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THE WEED FLORA OF CALIFORNIAN RICE FIELDS

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ABSTRACT

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Although cultivated rice (*Oryza sativa* L.) has been grown in the United States since the seventeenth century, it was not until 1912 that commercial rice production was practised in California. At present, approximately one quarter of the total annual U.S. rice crop is produced in the Central Valley of California. Due to the continually flooded conditions that prevail in Californian rice fields, the weed flora is highly specialised and is composed of some 62 species of aquatic vascular plants. The flora is unusual among crop weed floras of California in that it contains a substantial proportion (ca. two thirds) of native species. This is probably a result of the similarity in ecological conditions between rice fields and the original wetland habitats of the Central Valley that they replaced. Seventeen of the 20 alien species in the weed flora are of Old World origin and several (*Cyperus difformis* L., *Dopatrium junceum* (Roxb.) Ham., *Echinochloa crus-galli* (L.) Beauv., *Scirpus mucronatus* L., *Monochoria vaginalis* (Burm. f.) Presl, *Oryza rufipogon* Griff., *Ottelia alismoides* (L.) Pers. and *Rotala indica* (Willd.) Koehne are widely distributed and well-documented weeds associated with rice. It is proposed that the most likely method by which these aliens have been introduced to California is as seed contaminants of imported rice stocks. The small seed size, annual life form and autogamous breeding systems of the majority of these species probably aid in their dispersal, establishment and colonization of rice fields. A survey of 70 rice fields distributed throughout the rice-growing areas of the state indicated that the annuals *Sagittaria montevidensis* Cham. and Schlecht. ssp. *calycina* (Engelm.) Bogin., *Ammannia coccinea* Rottb., *Bacopa rotundifolia* (Michx.) Wettst. and taxa in the *Echinochloa crus-galli* complex are the most abundant and widely distributed rice weeds in California.

INTRODUCTION

Weed communities of agricultural land in California have received little attention from botanists. In a recent work on the terrestrial vegetation of the state (Barbour and Major, 1977) weed communities were not treated

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in detail, although one third of the area of California is cultivated or grazed. In addition, 674 alien species are represented in the flora of the state (Raven and Axelrod, 1978).

Baker (1962, 1965, 1972), Allard (1965), Stebbins (1965) and Jain (1969) among others have examined the population biology and evolution of individual Californian weed species. Robbins (1940) described the history of alien species introduction and compiled a manual of weeds of the state (Robbins et al., 1951). However, as Raven and Axelrod (1978) have recently mentioned, the preparation of an up-to-date weed flora of California is highly desirable. Perhaps the most detailed study of weed communities in California is Frenkel's analysis of the ruderal vegetation along Californian roadsides (Frenkel, 1970).

In the Central Valley of California, little of the original vegetation persists (Thompson, 1961; Ornduff, 1974; Jain, 1976; Barbour and Major, 1977) and most of the wetland plant communities have been replaced by agricultural crops. One of the major crops grown in this region is cultivated rice (*Oryza sativa* L.). Rice is unusual among crop plants in being an aquatic annual. Although 'upland' varieties can be grown under terrestrial conditions, the majority of the world's rice is produced under 'paddy' or flooded cultivation (Grist, 1953). In North America, all commercial rice production is under flooded conditions, although the depth and duration of flood varies from state to state. Due to the flooded conditions that prevail in the rice fields, only relatively specialised weeds capable of growing under aquatic conditions occur. Rice weed floras are often composed of species that are not found as weeds of terrestrial crops, and hence, rice weed communities are highly distinctive. Species lists and ecological studies of these communities have been reported for the following geographical locations: Australia (Clampett and Clough, 1975); China (Anonymous, 1973); Egypt (Imam and Kosinova, 1972); France (Tallon, 1958; Cornet, 1971); Italy (Koch, 1952, 1954; Pignatti, 1957; Cook, 1973); Japan (Noda, 1970; Morishima and Oka, 1977); India (Chakravarty, 1957; Singh, 1969); Lower Amazon (Barrett, 1975); Philippines (Pancho et al., 1969); Romania (Chirila and Melachrinos, 1976); Russia (Vasinger-Alektrova, 1931); Surinam (Dirven and Poerink, 1955); Taiwan (Sung and Chang, 1964); Thailand (Suwatabandhu, 1950) and the United States (Smith et al., 1977).

The objective of this paper is to describe the history of rice cultivation in California and to document the origin, distribution and biological characteristics of the rice weed flora of the state. In addition, the distribution and weed status of California's most serious rice weeds (the *Echinochloa crus-galli* (L.) Beauv. complex) are reviewed. Names used in this paper follow Mason (1957) and Munz and Keck (1959) except where more recent taxonomic treatments are available.

RICE CULTIVATION IN CALIFORNIA

Rice has been grown in the United States since the latter part of the seventeenth century (Gray and Thompson, 1941). Prior to the twentieth century, the major rice producing states were Louisiana, Arkansas and Texas. In an attempt to determine whether commercial rice production was feasible under Californian conditions, small quantities of rice were grown in widely separates sites during the summer of 1860. Sites were chosen in Alameda, Tehama, San Mateo, Santa Cruz and Sonoma Counties. Only 1975 kg of rice was harvested from all plots. None of these localities is currently used for rice cultivation.

In 1862, an attempt was made by the Californian legislature to stimulate the growth of the rice industry by offering financial incentives to growers. However, it was not until 1906 that rice, obtained from Japan, was grown and matured in Fresno County. In the following year, Louisiana rice seed was planted at Stockton and in Sacramento County but failed to produce a crop. In 1908—09 several acres of Japanese and Honduran rice, composed of some 300 varieties, were grown at Biggs, Butte County (Chambliss, 1912).

Experience with these early plantings of rice provided valuable information on the commercial possibilities for rice culture in the state. In 1912, 567 ha of commercial plantings were made near Biggs and a rice experiment station was constructed 7.25 km NW. of the town (Jones, 1923). Since then, the area utilized for rice production has increased steadily and by 1970 some 134 529 ha were under cultivation in California, representing 22% of the total United States' rice crop (Adair, 1973).

All rice currently produced in California is grown in the Central Valley, with 88% of the total area located in the Sacramento Valley (Fig. 1). The major rice-producing counties listed in approximate order of area under cultivation are: Colusa, Sutter, Butte, Glenn, Yolo, Yuba, Fresno, Sacramento, San Joaquin and Merced. The summer climate of this area is characterized by hot, dry conditions, particularly during May—September which constitutes the rice growing season. The principal soils on which rice is grown in California are heavy clay and clay adobes with impervious subsoils.

Throughout California, a single method of rice culture is practised. Levelled fields are flooded prior to aerial seeding of pre-soaked rice seed. This occurs from mid-April to early June with planting reaching a peak in early May. Rice fields remain flooded at a depth of 8—20 cm for the duration of rice growth and water is removed from fields several weeks prior to harvest in September and October. Due to cooler temperatures during the remainder of the year, only a single rice crop is grown annually in California.

The composition of rice weed communities is strongly influenced by the types of water management and rotational practices utilised in rice-growing areas. The 'continuous flood' technique, in which water is maintained on fields for most of the season, was developed in California during the 1920—30s in order to reduce certain weeds, principally *Echinochloa crus-galli* var. *crus-galli* and *Leptochloa fascicularis* (Lam.) Gray, which are unable to tolerate

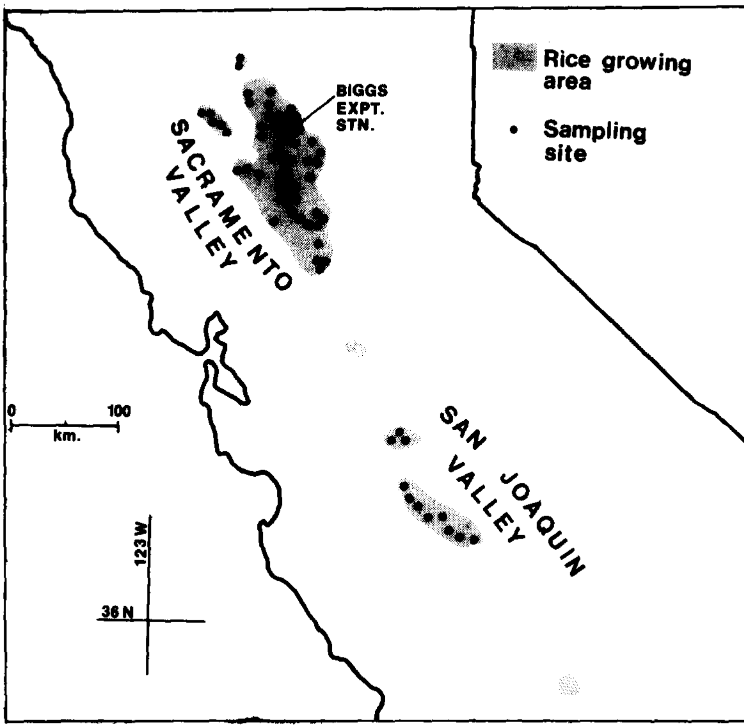

Fig. 1. The rice growing areas of California and the 70 sampling sites utilised in the rice weed survey.

prolonged flooding during seed germination and seedling establishment. This technique is not utilised to any great extent in the other rice growing regions of the United States (i.e. Texas, Louisiana, Arkansas and Mississippi) where seed is usually drilled or broadcast onto dry or saturated soil and germination and rice stand establishment is achieved by rainfall or a series of water flushes followed after 20—30 days by complete or 'permanent' flooding. The deeper water and continuously flooded conditions of Californian rice fields result in a relative more 'aquatic' weed flora compared to the rice weed floras of Southern rice growing states.

Unlike many other rice growing regions of the world, there is at present no established crop rotation pattern for Californian rice lands (Jones et al., 1950). This is because no serious rice disease has yet emerged during the relatively short cropping history (70 years). In addition the soils of rice growing areas of California are inherently quite fertile and soil nutrient depletion has not become a major problem (Johnston and Miller, 1973). Although some growers rotate rice with crops such as safflower (*Carthamus tinctorius* L.), sorghum, sunflower, tomatoes, and wheat, many areas, particularly in Butte, Colusa and Glenn Counties, have been in continuous rice production for over 20 years. Such farming practices have important consequences for the persistence of certain weed species.

With the exception of 400 ha of 'organically grown' rice at Richvale, Butte County, the majority of the rice crop in California receives at least two annual herbicide treatments (Smith et al., 1977). The first is a pre- or post-emergence application of S-ethyl hexahydro-1H-azepine-1-carbothioate (molinate) which controls grasses, particularly varieties of *Echinochloa crus-galli*. Between 35 and 50 days after sowing, an application of [(4-chloro-*o*-tolyl) oxy] acetic acid (MCPA) is made to control broad-leaved weeds and some sedges. Post-emergence applications of 3′, 4′-dichloropropionanilide (propanil) are made for control of these weeds on about 10% of the rice crop in the lower Sacramento and San Joaquin river valleys in lieu of MCPA or molinate. Despite the continuous use of herbicides over the past 10—20 years, weed populations persist and remain one of the major factors reducing yields of rice in California.

THE RICE AGROECOSYSTEM

Agricultural ecosystems are often characterized by a distinctive structure, readily discernable boundaries, and discrete habitats. Ecotones between habitats can be abrupt and temporal changes in the environment, associated with seasonal farming practices, highly predictable. These features are particularly evident in the rice agroecosystem of California (Fig. 2). From the standpoint of weed communities the agroecosystem can be divided into three broad habitat types (Fig. 3) hereafter referred to as the field, levee and

Fig. 2. Aerial view of rice agroecosystem, Sacramento Valley, California.

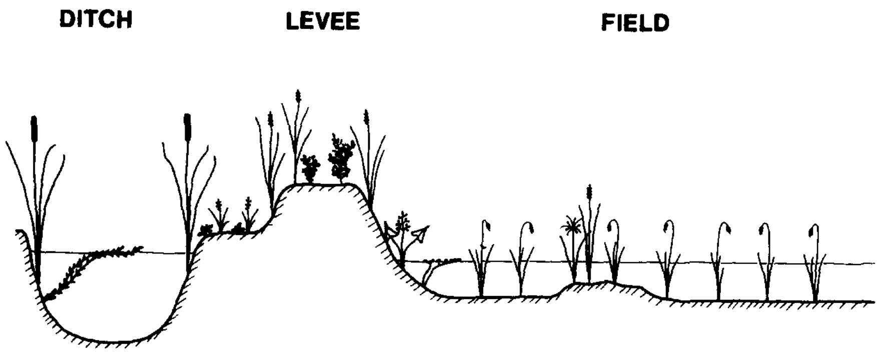

Fig. 3. Schematic diagram of rice agroecosystem illustrating the three major habitats (ditch, levee and field) of weed communities.

ditch habitats. Each of these habitats contains a distinct weed community.

Rice fields represent at least 75% of the total area of the ecosystem. In its simplest form, a rice field is a rectangular block of land subdivided by levees (raised banks) into smaller units known as checks. The checks are flooded and contain dense stands of cultivated rice (average of 120 rice plants m^{-2}). Water depths rarely exceed 0.5 m and shallow water and exposed mud occur at the periphery of each check adjoining the levee and in fields where land has not been adequately levelled. During September—October the fields are drained prior to harvest and from November—March they are left fallow allowing terrestrial weed communities mostly composed of winter annuals, e.g. *Capsella bursa-pastoris* (L.) Medic., *Coronopus didymus* (L.) Sm., *Erodium cicutarium* (L.) L'Her., *Poa annua* L. and *Veronica peregrina* L. to make their appearance.

Adjoining the rice fields are complex series of irrigation ditches, drainage ditches, and canals that convey water from rivers, reservoirs, or wells, to the flooded rice fields. These habitats are usually characterised by deep water to depths of 2—3 m, although shallow water is present in the smaller channels. Ditch habitats can contain flowing or relatively stagnant water depending on the season and water management technique employed. At the end of the rice season the majority of irrigation ditches are drained and remain empty until the commencement of rice culture the following year. Drainage ditches usually remain flooded throughout the year. Ditch habitats are mostly infested with native perennial species, including *Ceratophyllum demersum* L., *Elodea canadensis* Michx., *Ludwigia peploides* (HBK) Raven, *Polygonum coccineum* Muhl., *Potamogeton crispus* L., *P. nodosus* Poir., *P. pectinatus* L., *Scirpus acutus* Muhl., *Typha angustifolia* L., *T. domingensis* Pers. and *T. latifolia* L.

Throughout the rice agroecosystem are elevated earth banks or levees that are used for water-depth control within each field. The levees are usually constructed every three or four years by earth-moving machinery. They vary in width from 1—3 m and are elevated above the flooded fields by 0.25—1 m. In contrast to the field and ditch habitats, the weed communities that occur on levees and canal banks are terrestrial in nature and are usually composed of widespread ruderal species, including *Abutilon theophrasti* Medic., *Amaranthus albus* L., *Avena fatua* L., *Centaurea solstitialis* L., *Chenopodium album* L., *Echinochloa crus-galli* var. *crus-galli*, *Lactuca serriola* L., *Lolium temulentum* L., *Medicago hispida* Gaertn., *Melilotus alba* Desr., *Paspalum dilatatum* Poir., *Polygonum* spp., *Rumex crispus* L. and *Sorghum halepense* (L.) Pers. The majority of the levee weeds are aliens which were introduced to California prior to the start of rice cultivation.

Since the rice field habitat is the major and most distinctive component of the agroecosystem, much of the emphasis of this study was directed toward a description of its particular weed flora.

ORIGIN AND HISTORY OF THE WEED FLORA

The weed flora of Californian rice fields and associated ditch habitats is composed of some 62 species of vascular plant. A list of the species and information on their distribution, weed status, habitat and biology are presented in Table I. Weeds found exclusively on levees and other terrestrial habitats associated with the rice agroecosystem are not included. Doubtless the number of species reported here from rice fields of the state will increase with further exploration and collection. We feel confident however that all of the common rice field weeds are included in Table I.

Unlike other weed floras of agricultural crops grown in California, the native element of the rice weed flora is substantial, representing two thirds of the total flora (see Baker, 1962). The large number of native species is probably the result of the similarity in ecological conditions between rice fields and the original wetland habitats of the Central Valley that they replaced (Baker, 1972). Aquatic species of the natural vegetation possess adaptations enabling them to establish and proliferate in the flooded conditions of rice fields. It is noteworthy that species of the vernal pool flora of the Central Valley (see Jain, 1976) are not among the native representatives of the rice weed flora despite the superficial ecological similarity and seasonal nature of both habitats. This is presumably because of the seasonal differences in the availability of the two habitats. Rice fields are flooded from April—September whereas vernal pools occur from November—June depending on rainfall. Several vernal pool species such as *Veronica peregrina* can be found in poorly drained rice fields during winter and early spring. Populations of these species are usually destroyed during land preparation prior to flooding.

Among the 62 species of the rice agroecosystem are 21 aliens. These can be grouped into three geographical elements based on their areas of origin. The Paleotropical, European and American elements are composed of 11, 7 and 3 taxa, respectively (Table II). All species from the Old World tropics have been previously reported as weeds of the rice agroecosystem (see Table I).

TABLE I

Species list of Californian rice weeds indicating distribution, rice weed status, habitat in rice agroecosystem and life form

Taxon	Native/ alien[a]	Distribution	Geographical areas where reported as weed of rice agroecosystem (other than California)[b]	Major habitats[c]	Life forms[d]
Marsileaceae					
Marsilea mucronata A. Br.	N	N. America	Not reported elsewhere	F	Pe., F1.
Salviniaceae					
Azolla filiculoides Lam.	N	Cosmopolitan	Indonesia, Malaysia, southern U.S.A., France, Italy, Algeria	D, F	Pe., Ff.
Typhaceae					
Typha angustifolia L.	N	Cosmopolitan	Thailand	D, F	Pe., Em.
Typha domingensis Pers.	N	New World	Southern U.S.A.	D, F	Pe., Em.
Typha latifolia L.	N	Cosmopolitan	Southern U.S.A., France, Italy, Russia	D, F	Pe., Em.
Potamogetonaceae					
Potamogeton crispus L.	N	Cosmopolitan	Italy, Russia, Swaziland, China	D	Pe., Sub.
Potamogeton nodosus Poir.	N	Cosmopolitan	Italy, Egypt	D, F	Pe., Fl.
Potamogeton pectinatus L.	N	Cosmopolitan	Italy	D, F	Pe., Sub.
Najadaceae					
Najas graminea Raffeneau-Delile	N	Old World	Italy, Egypt, Thailand	D, F	An., Sub.
Najas guadalupensis (Spreng.) Morong	N	New World	Not reported elsewhere	D, F	An., Sub.
Zannichelliaceae					
Zannichellia palustris L.	N	Cosmopolitan	Not reported elswhere	D, F	Pe., Sub.
Alismataceae					
Alisma lanceolatum With.	A	Eurasia	France, Italy, Romania	F	An., Em.
Alisma triviale Pursh	N	N. America	Not reported elsewhere	F, D	An., Em.
Echinodorus berteroi (Spreng.) Fassett	N	N. America	Southern U.S.A.?	F, D	An., Em.
Sagittaria longiloba Engelm.	N	N. America	Not reported elsewhere	F, D	Pe., Em.
Sagittaria montevidensis Cham. & Schlecht. ssp. *calycina* (Engelm.) Bogin	N	N. America	Not reported elsewhere	F, D	An., Em.

Hydrocharitaceae					
Elodea canadensis Michx.	N	Cosmopolitan	Italy	D	Pe., Sub.
Ottelia alismoides (L.) Pers.	A	Cosmopolitan	Italy, Egypt, India, Thailand	D	Pe., Sub.
Gramineae					
Echinochloa colonum (L) Link	A	Cosmopolitan	Worldwide in rice	L, F	An., Em.
Echinochloa crus-galli (L.) Beauv. var. *crus-galli*	A	Cosmopolitan	Worldwide in rice	L, F	An., Em.
Echinochloa crus-galli (L.) Beauv. var. *oryzicola* (Vasing.) Ohwi	A	Cosmopolitan	Europe, India, S.E. Asia, Japan, Australia, Russia	F	An., Em.
Echinochloa muricata (Beauv.) Fern.	N	N. America	Australia (Vickery, 1975)	L, F	An., Em.
Leersia oryzoides (L.) Sw.	N	N. temperate	Southern U.S.A., Italy, Romania	D, F	Pe., Fl.
Leptochloa fascicularis (Lam.) Gray	N	Cosmopolitan	Southern U.S.A.	L, F	An., Em.
Leptochloa uninervia (Presl) Hitch. & Chase	N	N. temperate	Southern U.S.A.	L, F	An., Em.
Oryza rufipogon Griff.	A	Cosmopolitan	Worldwide in rice	F	An., Em.
Paspalum distichum L.	N	Cosmopolitan	Southern U.S.A., Brazil, Italy, Romania, Egypt, Swaziland, China	D, F	Pe., Fl.
Polypogon monspeliensis (L.) Desf.	A	Europe, Australia	Not reported elsewhere	D, F	An., Em.
Cyperaceae					
Cyperus difformis L.	A	Cosmopolitan	Worldwide in rice	F	An., Em.
Cyperus erythrorhizos Muhl.	N	N. America	Southern U.S.A.	F, L	An., Em.
Cyperus odoratus L.	N	Cosmopolitan	Southern U.S.A., Surinam, Brazil, Philippines	F, L	An., Em.
Eleocharis obtusa (Willd.) Schult.	N	N. America Europe	Southern U.S.A., Italy	F	An., Em.
Eleocharis palustris (L.) R. & S.	N	N. America	Russia, China, Japan	F	An., Em.
Scirpus fluviatilis (Torr.) Gray	N	N. America Australia	Not reported elsewhere	F	Pe., Em.
Scirpus mucronatus L.	A	Eurasia	France, Italy	F	An., Em.
Scirpus acutus Muhl.	N	N. America	Southern U.S.A.	F, D	Pe., Em.
Lemnaceae					
Lemna minor L.	N	Cosmopolitan	Italy, Russia, Egypt	F, D	Pe., Ff.
Pontederiaceae					
Heteranthera limosa (Sw.) Willd.	A	Neotropics	Southern U.S.A., Costa Rica, Venezuela	F	An., Em.
Monochoria vaginalis (Burm. f.) Presl	A	Asia	Russia, India, SE. Asia, Japan	F	An., Em.

Taxon	Native/ alien[a]	Distribution	Geographical areas where reported as weed of rice agroecosystem (other than California)[b]	Major habitats[c]	Life forms[d]
Polygonaceae					
Polygonum coccineum Muhl.	N	North America	Not reported elsewhere	L, F	Pe., Em
Polygonum persicaria L.	A	North-temperate	France, Italy	L, F	An., Em.
Polygonum lapathifolium L.	A	North-temperate	Italy, Taiwan	L, F	An., Em.
Rumex crispus L.	A	Cosmopolitan	Italy, Taiwan	L, F	Pe., Em.
Ceratophyllaceae					
Ceratophyllum demersum L.	N	Cosmopolitan	Italy, Thailand, China	D, F	Pe., Sub.
Elatinaceae					
Elatine californica Gray	N	N. America	Not reported elsewhere	F	An., Sub.
Elatine ambigua Wight	A	Eurasia	Italy, Czechoslovakia, Russia, S.E. Asia	F	An., Sub.
Elatine rubella Rydb.	N	N. America	Not reported elsewhere	F	An., Em.
Lythraceae					
Ammannia auriculata Willd.	N	Cosmopolitan	Egypt, Nigeria	F	An., Em.
Ammannia coccinea Rottb.	N	Cosmopolitan	Southern U.S.A., Spain, Portugal, Romania	F	An., Em.
Lythrum hyssopifolia L.	N	Cosmopolitan	Italy, Egypt	F	An., Em.
Rotala indica (Willd.) Koehne	A	Cosmopolitan	Italy, Romania, India, S.E. Asia, Taiwan, Japan, China	F	An., Em.
Rotala ramosior (L.) Koehne	N	Cosmopolitan	Southern U.S.A., Italy, Philippines (Cook, 1979)	F	An., Em.
Onagraceae					
Ludwigia peploides (HBK) Raven	N	New World	Southern U.S.A.	D, F	Pe., Fl.
Ludwigia repens Forster	N	N. America	Not reported elsewhere	F	Pe., Fl.
Scrophulariaceae					
Bacopa eisenii (Kell.) Penn.	N	N. America	Not reported elsewhere	F	An., Fl.
Bacopa rotundifolia (Michx.) Wettst.	A	N. America	Southern U.S.A.	F	An., Fl.
Bacopa repens (Swartz) Wettst.	A	Central America	Louisiana	F	An., Fl.
Dopatrium junceum (Roxb.) Ham.	A	Cosmopolitan	Southern U.S.A., Swaziland, India, SE. Asia, Taiwan, Japan, Australia	F	An., Em.
Lindernia anagallidea (Michx.) Penn.	N	N. America	Southern U.S.A.	F	An., Em.

Limnophila indica (L.) Druce X *sessiflora* Bl.	A	Paleotropics	Nigeria	F	Pe., Sub.
Lentibulariaceae					
Utricularia gibba L.	N	North and Central America	Not reported elsewhere	F	Pe., Sub.
Compositae					
Aster exilis Ell.	N	New World	Not reported elsewhere	L, F	An., Em.
Eclipta alba (L.) Hassk.	N	Cosmopolitan	Southern U.S.A., India, S.E. Asia, Japan	L, F	An., Em.

[a](A) alien, (N) native species.
[b]Information based on rice weed literature (see Introduction) and authors' observations.
[c](D) = ditch, (F) = field and (L) = levee.
[d]Most frequently exhibited life form: (An) annual; (Pe) perennial; (Em) emergent aquatic; (Ff) free-floating aquatic; (Fl) floating-leaved aquatic; (Sub) submersed aquatic.

TABLE II

Origin, history of introduction and current distribution of alien species in the Californian rice weed flora

Taxon	Origin	Earliest collections and references	Current distribution in California rice area
Paleotropical element			
Cyperus difformis	Asia	1915, Biggs, Butte Co. *Johnston W132J* UC. (Howell, 1934)	Widespread
Dopatrium junceum	Asia	1944, Biggs, Butte Co. *Davis s.n.* CDA. (Morton and Howell, 1945)	Widespread
Echinochloa colona	Asia	1849—1860 (Brewer et al. 1876; Watson, 1880)	Occasional in southern area
Echinochloa crus-galli var. *oryzicola*	Asia	1915, Biggs, Butte Co. *Johnston W151J* DAV (Crampton, 1964)	Widespread
Elatine ambigua	Asia	1949, Willows, Glenn Co. *Nobs & Smith* 1885 UC.	Widespread
Limnophila indica X sessiflora	Paleotropics	1977, Marysville, Yuba Co. *Ahart s.n.* CDA.	Restricted to Marysville
Monochoria vaginalis	Asia	1954, Biggs, Butte Co. *Tucker, McCaskill & Harvey 2753* UC.	Restricted to Biggs
Najas graminea	Paleotropics	1946, Grey Lodge Game Refuge, Butte Co. *Mason & Grant 13047* UC.	Northern Sacramento Valley
Oryza rufipogon	Asia	(Chambliss, 1920; Jones, 1923)	Rare seed contaminant
Ottelia alismoides	Asia	1977, Biggs, Butte Co. *Turner 541* UC.	Once restricted to Biggs (population destroyed)
Rotala indica	Asia	1946, Biggs, Butte Co. *Mason & Grant 13137* UC.	Restricted to Biggs and Marysville

European element			
Alisma lanceolatum	Eurasia	1946, Williams, Colusa Co. *Mason & Grant 13119* UC (Rubtzoff, 1964)	Rare in rice Butte and Sutter Co.
Echinochloa crus-galli var. *crus-galli*	Eurasia	1825—1848 (Torrey, 1856; Hendry, 1931)	Widespread
Polygonum lapathifolium	Europe	Widely distributed at beginning of 20th century (Robbins, 1940)	Widespread
Polygonum persicaria	Europe	1849—1860 (Brewer et al., 1876; Watson, 1880)	Widespread
Polypogon monspeliensis	Europe	1825—1848 (Hendry, 1931; Hendry and Bellue, 1936).	Widespread
Rumex crispus	Europe	1769—1824 (Bentham, 1844; Hendry, 1931).	Widespread
Scirpus mucronatus	Eurasia	1942, Codora, Glenn Co. (Bellue, 1947)	Widespread in Sacramento Valley
American elements			
Bacopa repens	Central America	1949, Biggs, Butte Co. *Bellue s.n.* CDA. (Barrett & Strother, 1978).	Restricted to Biggs
Bacopa rotundifolia	Central U.S.A.	1923, Nelson, Butte Co. *Copeland 843* POM (Barrett & Strother, 1978).	Widespread
Heteranthera limosa	Neotropics	1948, Willows, Glenn Co. *Bellue s.n.* CDA (Tucker and McCaskill, 1967).	Widespread in Sacramento Valley

Some, e.g. *Cyperus difformis* L., *Dopatrium junceum* (Roxb.) Ham., *Echinochloa colonum* (L.) Link; *Echinochloa crus-galli* (L.) Beauv. var. *oryzicola* (Vasing) Ohwi, *Oryza rufipogon* Griff., *Ottelia alismoides* (L.) Pers., and *Rotala indica* (Willd.) Koehne are among the most cosmopolitan weeds of rice (Sculthorpe, 1967; Pancho et al., 1969; Noda, 1970; Cook, 1973, 1979; Cook et al., 1974; Holm et al., 1977; Reed, 1977).

Species of the Paleotropical element are particularly common as rice weeds in SE. Asia and the Orient, and it is possible that their original introduction to Californian ricefields was as seed contaminants in shipments of rice seed from those regions. Support for this suggestion comes from several lines of evidence: (1) none of the species (except *Echinochloa colonum*, see Table II) is recorded in California prior to the start of rice cultivation and, with the exception of *Oryza rufipogon* and *E. colonum*, they are either absent or rare elsewhere in the U.S.A.; (2) all species were first collected from the rice agroecosystem; and (3), six of the 11 species were first recorded in the vicinity of Biggs Rice Experiment Station, one of the major entry points for imported rice seed stocks (Jones, 1923). *Oryza rufipogon* was introduced to California as a rice seed contaminant, from the southern U.S.A. at the beginning of rice culture (Chambliss, 1920).

With the exception of *Scirpus mucronatus* L. and *Alisma lanceolatum* With., the species that make up the European element are common weeds of wet, disturbed ground in California and were established in the state prior to the beginning of rice culture (Robbins, 1940). They frequently occur as weeds of irrigated crops other than rice (Robbins et al., 1951), and their introduction to California is associated with European colonization and agricultural settlement (Robbins, 1940; Frenkel, 1970). *Scirpus mucronatus* was first observed in California in 1942 (Bellue, 1947) and is currently restricted in the U.S.A. to rice fields of California. The species is a cosmopolitan rice weed (Mason, 1957; Reed, 1977). Earliest collections of *A. lanceolatum* in California, made in 1946, were incorrectly identified as *A. plantago-aquatica* L. (Rubtzoff, 1964). At present, *A. lanceolatum* is reported from Sonoma, Marin, Colusa and Placer Counties (Munz, 1968) and occurs rarely in rice fields. In Europe, the species is reported as a weed of rice in France (Cornet, 1971); Italy (Cook, 1973) and Romania (Chirila and Melanchrinos, 1976).

The alien American element in Californian rice fields is composed of three species, *Bacopa repens* (Swartz) Wettst., *B. rotundifolia* (Michx.) Wettst. and *Heteranthera limosa* (Sw.) Willd. Each species was first reported in California from rice fields (Table II), and virtually all herbarium collections from California (seen by the authors) are from rice field localities. These facts suggest that their introduction to the state was also as seed contaminants of rice stocks. The most likely source of origin of such stocks is the southern U.S.A., where all three species occur as weeds of rice (Smith et al., 1977; Barrett and Strother, 1978). The two species of *Bacopa* have been misunderstood taxonomically as *B. nobsiana* Mason, and considered endemic to the Central Valley (Mason, 1952; Raven and Axelrod, 1978). A recent taxonomic treatment (Barrett and Strother, 1978) clarifies the relationships among Californian Bacopas and discusses the history of their introduction to the state.

The small number of species in the American element probably reflects the absence of a well-developed flooded rice weed flora in the New World comparable to that found in the Old World. This is mainly due to the short period in which rice, an Old World domesticate (Purseglove, 1972), has been grown in the New World. In addition, much of the rice grown in the Americas (outside of the U.S.A.) is of upland varieties grown under terrestrial or upland conditions and there have been few Central or South American rice varieties introduced to North America.

DISTRIBUTION OF RICE WEEDS

There have been no published surveys of the distribution and abundance of rice weeds in California. Lists of major rice weeds were compiled by Kennedy (1923), Bellue (1932), and Robbins et al., (1951). These lists are useful for evaluating changes in the composition of the weed flora, although the identity of some of the weeds listed is difficult to determine because no taxonomic sources are mentioned.

In order to obtain quantitative estimates of the abundance and distribution of rice weeds in California, a survey was undertaken during the summer of 1976, an attempt being made to sample throughout the rice-growing areas of California. The location of sample sites is shown in Fig. 1, and detailed locality data are on file at Biggs Rice Experiment Station. Vegetation on levees, and that associated with ditches and canals was not included in the survey. Seventy sites (rice fields) were chosen for sampling, and at each site the identity of all emergent weed species occurring in twenty five 0.25-m^2 quadrats was recorded. Owing to the difficulty of observation and field identification, submersed aquatics were not included in the survey. Sites were chosen depending on access and the timing of herbicide spray. Quadrats were positioned at random within fields. All sampling was undertaken during early June and fields were sampled prior to MCPA herbicide sprays.

A total of 31 species was recorded from the 1750 quadrats sampled. The average number of taxa recorded per site was 9.3 (range 4—17). Table III lists the species recorded in the survey with their respective absolute presence, constancy and frequency values. Species are listed in order of abundance. The most widespread and abundant rice weeds of the state are *Sagittaria montevidensis* Cham. and Schlecht. ssp. *calycina* (Engelm.) Bogin, *Ammannia coccinea* Rottb. and *Bacopa rotundifolia.* These species occurred in 85% or more of the sites surveyed. None of the remaining species was as widely distributed, although many were locally abundant, e.g. *Bacopa eisenii* (Kell.) Penn., *Cyperus difformis, Eleocharis palustris* (L.) R. & S., *Heteranthera limosa, Sagittaria longiloba* Engelm. and *Scirpus mucronatus.* It should

TABLE III

Presence and frequency of weed species in a survey of Californian rice fields (n = 70 sites)

Species in order of presence	Absolute presence[a]	Constancy[b]	Av. frequency[c]	Av. frequency (where present)[d]
Sagittaria montevidensis ssp. *calycina*	65	0.929	0.521	0.561
Ammannia coccinea	62	0.886	0.349	0.394
Bacopa rotundifolia	60	0.857	0.558	0.651
Echinochloa crus-galli var. *oryzicola*	34	0.486	0.090	0.186
Typha latifolia	33	0.471	0.043	0.092
Heteranthera limosa	32	0.457	0.243	0.531
Scirpus mucronatus	32	0.457	0.177	0.386
Eleocharis palustris	31	0.443	0.133	0.299
Rotala ramosior	31	0.443	0.116	0.262
Alisma triviale	30	0.429	0.085	0.199
Cyperus difformis	30	0.429	0.113	0.263
Echinochloa crus-galli var. *crus-galli*	28	0.400	0.074	0.186
Leptochloa fascicularis	28	0.400	0.062	0.156
Polygonum coccineum	26	0.371	0.020	0.054
Lythrum hyssopifolia	20	0.286	0.033	0.114
Dopatrium junceum	19	0.271	0.071	0.263
Sagittaria longiloba	14	0.200	0.030	0.151
Bacopa eisenii	13	0.186	0.095	0.514
Scirpus fluviatilis	13	0.186	0.033	0.178
Echinodorus berteroi	11	0.157	0.047	0.298
Marsilea mucronata	8	0.114	0.026	0.230
Lindernia anagallidea	7	0.100	0.013	0.126
Cyperus odoratus	5	0.071	0.006	0.080
Lemna minor	3	0.043	0.016	0.373
Rumex crispus	3	0.043	0.002	0.040
Jussiaea californica	2	0.029	0.003	0.100
Scirpus acutus	2	0.029	0.001	0.040
Aster exilis	1	0.014	0.003	0.240
Eclipta alba	1	0.014	<0.001	0.040
Paspalum distichum	1	0.014	<0.001	0.040
Polypogon monspeliensis	1	0.014	<0.001	0.040
Potamogeton nodosus	1	0.014	0.007	0.520

[a]No. of sites where taxon occurred.
[b]Proportion of sites where taxon occurred.
[c]Proportion of quadrats in which taxon occurred averaged for all sites.
[d]Proportion of quadrats in which taxon occurred averaged for sites where taxon occurred.

be noted that the survey was undertaken after the application of herbicides utilised for control of grasses, primarily varieties of *Echinochloa crus-galli*. As a result, values obtained for these taxa as well as other grass species should be considered underestimates of their actual abundance in rice fields prior to herbicide applications.

Certain geographical patterns were evident from the survey data. Rice weeds with predominantly northern distributions include *Alisma triviale* Pursh, *Heteranthera limosa* and *Scirpus mucronatus*. *Bacopa rotundifolia* is rare in the southern rice areas of the San Joaquin Valley and is replaced by *Bacopa eisenii*, which is rare in the southern Sacramento Valley and absent from the northern part of the valley. *Aster exilis* Ell., *Cyperus difformis*, *Echinodorus berteroi* (Spreng.) Fassett, *Leptochloa fascicularis* and *Scirpus* *fluviatilis* (Torr.) Gray are more abundant in the San Joaquin Valley than in the Sacramento Valley. *Bacopa rotundifolia* and *Sagittaria montevidensis* ssp. *calycina* are not mentioned in the early observations on Californian rice weeds by Kennedy (1923) and Bellue (1932). This suggests that their present abundance may have been achieved over a relatively short time period. Several other species appear to be undergoing range extension. *Heteranthera limosa* was first reported from Glenn County in 1948 (Tucker and McCaskill, 1967); in the present survey, it was recorded from 32 sites in Butte, Glenn, Placer, Sutter and Yuba Counties. Records of early herbarium collections of *Bacopa eisenii*, *Dopatrium junceum*, *Echinochloa crus-galli* var. *oryzicola* and *Scirpus mucronatus* indicate that these species have also spread extensively during the past few decades.

Several introduced species have shown little tendency to spread outside of their original sites of entry. The earliest collections of *Rotala indica*, *Bacopa repens* and *Monochoria vaginalis* (Burm. f.) Presl. were made at Biggs in 1946, 1949 and 1954, respectively. Despite an extensive search, the authors have not located any populations of *B. repens* or *M. vaginalis* outside of the general vicinity of Biggs and only a single population of *R. indica* (*Williams, s.n.*, DAV, Marysville, Yuba Co., October 8, 1974). At present, *M. vaginalis* and *R. indica* are among the most abundant and conspicuous rice weeds at Biggs Experiment Station. *Bacopa repens* is more difficult to locate, occurring in small numbers from year to year. The causes behind the restricted nature of the Californian distributions of these species is a problem worthy of future study. In California, all three are autogamous annuals that reproduce exclusively by seed (see below). It seems unlikely that restricted seed dispersal is preventing range extension of the three species since they each produce large quantities of small seed. In the case of *B. repens* and *R. indica*, congeneric species (*B. rotundifolia*, *R. ramosior* (L.) Koehne) with apparently similar reproductive biologies are widespread weeds of rice.

The present distribution and weed status of taxa within the *Echinochloa crus-galli* complex (barnyard grass or water grass) are worth considering here in detail because of confusion in the literature and among agronomists concerning the identity and ecological characteristics of constituent taxa (Kennedy, 1923; Jones, 1933; Robbins et al., 1951). Barnyard grasses are the most serious threat to rice production in California, and are among the most widespread weeds of rice (Yabuno, 1966; Michael, 1973, 1978; Holm et al., 1977). The polymorphic nature of the complex has resulted in the naming of countless intraspecific taxa (see Wiegand, 1921; Hitchcock and Chase, 1950; Smith et al., 1977). In this discussion, Gould's treatment of *Echinochloa* for the U.S.A. (Gould et al., 1972) is followed throughout. Three major forms of barnyard grass occur in Californian rice fields (Kennedy, 1923); all three are introduced from the Old World. The most widespread form is *Echinochloa crus-galli* var. *crus-galli* which is morphologically variable with awned and awnless individuals occurring within populations. Its variable nature is no doubt the result of many separate introductions to North America coupled with an autogamous breeding system. It was recorded in California prior to the beginning of rice culture (Jones, 1923; Frenkel, 1970) and is abundant on levees and in shallow areas within fields. Deep water management controls this form in the majority of fields (Jones, 1933). In the present survey it was recorded from 40.0% of the fields studied although it was observed at all sites growing on levees.

Two morphologically and phenologically distinct forms of *Echinochloa crus-galli* var. *oryzicola* occur in Californian rice fields (Fig. 4). Both forms were probably introduced as rice seed contaminants at the beginning of rice

Fig. 4. Panicles of the major forms of *Echinochloa crus-galli* occurring in Californian rice fields. From left to right: *E. crus-galli* var. *crus-galli*, non-awned form; *E. crus-galli* var. *crus-galli*, awned form; *E. crus-galli* var. *oryzicola*, early flowering form; *E. crus-galli* var. *oryzicola*, late flowering form.

culture in California. Label data on early collections from Biggs and a temporary rice experiment station at Cortena, Colusa Co. distinguish these forms as "a new form of water grass" (*Kennedy s.n.*, DAV, Cortena, Colusa Co., Sept. 18, 1925) and "late form green throughout" (*Kennedy s.n.*, AHUC, Biggs, Butte Co., Sept. 9, 1921). Kennedy and other rice agronomists in California have referred to both forms as "Japanese, Oriental or White Water Grass" (Jones, 1923; Davis, 1950). The behaviour of the two forms since their original introduction to California has been strikingly different. The early flowering form (anthesis begins in June) with lax drooping panicles, awned spikelets and pale green foliage is widespread throughout the area of rice production and constitutes a major weed problem. It was recorded from 48.6% of the sites surveyed. This form corresponds to *E. oryzoides* (Ard.) Fritsch of European authors and is an important weed of rice in Eurasia and Australia (Vickery, 1975; Chirila and Melachrinos, 1976; Michael, 1978; Clayton, 1980). The second form of *E. crus-galli* var. *oryzicola* was not encountered in the weed survey, but occurs abundantly in the vicinity of Biggs Experiment Station and in scattered localities in Butte, Colusa, Glenn, Kern, Merced, Sacramento, Sutter and Yuba counties. This form has dark green, upright foliage, erect panicles and awnless spikelets. It begins flowering at the same time as rice (mid-August), resembles the rice plant in its vegetative condition, and is an example of a crop-mimic (Yabuno, 1966). Ohwi (1962), Bor (1968) and Gould et al. (1972) consider this taxon to be a variety of *E. crus-galli* whereas Crampton (1964) and Yabuno (1966) elevate the taxon to specific rank as *E. oryzicola* (Vasing.) Vasing. (Yabuno, 1966). The form corresponds to *E. phyllopogon* (Stapf.) Koss of some European authors (e.g. Chirila and Melachrinos, 1976) and occurs as a rice weed in China, Europe, India, Japan and Russia.

Both forms of *Echinochloa crus-galli* var. *oryzicola* can be distinguished from *E. crus-galli* var. *crus-galli* by an absence of any well-developed anthocyanin pigmentation, by their larger spikelets, and by seed size. Previous workers in California have not recognized the distinctive nature of the early flowering form of var. *oryzicola* and have considered it as part of the variation encompassed within *E. crus-galli* var. *crus-galli*. Hence, reference to the distribution and weed status of *E. crus-galli* var. *oryzicola* in Crampton (1964) and Gould et al. (1972) refer to the late flowering, crop-mimic form only. It is of interest to note that although *Echinochloa crus-galli* var. *crus-galli* causes a serious weed problem in the remaining rice growing states of the U.S.A. (Smith, 1960; Smith et al., 1977), *E. crus-galli* var. *oryzicola* is absent from these areas.

BIOLOGY

Life forms

There are 36 Monocotyledons, 24 Dicotyledons and 2 Pteridophytes represented in the Californian rice weed flora. The major families are the Gramineae (9 spp.), Cyperaceae (8 spp.), Scrophulariaceae (6 spp.) and Lythraceae (5 spp.). Compositae, Leguminosae and Cruciferae are absent or poorly represented in comparison to the Californian flora as a whole. These families include few herbaceous aquatic species. The weed flora can be considered aquatic and individual species can be classified by aquatic life forms following Sculthorpe (1967). The four life forms recognized are all represented in the flora: emergent aquatics (38 spp.), submersed aquatics

(13 spp.), floating-leaved aquatics (9 spp.) and free-floating aquatics (2 spp.). Cultivated rice exhibits the emergent life form and it is not surprising that the majority of species in rice fields (61%) are emergent aquatics since rice cultural practices favour this form. The smaller representation of the other life forms is probably due to their inability to tolerate dense shade at the water surface once the rice canopy has become established. Many of the species in these remaining groups begin flowering prior to canopy closure, or persist in open water areas at the periphery of fields and where rice stands are thinned by unfavourable growing conditions.

Submersed aquatics are well represented in the Californian rice weed flora in comparison to the southern rice growing states of the U.S.A., where they are generally absent. Their presence in Californian rice fields is probably aided by the continuous flood culture practised in the state combined with favourable water conditions. The water, obtained from the nearby Sierra Nevada mountains is cooler, less turbid and more oxygenated than water utilised in southern states where discontinuous flooding of rice fields is practised.

Those species which persist from year to year in the rice fields complete their reproductive activities before drainage and harvest or alternatively produce perennating organs which can survive burning, ploughing, drying and occasional winter-freezing. The weed flora is composed of 38 annuals and 24 perennials. Some species, e.g. *Alisma triviale*, *Eleocharis palustris* and *Scirpus mucronatus* exhibit both annual and perennial life histories but grow mainly as annuals. The balance between the two is determined by the specific farming practices employed. The type and depth of ploughing is of particular importance in determining the persistence of perennials. For example, deep ploughing and drying of soil after the autumn harvest tends to destroy perennating organs, whereas shallow ploughing in the spring multiplies and spreads vegetative propagules. Among the annual species, both obligate and facultative annuals occur. Taxa such as *Bacopa rotundifolia*, *Heteranthera limosa*, *Dopatrium junceum*, *Echinochloa crus-galli*, *Ammannia* and *Rotala* spp., die back after flowering regardless of environmental conditions. Facultative annuals such as *Bacopa eisenii* and *Monochoria vaginalis* are destroyed as a result of field drainage. Glasshouse-grown plants of these latter species have remained in active growth for over one year (Barrett and Strother, 1978; S.C.H. Barrett, unpublished data).

Closely related species in the weed flora usually exhibit similar life histories and reproductive methods. For example related taxa within the genera *Bacopa*, *Echinochloa* and *Rotala* are autogamous annuals reproducing exclusively by seed. However exceptions occur as in the genus *Sagittaria*, *S. longiloba* is a monoecious perennial that reproduces predominantly by vegetative means and *S. montevidensis* ssp. *calycina* is an andromonoecious annual capable of autogamy and reproducing exclusively by seed. Populations of both *Sagittaria* species are mostly destroyed by MCPA herbicide sprays applied 35—50 days after the rice is sown. In *S. montevidensis* ssp.

calycina flowering commences as soon as 25 days after flooding and enough seed matures to enable populations to persist from year to year. Populations of *S. longiloba* often take somewhat longer to flower and herbicides destroy many plants before their seeds are mature. Most regeneration is by underground stolons and tubers. The yearly applications of herbicides in Californian rice fields must exert strong selection pressures on sensitive species with regard to development rate and time to flowering.

Breeding systems and dispersal

Previous workers have described the adaptive value of autogamy in annual weeds (Baker, 1955; Stebbins, 1957; Mulligan and Findlay, 1970). The breeding systems of 14 annual species were tested in order to determine their facility for autogamous seed production. The following species were tested: *Sagittaria montevidensis* ssp. *calycina*, *Echinochloa crus-galli* var. *crus-galli* and *oryzicola*, *E. muricata* (Beauv.) Fern., *Cyperus difformis*, *Heteranthera limosa*, *Monochoria vaginalis*, *Ammannia coccinea*, *Lythrum hyssopifolia* L., *R. ramosior*, *R. indica*, *Bacopa eisenii*, *B. rotundifolia*, *B. repens* and *Dopatrium junceum*. Isolated plants of each species were grown in a pollinator-free glasshouse and observations of seed set were made. In each species, undisturbed flowers produced seed, suggesting that they are either self-compatible and autogamous or capable of apomixis. Several species (*Bacopa rotundifolia*, *B. repens*, *Dopatrium junceum*, *Heteranthera limosa*, *Monochoria vaginalis*) produce both chasmogamous and cleistogamous flowers. The latter type of flower is produced either on submersed shoots or on plants growing in the deep shade of the river canopy. Cleistogamous flowers are also reported in *Rotala* spp. (see Cook, 1979).

The majority of Californian rice weeds have small to minute, non-fleshy seeds with no obvious appendages. These seed types fall into the sporochore and sclerochore groups in Dansereau and Lems' (1957) classification of diaspore (dispersal unit) types. The major methods by which rice weed seeds are dispersed are by water, by birds, in soil adhering to farm machinery, and as contaminants of cultivated rice seed stocks. Many species produce diaspores which float, and well-developed buoyancy mechanisms occur in *Ammannia coccinea*, *Ottelia alismoides* and *Sagittaria* spp. (see Ridley, 1930). Dispersal in irrigation water is probably the most important method of local dispersal within the rice field agroecosystem.

Californian rice fields are a favourite habitat for birds, including migrating wildfowl and large flocks of granivorous species such as blackbirds. Ducks feed on *Sagittaria* and *Bacopa* spp. (Mason, 1957; S.C.H. Barrett, personal observation) and up to 10% of the diet of species of blackbird (*Agelaius* spp.) can be seeds of *Echinochloa* spp. (Smith and Shaw, 1966). Birds are important in both local and long-distance dispersal of aquatic plants (Ridley, 1930; Cruden, 1966), and they have undoubtedly played a major role in the dissemination and spread of rice weeds. The soils of Californian ricelands are mostly sticky clays. Mud not only adheres to the feet of wildfowl but also builds up on farm machinery. As vehicles move from one field to another, weed seeds are disseminated in the mud. The high diversity of weed species which can be observed at the corners of rice fields where vehicles routinely enter is evidence of the importance of farm machinery in local weed dispersal.

Perhaps the most effective method by which rice weeds have been introduced to California and have subsequently spread is in contaminated rice seed stocks. As mentioned earlier the most likely way in which many alien species were introduced to the state is with imported rice seed during the early days of rice culture in California. The lax seed purity standards, before present quarantine and seed certification procedures were in effect, and the small seed size of the species involved probably aided this process. Once weeds are established in California this method of dissemination is also important in dispersal from one rice growing area to another. Whether growers sow their own seed, harvested the previous year, or purchase certified seed some weed seeds are usually included. Between 1922 and 1932, 81% of the rice seed lots tested by Bellue (1932) contained seeds of *Echinochloa crus-galli* and 28% was contaminated with Red Rice (*Oryza rufipogon*). Today, although Red Rice is still a serious weed in southern states, it has almost been eradicated from Californian rice fields as a result of a vigilant seed certification programme. The smaller seeded *E. crus-galli* still contaminates cultivated rice seed lots.

Evidence for the importance of contaminated rice stocks as a means of rice weed dissemination comes from the weed survey described earlier. Two fields surveyed in the Corning area (Tehama Co.) contained first and second year crops and represent a new and somewhat isolated area of rice cultivation in California. Although overall species diversity was low (6 and 7 spp.) it is noteworthy that the aliens *Bacopa rotundifolia* and *Echinochloa crus-galli* var. *oryzicola* (early form) were present in small numbers scattered throughout these fields. Since both species are restricted to rice fields and neither had been collected in the general area prior to 1976 it would seem most likely that their introduction to the area was in rice stocks utilised in starting the crop in 1975—1976.

CONCLUSION

This review should be regarded as a preliminary attempt to synthesize information of a general nature on weed communities of the Californian rice agroecosystem. The information comes from scattered sources including floras, herbarium records, agronomy journals and reports, and the authors' own observations.

It is remarkable that despite the conspicuous appearance of rice farming, the highly specialised nature of the weed flora, and the interest shown by Californian botanists in colonizing species (e.g. see Baker and Stebbins, 1965) there has been no detailed botanical work on rice weeds. We hope this study will stimulate interest in further investigation of this distinctive group of aquatic plants.

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