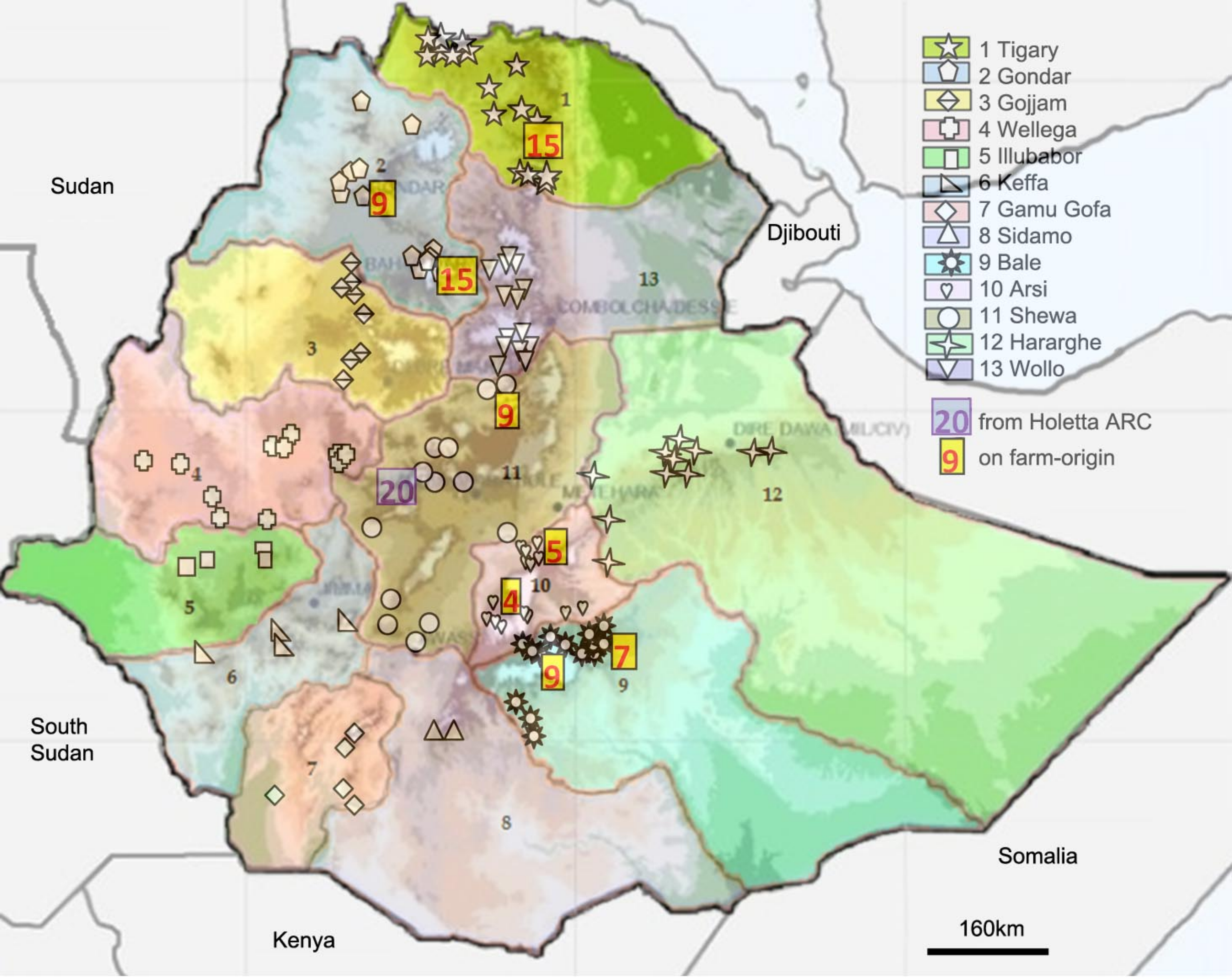

Figure 1. Worku et al. Diversity in Ethiopian linseed.


A
B
C
D

Figure 3. Worku et al. Morphology of Ethiopian linseed.


13538
237001
HARC-12
13105

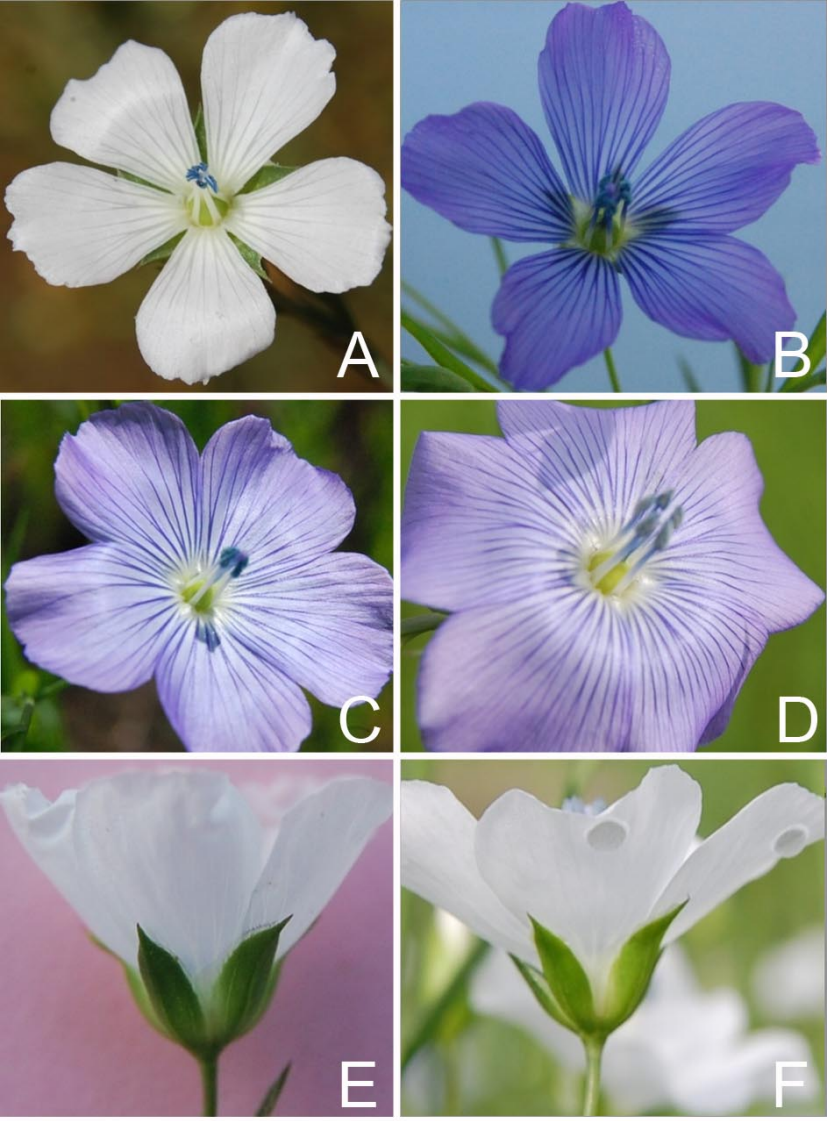

Fig. 5. Worku et al. Biodiversity in Ethiopian linseed

Fig. 6. Worku et al. Biodiversity in Ethiopian Linseed

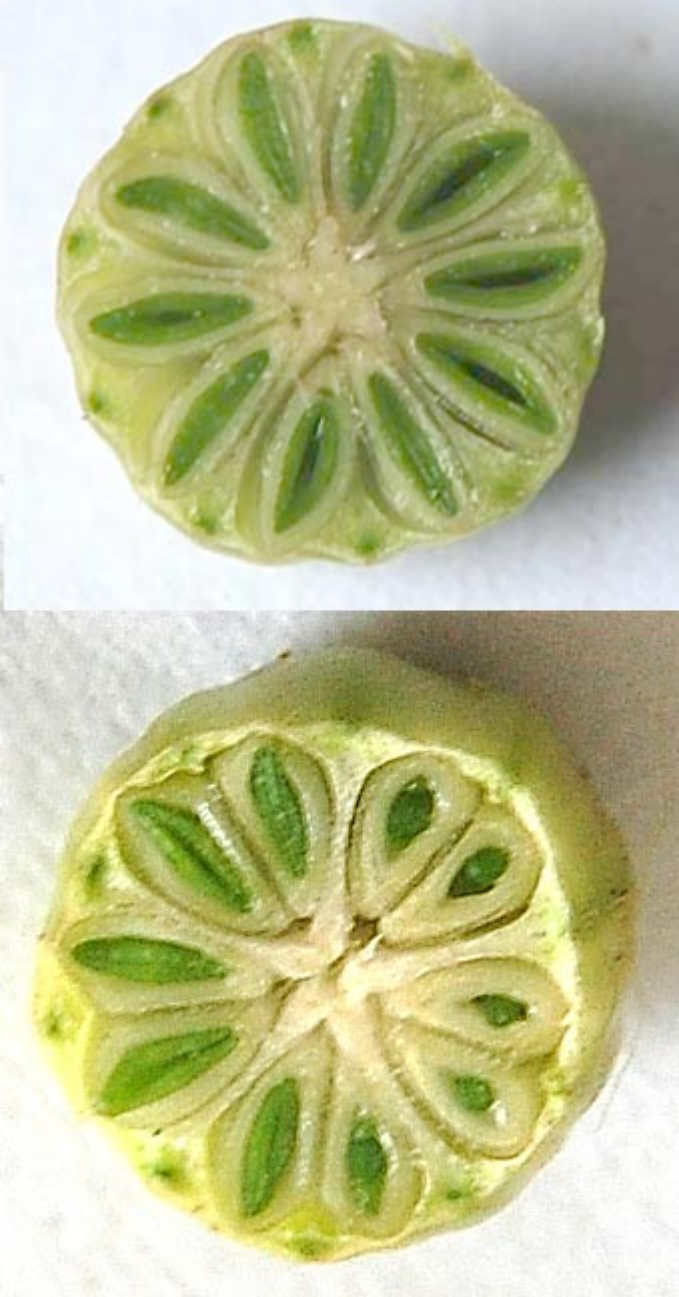

Table 1. Agronomic and morphological descriptors, descriptor scales and distribution for linseed accessions

	The trait/descriptor	Descriptor state	Class or scale of descriptor	Distribution by classes of descriptor
Seedling	1. Germination time (GT)	7th day of sowing	3 = slow	2 (1.01%)
		6th day of sowing	5 = medium	12 (6.06%)
		5th day of sowing	7 = fast	184 (92.93%)
	2. Germination percentage (GP)	<75%	1 = very poor	2 (1.01%)
		75%-85%	3 = poor	5 (2.52%)
		86%-90%	5 = intermediate	13 (6.56%)
		91%-95%	7 = efficient	63 (31.81%)
		d> 95%	9 = very efficient	115 (58.08%)
	3. Cotyledon leaf size (CL)	<14.7mm	3 = small	3014 (15.96%)
		14.7-20.1mm	5 = medium	12064 (63.91%)
		>20.1mm	7 = large	3800 (20.13%)
	4. Basal branch development (BD)	Late	3 = late	10 (5.05%)
		Medium	5 = medium	30 (15.14%)
		Fast	7 = fast	79 (39.90%)
		Heterogeneous	3, 5, 7	79 (39.90%)
Plant	5. Days to flowering (DF)	< 47 days	1 = very early flowering	2 (1.01%)
		48-57 days	3 = early flowering	57 (28.79%)
		58-67 days	5 = medium flowering	119 (60.10%)
		68-77 days	7 = late flowering	16 (8.12%)
		> 77 days	9 = vey late flowering	4 (2.02%)
	6. Days to maturity (DM)	< 100 days	1 = very early maturing	3 (1.52%)
		101-112 days	3 = early maturing	27 (13.64%)
		113-124 days	5 = medium maturing	71 (35.86%)
		125-136 days	7 = late maturing	68 (34.34%)
		> 137 days	9 = very late maturing	29 (9.59%)
	7. Flowering to maturity period (FM)	< 47 days	1 = very soon matured	3 (1.52%)
		47-57 days	3 = soon matured	51(25.76%)
		58-68 days	5 = medium matured	75 (37.88%)
		69-79 days	7 = late matured	53 (26.77%)
		> 79 days	9 = very late matured	16 (8.08%)
	8. Leaf colour (LC)	Dark green	3 = dark green	19 (9.60%)
		Green	5 = green	162 (81.82%)
		Light green	7 = light green	17 (8.58%)
	9. Growth habit (GH)	Bushy type	3 = bushy type	14 (7.07%)
		Semi-erect	5 = semi-erect	176 (88.89%)
		Erect	7 = erect	8 (4.04%)
	10. Plant natural height (NH)	< 40cm	1 = very short	2 (1.01%)
		41-51cm	3 = short	43 (21.71%)
		52-62cm	5 = medium	73 (36.86%)
		63-73cm	7 = tall	68 (34.34%)
		>73cm	9 = very tall	12 (6.06%)
	11. Systemic/technical stem height (SH)	< 26.00cm	1 = very short	2 (1.01%)
		26.00-36.50cm	3 = short	43 (21.71%)
		36.51-47.5cm	5 = medium length	85 (42.92%)
		47.51-58.50cm	7 = long	66 (33.33%)
		>58.5cm	9 = very long	2 (1.01%)
	12. SH:NH (S/N)	< 0.75	1 = oil type	113 (57.07%)
		≥ 0.75	9 = fibre type	85 (42.93%)
	13. Primary branches (PB)	< 18.0	3 = some	109 (55.05%)
		18.1-23.0	5 = many	84 (42.42%)
		>23.0	7 = too many	5 (2.53%)
	14. Secondary branches (SB)	Zero/1	1 = no or one	0 (0.0%)
		1.1-3.0	3 = few	0 (0.0%)
		3.1-7.0	5 = some	11 (5.55%)
		7.1 – 11.0	7 = many	168 (84.85%)
		>11	9 = very many	19 (9.609%)

Table 1. continued

	The trait/descriptor	Descriptor state	Class or scale of descriptor	Distribution by classes of descriptor
Flower/boll	15. Crown stage petal colour (CP)	White	1 =white	3 (1.48%)
		Pale-blue	2 = pale-blue	2 (0.98%)
		Blue	3 = blue	189 (93.10%)
		Blue-violet	4 = blue-violet	4 (1.97%)
		Violet	5 = violet	3 (1.48%)
		Red-violet	6 = red-violet	1(0.49%)
		Pink	7 = pink	1(0.49%)
	16. Petal aestivation (PA)	Valvate	3 = valvate	7 (3.41%)
		Semi- twisted	5 = Semi-twisted	162 (79.02%)
		Twisted	7 = twisted	36 (17.56%)
	17. Corolla/petal colour (CC)	White	1 = white	3 (1.43%)
		Pale-blue	2 = pale-blue	195 (93.30%)
		Blue	3 = blue	10 (4.78%)
		Blue-violet	4 = blue-violet	5 (2.39%)
		Red-violet	5 = red-violet	5 (2.39%)
		Pink	6 = pink	1(0.48%)
	18. Corolla or flower diameter (CD)	< 20 mm	3 = small	34 (17.17%)
		20 mm-25 mm	5 = medium	134 (67.67%)
		> 25 mm	7 = large	30 (15.15%)
	19. Anther colour (AC)	Yellowish	1 = yellowish	14 (5.11%)
		Salmon pink	3 = salmon pink	39 (14.60%)
		Silver/Azure	5 = silver/Azure	4(1.46%)
		Greenish	7 = greenish	19 (6.93%)
		Bluish	9 = bluish	197 (71.90%)
	20. Boll size/diameter (BS)	< 5.58 mm	3 = small	19 (9.60%)
		5.58 mm-6.32 mm	5 = medium	137 (69.19%)
		> 6.32 mm	7 = large	42 (21.21%)
	21. Boll number (BN)	< 83.0	3 = some	84 (42.42%)
		83.1 – 99.0	5 = many	108 (54.55%)
		> 99.0	7 = too many	16 (8.08%)
	22. Seed number (SN)*	< 8.0	3 = less	2 (1.01%)
		8.1-9.0	5 = high	1 (0.51%)
		> 9.0	7 = maximum	195 (98.48%)
Seed	23. Seed length (SL)	< 4.0 mm	3 = short	80 (40.40%)
		4.0-5.0 mm	5 = medium	115 (58.08%)
		> 5.0 mm	7 = long	3 (15.15%)
	24. Seed width (SW)	< 2.0mm	3 = narrow	71 (35.86%)
		2.0-2.5mm	5 = medium	122 (61.62%)
		> 2.5mm	7 = wide	5 (2.52%)
	25. Thousand-seed weight (TW)	< 4.01g	1 = very low weight	89 (44.95%)
		4.01g-5.00g	3 = low weight	65 (32.83%)
		5.01g-6.00g	5 = medium weight	29 (14.65%)
		6.01g-7.00g	7 = high weight	11 (5.56%)
		> 7.01g	9 = very high weight	4 (2.02%)
	26. Twinning of seeds (TS)	Single	1 = single	196 (98.99%)
		Twinned	9 = twinned	2 (1.01%)
	27. Seed coat colour (SC)	Yellow	1 = yellow	7 (3.29%)
		Light-brown	2 = light brown	6 (2.82%)
		Medium brown	3 = medium brown	95 (44.60%)
		Dark brown	4 = dark brown	105 (49.30%)
		Olive	5 = olive	None
		Others	6= variegated	None

Table 1. continued

	The trait/descriptor	Descriptor state	Class or scale of descriptor	Distribution by classes of descriptor
Oil	28. Oil content (OC)	< 35.00%	1 = very low	81 (40.91%)
		35.00-37.00%	3 = low	60 (30.30%)
		37.01-39.00%	5 = medium	43 (21.72%)
		39.01-42.00 %	7 = high	13 (6.56%)
		> 42.00 %	9 = very high	1 (0.51%)
	29. Palmitic fatty acid (PF)	< 5.62%	3 = low	9 (4.54%)
		5.62 – 6.21%	5 = medium	63 (31.82%)
		> 6.21%	7 = high	126 (63.64%)
	30. Stearic fatty acid (SF)	< 4.81%	3 = low	40 (20.20%)
		4.81- 5.43%	5 = medium	132 (66.67%)
		> 5.43%	7 = high	26 (13.13%)
	31. Oleic fatty acid (OF)	<16.90	3 = low	20 (10.10%)
		16.90 - 19.83%	5 = medium	159 (80.30%)
		> 19.83%	7 = high	19 (9.60%)
	32. Linoleic fatty acid (LF)	< 14.50%	3 = low	29 (14.65%)
		14.50-15.30%	5 = medium	159 (80.30%)
		> 5.30%	7 = high	10 (5.05%)
	33. Linolenic fatty acid (LnF)	< 54%	3 = low	35 (17.68%)
		55-58%	5 = medium	138 (69.70%)
		>57%	7 = high	25 (12.63%)

*Character 22 SN: variation is only found in three accessions where late maturity extends into the main rainy season.

Table 2. Principal component (PC) analysis of 198 linseed accessions for 22 morphological variables/characters (Table 1). Tables S2 and S3 give the Factor Analysis, correlations and component weights.

PC	Eigen value	% variance	% cumulative variance
1	5.49	26.08	26.08
2	3.96	18.83	44.91
3	2.75	13.09	58.00
4	1.80	8.56	66.56
5	1.39	6.61	73.17
6 to 22	<1.00	<5.00	

Table S1. List of germplasm accessions analysed and their geographical origin. NK: not known

S.N	Accession code/Name	Source Region	Altitude (masl)	Lat-Longitude	S.N	Accession code/Name	Source Region	Altitude (masl)	Lat-Longitude
1	10064	G.Gofa	1410	0549N 3636E	60	13700	Wollo	2550	1029N 3917E
2	10067	Gojjam	1990	1125N 3712E	61	13718	Wollo	3190	1102N 3914E
3	10069	Gojjam	1980	1039N 3724E	62	13720	Wollo	3060	1108N 3913E
4	10084	Illubabur	2000	0817N 3628E	63	13753	Welega	1680	0838N 3457E
5	10086	Kefa	1740	0744N 3715E	64	13754	Illubabur	1680	0816N 3507E
6	10087	Kefa	1740	0744N 3716E	65	13755	Illubabur	1750	0832N 3540E
7	10093	Shewa	1480	0841N 3932E	66	13756	Illubabur	1900	0821N 3621E
8	10097	Shewa	1500	0741N 3821E	67	13757	Kefa	1860	0733N 3637E
9	10100	Shewa	2350	0901N 3825E	68	13758	Kefa	1790	0710N 3625E
10	10106	Shewa	1800	0707N 3802E	69	208358	Shewa	1960	0740N 3755E
11	10117	Shewa	1950	0859N 3748E	70	208663	Harergh	2200	0905N 4021E
12	10121	Sidamo	2600	0623N 3838E	71	208664	Hararghe	2540	0918N 4148E
13	10124	Sidamo	1853	0623N 3820E	72	208665	Harergh	2180	0910N 4132E
14	10127	Tigray	1980	1407N 3838E	73	208796	Arsi	2970	0735N 3905E
15	10136	Welega	1980	0859N 3550E	74	211477	G.Gofa	1780	0520N 3725E
16	10137	Welega	1650	0927N 3508E	75	211478	G.Gofa	1560	0517N 3722E
17	10145	Wollo	1964	1105N 3945E	76	212515	Shewa	2610	1023N 3912E
18	13510	Arsi	2580	0748N 3908E	77	212517	Shewa	3100	1015N 3935E
18	13520	Shewa	3110	0948N 3836E	78	212518	Shewa	3110	1015N 3900E
19	13524	Gondar	2900	1245N 3722E	79	212747	Gojjam	2340	1111N 3715E
20	13526	Bale	2610	0713N 3950E	80	212748	Gondar	2800	1250N 3741E
21	13528	Bale	2060	0721N 4029E	81	212753	Gondar	2950	1142N 3818E
22	13529	Shewa	2160	0711N 3838E	82	212854	Bale	1800	0700N 4028E
23	13531	Arsi	2925	0810N 3954E	83	212855	Bale	1900	0701N 4027E
24	13533	Arsi	2480	0749N 3947E	84	212857	Bale	1800	0629N 3913E
25	13534	Bale	2450	0718N 3949E	85	219963	Tigray	1850	1470N 3858E
26	13535	Bale	2400	0722N 4005E	86	219964	Tigray	2550	1410N 3857E
28	13537	Bale	2530	0710N 3959E	87	223229	Tigray	2320	1241N 3931E
29	13538	Bale	1520	0706N 4045E	88	226033	Gojjam	1960	1119N 3713E
30	13545	Arsi	3090	0813N 3955E	89	230022	Bale	2700	0606N 3904E
31	13547	Arsi	2660	0801N 3950E	90	230025	Bale	1830	0664N 3901E
32	13549	Arsi	2635	0819N 3942E	91	230026	Bale	2530	0706N 3938E
33	13550	Arsi	2500	0749N 3949E	92	230029	Bale	2560	0707N 3952E
34	13567	Gojjam	2810	1051N 3734E	93	230033	Bale	2110	0706N 4038E
35	13596	Shewa	2940	0916N 3805E	94	230034	Bale	2100	0706N 4035E
36	13599	Shewa	2510	0901N 3856E	95	230816	Harerghe	1980	0929N 4240E
37	13607	Gojjam	2400	1017N 3749E	96	230818	Harerghe	2450	0929N 4213E
38	13610	Gondar	2550	1258N 3745E	97	230821	Harerghe	1700	0908N 4141E
39	13611	Gondar	2680	1352N 3744E	98	230822	Harerghe	2270	0925N 4137E
40	13615	Gondar	2610	1151N 3802E	99	230824	Harerghe	2510	0917N 4128E
41	13617	Gondar	3114	1148N 3828E	100	230827	Harerghe	2410	0909N 4116E
42	13625	Gondar	2900	1138N 3830E	101	230828	Harerghe	1956	0857N 4049E
43	13626	Gondar	3120	1144N 3829E	102	231253	Arsi	2330	0835N 3952E
44	13628	Harergh	1500	0807N 4041E	103	232215	Arsi	1610	0835N 3946E
45	13633	Wollo	2820	1141N 3850E	104	234004	Tigray	1910	1412N 3811E
46	13644	Welega	2420	0846N 3630E	105	234006	Tigray	1820	1423N 3806E
47	13647	Gondar	3100	1147N 3815E	106	235162	Tigray	2250	1246N 3933E
48	13648	Gondar	3220	1313N 3801E	107	235163	Tigray	2500	1252N 3932E
49	13651	Arsi	2520	0751N 3908E	108	235165	Tigray	1850	1257N 3932E
50	13655	Arsi	3190	0748N 3920E	109	235167	Tigray	2060	1333N 3929E
51	13656	G.Gofa	2710	0621N 3736E	110	235169	Tigray	1650	1344N 3904E
52	13657	G.Gofa	2000	0558N 3718E	111	235177	Tigray	1780	1340N 3914E
53	13659	Welega	2300	0954N 3634E	112	236996	Arsi	2790	0719N 3916E
54	13662	Welega	2090	0954N 3636E	113	237000	Arsi	2340	0708N 4000E
55	13663	Welega	2030	0957N 3655E	114	237001	Arsi	2110	0740N 4012E
56	13664	Welega	2430	0945N 3702E	115	237491	Wollo	1480	1032N 3955E
57	13665	Welega	2360	0932N 3707E	116	238282	Gojjam	2440	1020N 3709E
58	13666	Welega	2340	0926N 3707E	117	242589	Tigray	1981	1394N 3948E
59	13692	Wollo	2850	1049N 3927E	118	242590	Tigray	1710	1438N 3880E

Table S1 continued.

S.N	Accession code/Name	Source Region	Altitude (masl)	Lat-Longitude	S.N	Accession code/Name	Source Region	Altitude (masl)	Lat-Longitude
119	242595	Tigray	1950	1428N 3833E	159	WL1290	Gondar	NK	NK
120	243797	Wollo	2290	1113N 3950E	160	WL1300	Gondar	NK	NK
121	243798	Wollo	3335	1059N 3931E	161	WL1320	Gondar	NK	NK
122	243799	Wollo	2920	1057N 3934E	162	WL1330	Gondar	NK	NK
123	243800	Wollo	3440	1054N 3921E	163	WL1340	Gondar	NK	NK
124	243807	Wollo	3090	1151N 3924E	164	WL1350	Gondar	NK	NK
125	243808	Wollo	2980	1151N 3930E	165	WL1360	Gondar	NK	NK
126	243809	Wollo	3360	1151N 3925E	166	WL1380	Shewa	NK	NK
127	243811	Tigray	1990	1337N 3900E	167	WL1390	Shewa	NK	NK
128	243816	Gondar	1920	1221N 3731E	168	WL1400	Shewa	NK	NK
129	243817	Gondar	2145	1219N 3733E	169	WL1410	Shewa	NK	NK
130	243819	Gojjam	1870	1138N 3720E	170	WL1420	Shewa	NK	NK
131	WL1010	Arsi	NK	NK	171	WL1430	Shewa	NK	NK
132	WL1020	Arsi	NK	NK	172	WL1440	Shewa	NK	NK
133	WL1030	Arsi	NK	NK	173	WL1450	Shewa	NK	NK
134	WL1040	Arsi	NK	NK	174	WL1460	Shewa	NK	NK
135	WL1050	Arsi	NK	NK	175	WL1470	Tgray	NK	NK
136	WL1060	Bale	NK	NK	176	WL1480	Tgray	NK	NK
137	WL1070	Bale	NK	NK	177	WL1490	Tgray	NK	NK
138	WL1080	Bale	NK	NK	178	WL1500	Tgray	NK	NK
139	WL1090	Bale	NK	NK	179	WL1510	Tgray	NK	NK
140	WL1100	Bale	NK	NK	180	Belay-96	ARC01	NK	NK
141	WL1110	Bale	NK	NK	181	Berene	ARC02	NK	NK
142	WL1120	Gondar	NK	NK	182	CDC-1747	ARC03	NK	NK
143	WL1130	Gondar	NK	NK	183	Chilalo	ARC04	NK	NK
144	WL1140	Gondar	NK	NK	184	CI-525	ARC05	NK	NK
145	WL1150	Gondar	NK	NK	185	Jeldu	ARC06	NK	NK
146	WL1160	Gondar	NK	NK	186	Kasa1	ARC07	NK	NK
147	WL1170	Gondar	NK	NK	187	Kasa2	ARC08	NK	NK
148	WL1180	Gondar	NK	NK	188	Kulumsa-1	ARC09	NK	NK
149	WL1190	Gondar	NK	NK	189	LLAS'PS' 21	ARC10	NK	NK
150	WL1200	Gonda	NK	NK	190	Local Check	ARC11	NK	NK
151	WL1210	Gonda	NK	NK	191	PGRC/E10306	ARC13	NK	NK
152	WL1220	Gonda	NK	NK	192	PI-523353	ARC15	NK	NK
153	WL1230	Gonda	NK	NK	193	R12-D33C	ARC16	NK	NK
154	WL1240	Gonda	NK	NK	194	R12-M20G'	ARC17	NK	NK
155	WL1250	Gonda	NK	NK	195	R12-N10D	ARC18	NK	NK
156	WL1260	Gonda	NK	NK	196	R12-N27G'	ARC19	NK	NK
157	WL1270	Gonda	NK	NK	197	Tole	ARC20	NK	NK
158	WL1280	Gonda	NK	NK	198	Geregera	ARC21	NK	NK

Table S2. Correlations between the 22 variables (Table 1) and the first five Eigenvectors factors from a Factor Analysis of the morphological data from 198 Ethopian linseed accessions. Colours highlight larger values for each factor.

Trait/descriptor	Factor1	Factor2	Factor3	Factor4	Factor5
NH	**0.741**	0.458	0.240	0.090	-0.056
SH	**0.690**	0.514	0.297	0.007	-0.107
PB	**-0.660**	0.175	-0.056	0.477	-0.068
SB	-0.395	0.350	-0.074	**0.767**	0.071
BN	-0.249	0.384	-0.080	**0.802**	0.130
SN	-0.050	**0.618**	0.033	-0.174	0.464
TW	0.569	**-0.611**	-0.062	0.257	-0.252
BS	**0.717**	-0.440	-0.053	0.260	0.008
DF	-0.251	**0.673**	0.238	-0.118	-0.357
DM	0.353	**0.723**	0.365	0.014	-0.140
FM	**0.563**	0.424	0.275	0.087	0.054
CD	**0.728**	0.148	-0.025	0.212	0.035
SL	**0.778**	-0.379	0.015	0.137	0.163
SW	**0.715**	-0.405	0.051	0.178	0.114
OC	**0.777**	-0.063	-0.074	0.084	0.148
PF	-0.386	-0.307	**0.546**	0.158	0.215
SF	-0.058	-0.148	**0.867**	0.059	0.106
OF	-0.286	-0.438	**0.747**	0.016	-0.039
LF	-0.261	**-0.504**	-0.426	0.098	0.240
LnF	0.303	0.506	**-0.765**	-0.075	-0.091
GP	0.080	0.177	0.045	-0.192	**0.574**
GT	0.006	-0.182	0.030	0.057	**-0.777**

Table S3. Mean values and Coefficient of Variation (CV) for traits in regional groups of linseed germplasm. (Colour and some qualitative or derived traits from Table 1 are not included.)

		Traits																				
Reg[a]	Parameter	NH[b]	SH	PB	SB	BN	SN	TW	BS	DF	DM	CD	SL	SW	GP	GT	OC	PF	SF	OF	LF	LnF
1	Mean	53.87	37.10	2.38	9.16	31.26	9.89	4.83	6.16	53.05	113.38	20.29	4.29	2.16	94.62	5.09	36.32	6.34	5.17	19.03	15.11	54.13
	CV	13.79	18.36	22.42	25.26	30.51	1.05	9.10	4.74	6.52	10.55	12.39	2.86	4.50	5.88	3.43	3.13	2.47	3.47	5.54	1.95	2.29
2	Mean	61.43	45.55	2.82	10.90	34.85	9.92	4.20	5.94	61.30	131.11	21.81	4.06	2.03	96.73	5.08	36.66	6.13	5.10	17.59	14.69	56.12
	CV	11.36	13.97	19.16	22.98	25.59	1.41	21.60	6.30	9.20	7.89	12.55	5.54	6.25	3.16	2.49	4.22	4.65	10.03	11.61	1.79	4.16
3	Mean	58.29	42.30	2.94	12.27	38.31	9.91	3.99	5.83	61.88	123.25	21.75	3.92	1.98	96.50	5.05	34.74	6.25	5.24	18.54	14.69	54.90
	CV	14.37	13.21	27.57	15.33	18.59	2.47	28.39	4.42	6.72	3.03	14.69	9.70	10.85	3.32	3.01	5.60	4.98	4.03	2.83	1.06	0.97
4	Mean	56.43	41.36	3.13	12.66	42.39	9.95	3.42	5.75	64.00	120.30	21.20	3.71	1.87	96.30	5.08	33.26	6.29	4.97	18.43	14.63	55.42
	CV	16.72	14.12	17.77	25.34	21.79	0.40	32.97	8.09	4.89	8.21	16.31	6.73	7.87	3.02	2.74	5.42	5.33	3.38	4.57	2.05	2.11
5	Mean	64.88	48.34	2.60	10.85	37.86	9.90	3.07	5.46	69.75	120.50	18.75	3.53	1.75	98.50	5.12	32.05	6.28	4.88	18.63	14.80	55.31
	CV	16.37	22.08	8.24	12.80	10.20	1.38	26.20	5.05	22.38	13.66	9.11	7.43	7.06	3.05	4.17	3.51	0.91	5.48	3.17	3.10	2.10
6	Mean	57.14	41.49	2.33	10.24	37.22	9.96	2.64	5.25	70.75	126.25	20.25	3.45	1.79	94.75	5.19	32.33	6.36	4.83	19.06	14.88	54.68
	CV	23.25	27.12	15.23	20.87	17.30	0.62	7.46	2.57	24.19	17.18	11.67	5.29	4.13	1.80	1.49	4.07	4.14	6.36	6.69	3.32	3.05
7	Mean	51.25	36.61	2.80	9.99	35.32	9.92	3.68	5.84	59.60	115.60	20.40	3.93	2.09	95.40	5.29	33.62	6.20	4.67	18.35	14.84	55.56
	CV	14.45	16.26	17.91	17.63	25.91	0.67	12.94	1.57	2.54	4.35	5.59	3.86	10.42	6.32	6.50	3.74	2.02	4.93	2.57	1.44	1.19
8	Mean	52.49	37.72	6.44	17.89	88.40	9.99	3.26	5.64	62.00	119.50	21.50	3.70	1.88	95.00	5.05	31.97	6.34	5.30	19.04	14.89	54.38
	CV	6.97	8.68	17.91	6.75	0.26	0.21	5.64	0.50	9.12	2.96	16.44	1.15	3.76	2.98	2.66	0.00	2.79	3.20	0.04	1.42	0.39
9	Mean	62.04	44.95	2.79	11.39	40.50	9.63	4.89	6.08	57.19	126.14	23.90	4.18	2.15	93.38	5.15	35.75	6.26	5.12	18.94	14.67	54.73
	CV	17.86	21.35	17.83	17.71	23.73	12.01	44.38	4.60	9.30	11.51	12.75	4.50	8.10	10.30	4.52	5.30	1.88	5.68	5.29	1.23	2.03
10	Mean	62.59	46.36	2.76	11.07	36.76	9.90	4.45	6.01	61.60	128.95	23.95	4.07	2.10	95.85	5.17	35.22	6.18	4.99	18.30	14.69	55.53
	CV	9.59	11.03	16.81	20.49	25.39	0.91	15.73	4.52	5.97	7.99	10.09	6.69	8.62	3.16	4.33	5.10	5.86	7.09	5.52	1.19	2.38
11	Mean	53.18	38.42	3.27	11.89	38.52	9.96	3.60	5.74	63.36	124.00	20.86	3.89	1.97	94.64	5.17	34.43	6.26	5.06	18.42	14.77	55.25
	CV	9.11	10.95	16.53	20.09	20.98	0.47	11.44	4.43	6.98	4.79	10.70	5.21	5.42	4.73	8.83	5.10	3.78	6.30	4.06	1.52	2.01
12	Mean	53.24	37.18	2.99	11.82	41.71	9.90	4.28	5.86	58.64	115.64	21.55	3.93	1.99	94.18	5.13	35.20	6.18	4.90	18.60	14.83	55.16
	CV	15.19	20.23	8.08	18.48	15.81	0.69	18.60	2.84	5.92	7.28	10.45	4.57	5.85	6.78	3.57	2.37	3.90	6.62	5.17	0.72	2.36
13	Mean	63.78	48.01	2.45	9.50	27.86	9.38	5.75	6.26	58.93	125.07	22.64	4.39	2.24	93.79	5.33	35.98	6.17	5.26	19.08	14.68	54.54
	CV	17.76	20.93	27.10	25.30	24.17	13.84	46.89	7.86	13.42	12.34	11.83	10.47	12.66	8.24	8.68	7.62	7.31	7.27	8.84	2.13	3.84
14	Mean	68.49	50.08	2.12	8.92	32.94	9.79	5.61	6.42	58.79	126.16	25.89	4.50	2.32	96.21	5.21	38.65	6.08	5.14	18.11	14.55	55.73
	CV	7.81	7.05	20.88	19.74	23.44	1.97	14.40	4.57	4.59	4.45	10.45	6.86	8.08	3.37	4.80	4.88	3.73	5.85	8.88	1.66	2.33
Total	Mean	59.54	43.35	2.74	10.78	36.05	9.84	4.42	5.99	60.18	124.25	22.25	4.08	2.08	95.34	5.15	35.64	6.21	5.08	18.43	14.74	55.24
	CV	15.43	18.31	22.10	23.08	25.25	5.41	31.82	6.53	10.71	9.54	13.95	8.45	9.95	5.50	5.15	6.37	4.41	7.02	7.55	1.92	2.94

Reg [a] Regions code and 1 = Tigray(31) ; 2 = Gondar(37); 3 = Gojjam(8); 4 = Wellega(10); 5 = Illubabor(4); 6 = Keffa(4); 7 = Gamogofa(5); 8 = Sidamo(2); 9 = Bale(31); 10 = Aris(20); 11= Shewa(22); 12 = Hararghe(11); 13 = Wollo(14); and 14 =. ARC(19);Numbers in parentheses are sample sizes for the regions. See Table 1 for trait code descriptions. For the location of regions on the map of Ethiopia see Fig. 1.

Table S4. Mean values and Coefficient of Variations (CV) for altitude groups of linseed germplasm quantitative characters

		Traits																			
Alt*	Parameter	NH[b]	SH	PB	SB	BN	SN	TW	BS	DF	DM	CD	SL	SW	GP	GT	OC	PF	SF	OF	LF	LnF
1	Mean	49.90	34.52	5.91	16.73	88.70	9.40	4.64	5.82	56.90	112.20	19.90	3.88	2.01	96.10	5.23	33.44	6.16	4 .86	19.12	14.94	54.89
	CV	22.65	26.62	11.72	28.23	28.97	17.98	72.41	7.14	14.14	10.73	9.31	6.89	9.46	4.56	5.08	5.44	7.33	7.31	3.94	1.68	2.76
2	Mean	57.27	40.21	5.68	16.30	87.51	9.90	3.92	5.76	60.43	116.04	20.78	3.94	2.02	94.57	5.11	34.32	6.32	4.99	18.95	14.89	54.61
	CV	17.31	20.32	24.03	19.05	18.41	1.47	29.19	7.36	16.83	9.73	15.96	9.20	10.09	6.03	2.79	6.08	3.00	5.82	6.09	2.18	2.73
3	Mean	58.82	43.31	5.60	14.96	83.06	9.87	4.24	5.99	60.60	121.72	21.92	4.06	2.04	96.80	5.13	34.90	6.23	5.07	18.81	14.78	54.91
	CV	15.68	19.53	25.98	24.71	28.76	1.76	26.14	6.11	12.46	10.21	11.70	8.59	9.54	2.46	3.97	6.22	4.55	6.28	4.49	2.35	2.45
4	Mean	57.39	42.33	6.09	16.14	87.61	9.90	4.23	5.92	61.18	124.00	21.71	3.95	2.00	96.29	5.10	34.42	6.29	5.09	18.64	14.70	54.95
	CV	18.14	20.96	22.81	15.93	19.96	0.80	24.02	4.62	7.91	9.05	12.49	7.73	8.75	3.90	3.32	4.57	2.35	4.55	5.04	0.98	1.84
5	Mean	57.64	41.57	5.88	16.69	88.09	9.73	4.56	5.91	58.44	124.08	22.56	4.01	2.05	93.56	5.17	34.46	6.23	5.14	18.86	14.79	54.71
	CV	15.83	20.24	15.89	19.83	23.15	10.11	43.79	5.74	9.87	10.83	13.36	7.04	8.94	7.44	6.31	4.69	3.43	6.29	7.47	2.17	2.76
6	Mean	60.19	44.58	5.64	14.08	80.43	9.91	4.04	5.96	61.00	127.36	20.73	4.08	2.11	97.18	5.19	35.11	6.14	5.18	18.56	14.68	55.07
	CV	9.68	12.58	15.13	14.99	27.15	0.90	17.91	4.65	9.56	7.89	14.16	5.52	10.33	2.87	6.35	3.56	7.42	8.46	5.18	1.47	2.43
7	Mean	60.11	45.23	6.06	16.72	85.91	9.90	3.85	5.80	63.73	128.13	21.40	3.98	1.99	95.13	5.16	34.75	6.33	5.31	18.61	14.63	54.95
	CV	13.23	15.58	17.17	22.66	23.93	2.37	26.46	7.16	6.06	7.24	9.80	10.47	10.02	5.10	4.09	4.03	2.21	6.17	4.19	1.26	1.50
8	Mean	68.59	51.81	4.89	12.17	83.78	9.57	6.18	6.47	60.25	125.25	23.50	4.61	2.30	96.50	5.26	38.06	6.42	5.58	19.90	14.48	53.48
	CV	11.15	10.58	32.89	11.42	7.90	4.96	28.22	8.05	13.71	4.24	16.11	10.49	16.41	2.74	0.95	4.59	4.45	4.35	9.95	1.11	4.30
Total	Mean	58.74	42.95	5.72	15.47	85.64	9.77	4.46	5.95	60.32	122.35	21.56	4.06	2.07	95.77	5.17	34.93	6.27	5.19	18.93	14.74	54.70
	CV	15.46	18.30	20.70	19.60	22.28	5.04	33.52	6.35	11.32	8.74	12.86	8.24	10.44	4.39	4.11	4.90	4.34	6.15	5.79	1.65	2.60

Alt* is Altitude classes code and 1 = 1410-1664 (10); 2 = 1665-1919(23); 3 = 1920-2174(25); 4 = 2175-2429(17); 5 = 2430-2684(25); 6 = 2685-2939(11); 7 = 2940-3194(15); and 8 = 3195-3449(4). Numbers in parenthesis are sample sizes for respective group.

[b] Traits' code and NH = Natural plant height; SH = systemic plant height; PB = primary branch number; SB= secondary branch number; BN = boll number per plant; SN = seed number per boll; TW = 1000-seed weight; BS = boll size; DF = days to flowering; DM = days to maturity; CD = corolla diameter; SL = seed length; SW = seed width; GP = germination percentage; GT = germination time; OC = oil content; PF = palmitic fatty acid; SF = steric fatty acid; OF = oleic fatty acid; LF linoleic fatty acid; LnF = linolenic fatty acid.

Table S5. ANOVA for quantitative characters of linseed samples by a) regional groups and b) altitude groups

a.

	Descriptor code (table 1)																			
Parameter	NH	SH	PB	SB	BN	SN	TW	BD	DF	DM	CD	SL	SW	GP	GT	OC	PF	SF	OF	LF	LnF
TMS	377.97	292.70	1.68	19.95	234.13	0.38	8.74	0.874	203.14	483.83	46.31	0.90	0.28	23.35	0.08	35.77	0.10	0.22	3.84	0.33	5.95
EMS	63.70	46.73	274	5.22	72.17	0.28	1.50	0.102	30.109	116.14	7.04	0.06	0.03	27.78	0.07	2.99	0.07	0.12	1.80	0.06	2.41
F	5.93	6.26	6.117	3.82	3.24	1.35	5.81	8.565	6.747	4.166	6.578	13.89	10.49	0.84	1.13	11.98	1.33	1.85	2.13	5.32	2.47
Sig.	0.000	0.000	0.000	0.000	0.000	**0.186**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.62**	**0.34**	0.000	**0.199**	**0.039**	**0.014**	0.000	0.004

TMS = total mean square; EMS = error mean square; F = F-statistic. Degrees of freedom (df) is 13; Sig = significance level

b.

	Descriptor code (table 1)																			
Parameter	NH	SH	PB	SB	BN	SN	TW	BD	DF	DM	CD	SL	SW	GP	GT	OC	PF	SF	OF	LF	LnF
TMS	344.80	258.56	1.75	25.63	207.23	0.36	6.01	0.77	48.93	535.72	46.72	0.66	0.19	27.92	0.04	53.82	0.17	0.36	8.50	0.26	9.80
EMS	71.974	53.601	0.301	5.261	76.91	0.28	1.79	0.12	41.17	121. 48	7.86	0.09	0.04	27.47	0.07	2.82	0.07	0.12	1.62	0.07	2.30
F	4.791	4.824	5.825	4.873	2.70	1.29	3.36	6.19	1.19	4.41	5.95	7.07	5.49	1.02	0.51	19.08	2.36	3.12	5.24	3.38	4.26
Sig.	0.000	0.000	0.000	0.000	0.006	**0.247**	0.001	0.000	**0.305**	0.000	0.000	0.000	0.000	**0.428**	**0.866**	0.000	**0.015**	0.002	0.000	0.001	0.000

TMS = total mean square; EMS = error mean square; F = F-statistic. Degrees of freedom (df) is 7; Sig = significance level