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A comparison of weed communitues of rice in Australia and California

SUSAN McINTYRE[1] and SPENCER C. H. BARRETT[2]

[1]*School of Botany, University of Melbourne, Parkville, Vic., Australia 3052 and*
[2]*Department of Botany, University of Toronto, Ontario, Canada, M55 1A1*

Abstract

A comparison of weeds inhabiting flooded rice fields in New South Wales (NSW) and California was made in an effort to understand the historical and ecological factors influencing the development and composition of weed communities. In both regions rice cultivation involves a high level of mechanization and is practised in areas with similar climatic regimes and soils. A total of 55 and 60 species were recorded from rice fields in New South Wales and California, respectively, of these 13 are shared. In contrast to most crop weed floras occurring in the two regions, a high proportion of the species (NSW 73%, Cal. 68%) are native. This suggests that many aquatic species shifted habitat from native wetland communities following the development of rice cultivation.

Representation of aquatic life forms and the proportion of annuals and perennials in the two floras are similar. Surveys in both regions indicate that Australian communities are composed of a few common species with widespread distributions and a large number of rare, restricted taxa. In California the number of restricted species is considerably less. In addition Australian communities contain a greater representation of wetland species capable of surviving under terrestrial conditions than California, where flooded conditions predominate. These contrasting patterns are probably associated with greater spatial and temporal variation in habitat availability in Australia where rice fields are patchily distributed and rotation with terrestrial crops is widely employed.

Introduction

The wide geographical distribution of many crops enables comparison of weed communities originating in different regions as well as providing an opportunity for examining the behaviour of individual species shared between regions. Studies of this type are likely to aid in unravelling the complex of ecological, genetic and historical factors which influence the colonization process and the subsequent development of weed communities. In addition, they provide an opportunity for identification of species which may constitute potential weed problems in newly invaded regions.

Among the weed communities of arable land, weeds of cultivated rice fields are unique in their capacity to survive and regenerate under prolonged periods of flooding. In areas of the world in which 'paddy' (flooded) rice is grown, the weed community is composed primarily of aquatic plants. Studies of rice weeds from various regions (e.g. Pignatti, 1957; Imam & Kosinova, 1972; Cook, 1973; Barrett & Seaman, 1980) indicate that the community is usually composed of an assemblage of cosmopolitan species, closely associated with rice and frequently introduced as rice seed contaminants, as well as native species recruited from local wetland habitats. The relative importance of these groups will vary and depend on the history of rice growing in the region, the extent and nature of native wetland habitats in the area of rice farming, and the cultural practices employed.

Rice cultivation in Australia and California is recent in comparison with most other regions of the world, particularly the Old World (Grist, 1965). The weed communities are therefore of recent origin and are still actively evolving. A study of Californian rice weeds by Barrett and Seaman (1980) demonstrated that weed communities were composed of a large native element. This contrasts with other arable crops grown in the state in which the majority of species are alien (Baker, 1972, 1974). In Australia alien species frequently dominate weed communities of arable land and it is therefore of interest to examine whether or not native species are well represented in the major area of rice production in Australia.

Here we compare data from Australia with that already available from California (Barrett & Seaman, 1980). We first describe the rice field environments and cultural practices employed in the two regions and then examine the floristic composition, phytogeographic origins and life history characteristics of weed communities found in rice fields.

Ecological setting

In Australia, over ninety-five per cent of rice production occurs in south-west New South Wales (NSW) on the Riverine Plain, a depositional landform developed from prior streams and ancestral rivers (Pels, 1964). Californian rice production occurs in the Central Valley, a wide valley flanked by mountain ranges with a broad floodplain, originally supporting extensive wetlands.

Both regions have a Mediterranean climate with a widely fluctuating annual rainfall. High evaporation rates render the limited summer rainfall largely ineffective for plant growth and irrigation schemes were developed in both regions for crop production. Rice farming is generally restricted to the heavy-textured clay soils with relatively impervious subsoils which are characteristic of both regions (Davis, 1950; Hallsworth *et al.* 1952; Talsma & van der Lelij, 1976).

European settlement has had a profound effect on the original vegetation in these parts of NSW and California with little, if any, relict areas remaining unmodified by agriculture, fire or grazing (Moore, 1953; Barbour & Major, 1977). On the Riverine Plain, the structural nature of the vegetation is still recognisable and three major formations occur: sclerophyll forest, woodland, and shrub steppe (Leigh and Noble, 1972). Within all formations there are areas in which free water may be present permanently or otherwise. Wetland communities occur in rivers, billabongs, streams, swamps, claypans and small local depressions (gilgais) throughout the Riverina (Beadle, 1948; Williams, 1955, 1956). In contrast, in the Central Valley of California, little of the original vegetation remains owing to intensive agriculture and urban settlement throughout the valley floor. Small pockets of freshwater marsh, vernal pool communities, and valley grassland remain, and riverine woodland borders the major river systems (Jain, 1976; Barbour & Major, 1977). In both regions a combination of low relief and low soil hydro-conductivity encourages local flooding after rainfall. High temperatures (35-45 °C) and evaporation rates, especially during summer, ensure the transitory nature of these inundated areas.

A major difference between the two regions concerns the spatial distribution of rice fields. In NSW, rice farming is confined to several geographically separate areas in which rice fields vary in density (Fig. 1). Thus large areas of intervening country occur between irrigation areas and in some districts, between individual rice crops. Here, semi-natural plant communities, grazing and terrestrial cropping occur. By comparison, Californian rice growing areas are intensively cultivated, with rice fields occupying a greater proportion of the land.

History of rice cultivation

Following a series of experimental crops, commercial production of rice began in California's Sacramento Valley in 1912. Its success provided the impetus to develop rice growing in NSW after observations of the similarity of Californian rice soils to the heavy soils of the recently developed Murrumbidgee Irrigation Areas (M.I.A.). The first successful rice crop in Australia was sown in 1922 at Yanco in the M.I.A. using imported Californian varieties (Anon 1967). In the ensuing years, the area devoted to rice production increased rapidly in both regions. In NSW, rice was a major crop involved in the subsequent development of the Murray Valley Irrigation Districts in the 1940's and the Coleambally Irrigation Area in the 1950's. Today in NSW approximately 45% of rice production occurs in the Murray Valley districts, 20% in the

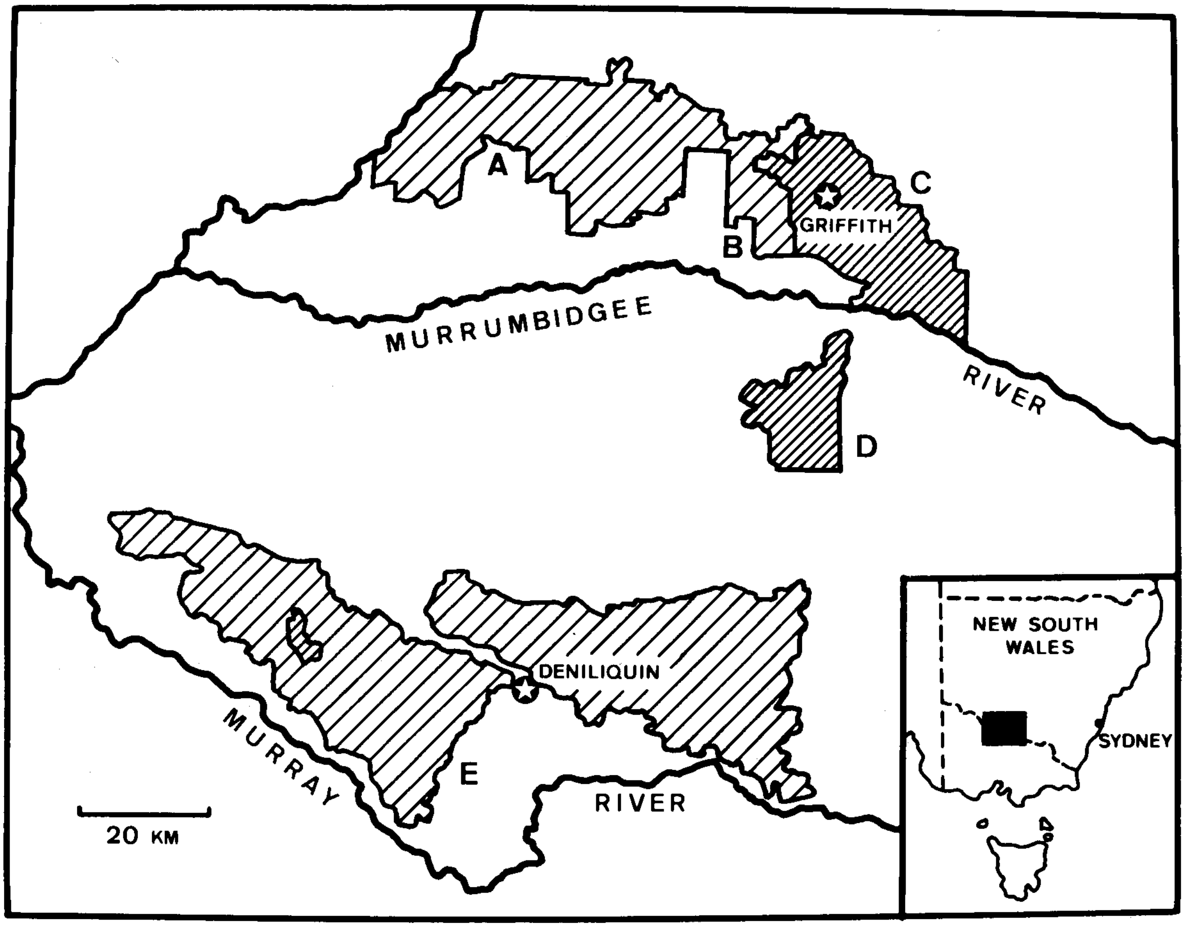

Fig. 1. Rice growing areas of NSW. Light hatching — low intensity rice cultivation; Dense hatching — intensive rice cultivation. A. Wah Wah Irrigation District, B. Benerembah Irrigation District, C. Murrumbidgee Irrigation Areas, D. Coleambally Irrigation Area, E. Murray Valley Irrigation Districts.

Coleambally area and 35% in the Murrumbidgee Irrigation Areas and associated districts.

Cultural practices

In both NSW and California highly developed technology is used in all stages of rice production. Mechanization enables fields to be laid out on a relatively broad scale, in blocks of up to 26 ha. Within each field, internal banks (levees) are formed along the natural contours of the land with a fall of approximately 7 cm between them. The intervening areas (bays or checks) are sown with rice and vary in size up to about 3 ha, depending on topography. Soil within the bays is routinely graded to promote even water depth. The fields are served by a system of channels and ditches for irrigation supply and drainage of waters.

During the rice season, fields are flooded for approximately five months (mid-spring to early autumn) to a depth of 8-20 cm. Water depths can, however, vary from 0-50 cm owing to temporary fluctuations in water or uneven land preparation. Depths of up to 50 cm are common in drainage furrows which run parallel to the contour banks. The banks themselves rise 25-100 cm above the water level and provide a terrestrial habitat in contrast to the aquatic conditions which occur a short distance away.

TABLE 1. Comparison of current rice growing practices in New South Wales and California

	NSW	*California*
First commercial production	1924/25	1912
Total area under production 1970/71	37,401 ha	134,529 ha
Sowing methods (see text)	aerial, combine, sod	aerial
Rotation	varies with locality continuous rice uncommon	continuous rice cropping common
Alternative land use	legume pasture wheat fallow summer crops	summer crops wheat fallow
Rice crops per year	one	one
Herbicide usage in rice crops	one treatment (MCPA, molinate, thiobencarb, propanil)	two treatments (MCPA, molinate, thiobencarb, propanil)
Nitrogen source	urea or legume pasture	sulphate of ammonia
Water regime (rice)	continuous flood for all or most of cropping period	continuous flood for all of cropping period

While field layout is much alike, cultivation practices in NSW and California differ to some extent (Table 1). In all Californian and approximately 40% of NSW rice fields an aerial sowing technique is used. This method is characterized by the early application of permanent water. Roughly tilled fields are flooded and pre-germinated rice seed is aerially broadcast into the bays which remain flooded until several weeks before harvest.

In NSW, two other sowing methods are employed. In both, rice establishment occurs under non-flooded conditions. Seed is sown into dry ground which may be previously tilled (combine sowing) or into unworked stubble or pasture (sod sowing). Fields are flooded briefly to initiate germination and may be flushed a second time to encourage emergence from dry or crusted soil. Permanent water is applied approximately four weeks after sowing. Pasture species which may be present are weakened by grazing or herbicides before permanent water is applied and usually die with subsequent flooding.

Some differences between the two regions are also found in rotational practices. Continuous rice cropping is common in California; the inherently fertile soil and lack of serious rice diseases has not necessitated the establishment of a particular rotation, although summer crops and wheat are used as alternative crops by some growers. In NSW, continuous rice cropping rarely occurs, and short-term irrigated legume pasture and cereals are the main alternative crops.

Weeds are a major factor in yield reduction of rice (Swain, 1973; Clampett and Clough, 1975) and herbicides are universally employed by growers. Species for which herbicide control is used routinely in NSW are: *Echinochloa crus-galli* in combine and sod grown crops and *Cyperus difformis* and *Damasonium minus* in aerially sown crops. *Echinochloa oryzoides* is the major grass weed in California and a second herbicide treatment is usually applied to control various broad-leaved species and sedges (Smith *et al.* 1977).

The flora

i. Methods

Species lists were compiled from the authors' field observations and from additional records. While not considered exhaustive, both lists include the great majority of rice weeds in both regions. Only species occurring within rice fields are included as this was considered to be the major and most distinctive component of the agroecosystem. Plants restricted to the terrestial bank habitats were therefore not recorded. A comparison of species abundance was obtained from the results of a survey of 94 sites in NSW and 70 sites in California. In both surveys, efforts were made to sample evenly throughout the rice growing areas. Presence/absence data for each site was obtained from 50 m transects (NSW) or 25 randomly placed 0.25 m^2 quadrats (California). Fields were sampled once during the season after herbicides had been

TABLE 2. Number of families, genera and species and proportion of introduced and alien taxa in NSW and Californian rice fields.

	NSW	*California*
Families	17	19
Genera	35	36
Species	55	60
Native species (% of total for country)	73%	68%
Alien species (% of total for country)	27%	32%

applied. Submersed aquatics were included in the Australian survey but not in California. Further details of the Californian survey are presented in Barrett & Seaman (1980).

ii. Composition

A total of 55 and 60 species were recorded in NSW and Californian rice fields respectively (Appendix 1). The designation of species as introduced (alien) or native follows Jacobs and Pickard (1981), recognising that uncertainty exists about the status of some species (Kloot, 1984). A similar number of native species occurs in both countries (Table 2) and these form a major component of the total flora. The two floras do not differ significantly in their proportion of native and alien species ($X^2=0.43$, $df=1$, $P>0.05$). The numbers of families and genera which occur in NSW are also very similar to those in California. Of the total number of species listed for both regions, 13 species (11%) were found to be common to both regions (Table 3). Four of these are cosmopolitan aquatics *(Azolla filiculoides, Typha*

TABLE 3. Taxa recorded in both NSW and Californian rice fields.

	Families	*Genera*	*Species*
Number shared	13	19	13
% of combined total shared	56%	37%	11%
	Marsileaceae	*Marsilea*	
	Azollaceae	*Azolla*	*A. filiculoides*
	Typhaceae	*Typha*	*T. domingensis*
	Najadaceae	*Najas*	
	Alismataceae	*Alisma*	*A. lanceolatum*
		Sagittaria	*S. montevidensis*
	Poaceae	*Echinochloa*	*E. crus-galli*
			E. colona
			E. oryzoides
			E. microstachya
		Paspalum	
		Polypogon	*P. monspeliensis*
	Cyperaceae	*Cyperus*	*C. difformis*
		Eleocharis	
	Polygonaceae	*Polygonum*	
		Rumex	*R. crispus*
	Lythraceae	*Lythrum*	*L. hyssopifolia*
		Ammannia	
	Onagraceae	*Ludwigia*	*L. peploides*
	Scrophulariaceae		
	Elatinaceae	*Elatine*	
	Asteraceae	*Eclipta*	
		Aster	

TABLE 4. Species classified according to life history and the most frequently exhibited life form in rice fields: (Em.) emergent aquatic; (Ff.) free-floating aquatic; (Fl.) floating-leaved aquatic; (Sub.) submersed aquatic.

	Annual				*Perennial*			
No species	*Em.*	*Ff.*	*Fl.*	*Sub.*	*Em.*	*Ff.*	*Fl.*	*Sub.*
NSW	22	0	1	5	21	1	4	1
California	32	0	3	4	8	2	6	5

domingensis, Lythrum hyssopifolia and *Ludwigia peploides),* two species *(Sagittaria montevidensis, Echinochloa microstachya)* are native to California, and one species *(Cyperus difformis)* is native to NSW. The most strongly represented families in both regions are the Poaceae (NSW 13 spp., Cal. 10 spp.) and Cyperaceae (NSW 7 spp., Cal. 8 spp.). A number of typically aquatic families are shared Marsileaceae, Azollaceae, Typhaceae, Najadaceae, Alismataceae and Elatinaceae.

iii. Ecological characteristics

To persist in rice fields, weeds must establish and compete successfully with rice under flooded conditions for approximately five months of the year during spring and summer. Subsequent drainage of fields requires populations to survive under conditions which can vary from severe desiccation to waterlogging depending on rainfall. Populations must also tolerate disturbance in the form of tillage, stubble burning and herbicide application.

The distinctions between terrestrial, wetland and aquatic communities are often unclear (Briggs, 1981). In rice fields, opportunities exist for the establishment or persistence of species ranging from true aquatics to terrestrial plants able to tolerate some degree of flooding. Australian rice weeds which are usually associated with terrestrial habitats include *Agrostis avenacea, Gnaphalium sphaericum, Paspalum dilatatum, Eragrostis parviflora, Polygonum aviculare* and *Rumex* spp. Terrestrial species are less well represented in the Californian flora which can be considered more truly aquatic (Barrett & Seaman, 1980). When classified by aquatic life form following Sculthorpe (1967), all four categories are represented in both floras and the proportion of species in each category does not differ significantly between regions ($X^2 = 1.77$, df = 3, $P > 0.05$) (Table 4). In each case, emergent aquatics predominate. This life form most effectively competes for light in a vigorous stand of rice (also an emergent) and is found in many rice weeds of major importance such as *Echinochloa spp., Cyperus difformis* and *Typha spp.* Submersed, free-floating and floating-leaved aquatics are less well represented, presumably because they are at a competitive disadvantage in dense rice stands.

Taxa exhibiting variation in life history occur in both countries. Perennials may adopt an annual life cycle if farming practices dictate. The type of land preparation and crop rotation determine whether perennating organs can survive or whether plants must rely on seedling recruitment to establish in subsequent crops. In Table 4, species have been classified according to the life history most frequently exhibited in rice crops. Among Californian rice weeds, 65% behave predominantly as annuals, compared with 51% in NSW. These proportions are not significantly different ($X^2 = 1.31$, df = 1, $P > 0.05$).

iv. Origins of the floras

Among the native flora of both regions are rice weeds of major economic importance and widespread distribution. Of the ten most frequently recorded rice weeds, six in California, and nine in Australia are of local origin (Table 5). Of the alien rice weeds, 13% (2 spp.) in NSW are of Paleotropical origin compared with 50% (10 spp.) in California (Table 6). It seems likely that their original introduction to California was as rice seed contaminants from SE Asia and the Orient (Barrett & Seaman 1980). The major source of Australian rice seed has been California (Anon, 1967) and it is noteworthy that 47% (7 spp.) of the alien rice weeds in NSW are of American origin. Of these *Sagittaria montevidensis* and *Echinochloa microstachya* were first recorded in the M.I.A. (Aston 1973; Vickery, 1975) and were almost certainly contaminants of seed rice imports.

TABLE 5. Ten most frequently recorded species in NSW (n = 94 sites) and Californian (n = 70 sites) rice fields.

NSW	*Constancy* %	*California*	[1]*Constancy* %
Cyperus difformis	90	Sagittaria montevidensis	93
Elatine gratioloides	82	Ammannia coccinea	89
Damasonium minus	76	*Bacopa rotundifolia	86
*Echinochloa crus-galli	74	*Echinochloa oryzoides	49
Typha spp.	44	Typha latifolia	47
Marsilea drummondii	43	*Heteranthera limosa	46
Diplachne fusca	34	*Scirpus mucronatus	46
Paspalum paspalodes	32	Eleocharis palustris	44
Centipeda cunninghamii	20	Rotala ramosoir	44
Rumex tenax	18	Alisma triviale	43

[1]Proportion of sites where taxon occurred.
*Denotes alien species.

Echinochloa oryzoides and a long-awned form of *E. crus-galli* may also have been introduced via California (Michael, 1981) even though their origins are elsewhere.

The proportion of alien species that are of European origin is similar in both countries, (≈37%). In general, these are common weeds of irrigated crops and wet disturbed ground, and their introduction to both regions in most cases preceeded the establishment of rice culture. Exceptions are *Echinochloa crus-galli,* and *Scirpus mucronatus* (the latter in California only) which are both cosmopolitan rice weeds and *Alisma lanceolatum* which is a weed of rice in France (Cornet, 1971) Italy (Cook, 1973) and Romania (Chirila & Melachrinos, 1976) but occurs rarely in Californian rice fields and has only recently been collected from Australian rice fields *[S. McIntyre* 49C, Farm 53, Coleambally Irrigation Area, 3 Mar. 1983 (NSW)].

v. Species distributions

In both NSW and California a small number of rice weeds are widespread throughout the rice growing areas. Two species in NSW and three in California were recorded at over 80% of sites (Fig. 2). The two regions differ however, in NSW having fewer moderately common rice weeds and many more species that are limited in their occurrence. A significantly greater proportion of species were recorded at 20% or fewer of the sites sampled in NSW ($X^2 = 5.6$, df = 1, $p < 0.05$). These differences may be related to the spatial and temporal distribution of rice yields and wetland habitats in the two areas and their effects on the dispersal and size of weed populations.

The disruption of regular seasonal flooding that results from crop rotation would reduce the build-up of seed populations, particularly for species with short-lived or non-dormant seeds (e.g. *Echinochloa oryzoides,* see below). Low field density may reduce opportunities for dispersal especially among large seeded species. These land use patterns may prevent some species in NSW from reaching their potential distribution and abundance. Crop rotation would also provide greater opportunities for terrestrial species to establish in rice fields and persist in subsequent rice crops. The widespread occurrence

TABLE 6. Origin of alien species in the NSW and Californian rice weed flora.

No. species (% of total)	*Asia Paleotropics*	*Europe*	*New World*
NSW	2(13%)	6(40%)	7(47%)
California	10(50%)	7(35%)	3(15%)

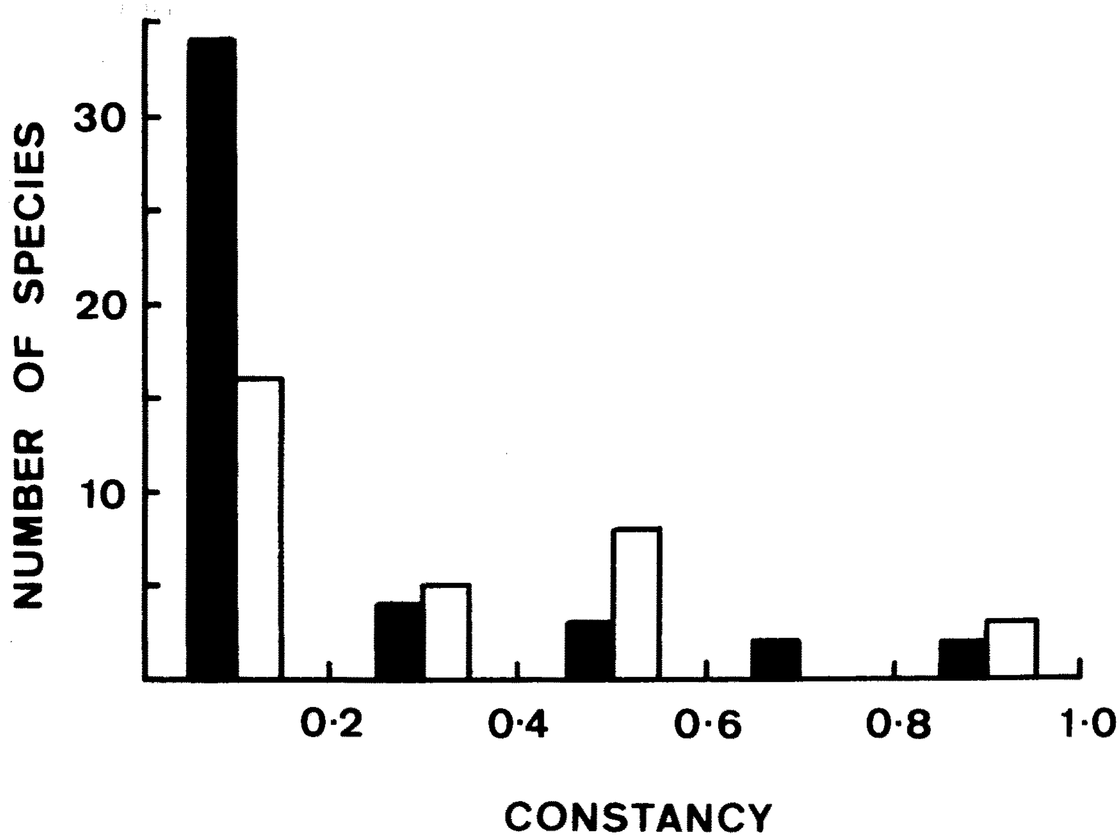

Fig. 2. Distribution of rice weed species of NSW (shaded bars) and California (open bars) over a range of constancy classes. Data obtained from quadrat samples of 94 and 70 rice fields in NSW and California, respectively.

of alternative wetland habitats in NSW (remnant communities and ruderal sites) could ameliorate the effect of spatial isolation of crops by providing 'stepping stones' for the dispersal of rice weeds. *Echinochloa crus-galli, E. microstachya* and *Diplachne fusca* are examples of successful rice weeds which are common ruderal species in NSW. These habitats may also act as refuges for wetland species which may not be particularly well adapted to rice culture but are capable of limited persistance in rice fields (e.g. *Centipeda cunninghamii, Eleocharis* spp. and *Myriophyllum* spp.).

vi. *Echinochloa*

Examination of the geographical distribution of alien species within the NSW rice-growing areas is useful for understanding the process of colonization by weeds. In particular, comparisons of closely related species provide an opportunity to assess plant attributes which may be responsible for differences in colonizing success (Baker, 1965).

Six species of *Echinochloa* are reported from NSW rice fields (Appendix 1). Of these, five are alien and are reported from rice weed communities elsewhere in the world. Distribution maps of four of the alien species in the NSW rice-growing area are presented in Fig. 3. The maps are based primarily on our own herbarium collections. As can be seen the four species have different distribution patterns and we now briefly consider some of the factors which account for their contrasting success as rice weeds.

The widespread abundance of the cosmopolitan *E. crus-galli* is typical of its behaviour in many

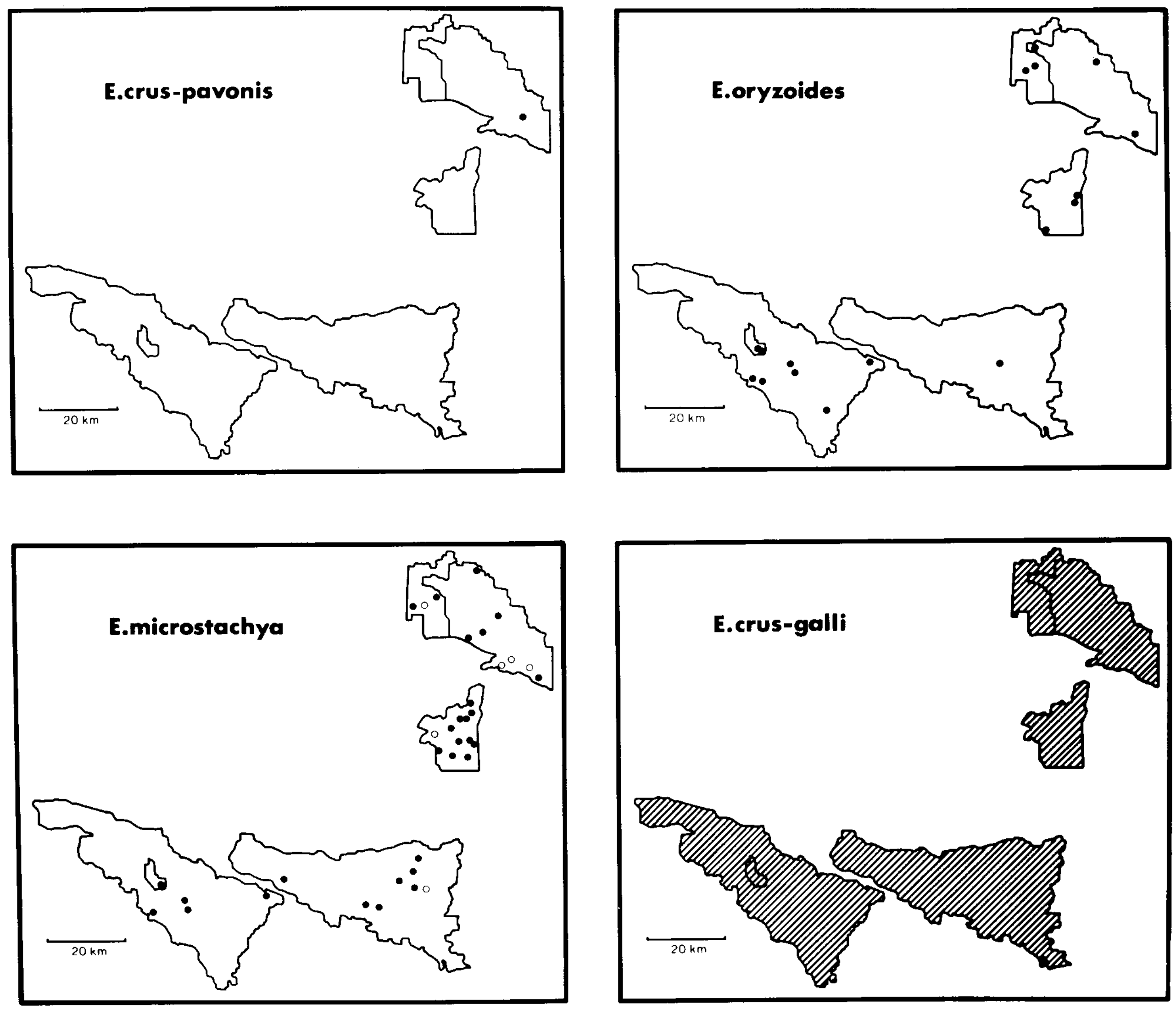

Fig. 3. Distribution of four alien *Echinochloa* species in NSW rice growing areas. Open and closed symbols refer to ruderal and rice field collections, respectively. The hatched area indicates that *E. crus-galli* is abundant in ruderal and rice field sites throughout the area.

temperate rice-growing countries, where it is often the most serious weed (Holm *et al* 1977; Michael, 1983). The species was introduced prior to the commencement of rice culture and is common in many parts of Australia (Vickery, 1975). Several distinct biotypes occur in NSW rice fields indicating multiple introduction of genetic material. *Echinochloa crus-galli* has a range of life history traits which contribute toward its success as a weed of ruderal and crop habitats, these include: rapid development to reproductive maturity, high phenotypic plasticity, production of large numbers of small, easily dispersed seeds and seed dormancy (Barrett & Wilson, 1981, 1983). Despite attempts at herbicide control the species remains a serious weed of rice in NSW, particularly in northern irrigation areas where sod and combine sowing are most widely employed.

The occurrence of the N. American *E. microstachya* [referred to as *E. muricata* var. *microstachya* by N. American authors, see Gould *et al.* (1972)] in NSW rice fields is of some interest because the species rarely occurs as a weed of rice in its native region and is not reported as a rice weed elsewhere in the world. Its introduction to Australian rice fields is almost certainly associated with the importation of contaminated rice seed from California, early in the history of rice culture in NSW. An herbarium collection of *E. microstachya* from Leeton Rice Research Station, MIA in 1938 (Vickery, 1975), where imported rice strains are grown, suggests an early entry point. The species has since spread over much of the rice-growing region although plants are rarely as numerous as *E. crus-galli*. Populations of *E. microstachya* are capable of persisting in roadside ditches and other seasonally-wet, disturbed habitats and the species is in the process of becoming firmly established as a component of the weed flora of the Riverina. In NSW rice fields *Echinochloa microstachya* exhibits some polymorphism for morphological characters indicating multiple introduction from N. America.

Echinochloa oryzoides is a widespread companion weed of rice reported from many areas including China, India, Japan, Soviet Union, S.E. Asia, Europe and California (Michael, 1983). In California where very large populations occur within flooded rice fields the species has remarkably limited ecological tolerance and populations are rarely found away from the rice field agroecosystem (Barrett, 1983). In NSW, populations are also restricted to rice crops and are usually composed of scattered colonies of few plants. In the southern rice-growing districts where aerial sowing predominates, large populations of *E. oryzoides* can occur. This pattern corresponds to historical changes in California where the ability to establish in flooded conditions have favoured the build up of *E. oryzoides* populations over *E. crus-galli* following the introduction of aerial sowing (Barrett & Wilson, 1983). In contrast to *E. crus-galli,* the dormancy of *E. oryzoides* seed is weakly developed and the practices of crop rotation and fallowing used in NSW are therefore likely to lead to rapid exhaustion of the soil seed bank. In addition the lower reproductive potential and much heavier seeds of *E. oryzoides,* in comparison with *E. crus-galli* and *E. microstachya* (Barrett & Wilson, 1981; Barrett, 1983), may also restrict population increase and dispersal potential. Populations of *E. oryzoides* in NSW are relatively uniform in morphology and closely resemble biotypes from California so it is possible that it was introduced in the same manner as *E. microstachya.* The earliest record of *E. oryzoides* in the rice-growing region of NSW is also from Leeton Rice Research Station in 1938 (Vickery, 1975).

A single herbarium collection of *E. crus-pavonis* from a rice crop in the Murrumbidgee Irrigation Area *[B. Cox* YR811, Glen Rd., Murrami via Leeton, 10 April, 1980 (NSW)] constitutes the only known record of the species in the rice-growing regions of NSW. Although *E. crus-pavonis* occurs in abundance in all South American countries where rice is grown, it is rarely reported as a rice weed elsewhere. The factors which limit its spread in temperate rice growing areas such as NSW and elsewhere are unknown, but may be associated with its tropical origin.

Conclusions

The environmental characteristics of the Californian and NSW rice agroecosystems are similar with regard to climate, soil, field layout and general crop husbandry, and it is not surprising to find the weed communities alike in diversity, life-forms and to some extent, floristically.

The composition of the alien flora in an ecosystem is related to historical and chance events as well as the degree of preadaptation to local conditions. Some alien species in both rice growing regions can be traced to original sources of rice seed. Introductions of this nature are thought to be responsible for the high incidence of Asian species in Californian crops, and the American element in Australian rice fields. The European component of both floras reflects strong historical links with these countries. Few specialized rice weeds are found amongst the aliens of European origin, probably because of the independant development of the European rice industries from California and Australia.

Weed communities of terrestrial cereal crops in Australia and California are overwhelmingly dominated by aliens both in species numbers and abundance (Baker, 1972; Velthuis & Amor 1982). Most activities associated with European settlement have resulted in the displacement of native species in favour of aliens with characteristics that confer success in disturbed habitats of high potential productivity (Amor & Piggin, 1977; Michael, 1981; Clements, 1983). These conditions are often associated with land development. Activities such as vegetation clearing, tillage, irrigation, fertilization may select for plants with rapid growth rates and high seed production (Baker, 1965; Grime, 1977; Amor & Piggin, 1977). In such species, tolerance to environmental stress is low in contrast to that found in many natives of undisturbed communities in Australia. The arid climate and predominantly infertile soils (Beadle, 1953; Stephens & Donald, 1958) in Australia would select for the 'stress-tolerant' strategy described by Grime (1977). Within this general pattern however, wetland communities are exceptional. Water is abundant and the process of flooding increases the availability of phosphorus (Ponnamperuma, 1972) to the extent that phosphorus fertilization is unnecessary in flooded rice. Additionally, the temporary and unpredictable nature of Australian and Californian wetlands subjects aquatic plants to disturbance in the form of drought, giving plants with rapid growth rates and early reproductive maturity an advantage. It has been noted that in Europe, agrestrals have been recruited from the native flora, particularly from naturally occurring open and disturbed habitats such as marshes, beaches and river banks (Harper, 1965; Baker, 1965; Grime, 1977), in a similar manner to that described here. What is unusual about the rice field floras of California and NSW is the extent to which indigenous species dominate the weed communities. Two factors may account for this; first the similarity of the aquatic rice field habitat to that of wetlands increases the potential number of weeds. Agriculture is more commonly associated with terrestrial habitats which are prohibitive to most wetland species. Second, the geographical proximity of the original wetlands allowed colonization to occur without the requirement of long-distance dispersal. Thus wetland communities of two different continents are similar in their inclusion of species pre-adapted to the highly modified, man-made environment of the rice agroecosystem.

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References

Amor R. L. & Piggin C. M. (1977) Factors influencing the establishment and success of exotic plants in Australia. In: *Proc. Ecol. Soc. Aust.* **10,** 15-26.

Anon (1967) *Ricegrowing in New South Wales, Australia.* A report of the Rice Industry Sub-Committee. Irrigation Research & Extension Committee.

Aston H. I. (1973) *Aquatic Plants of Australia.* Melbourne University Press.

Baker H. G. (1965) Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (ed. H. G. Baker & G. L. Stebbins). pp. 147-169. Academic Press, New York & London.

Baker H. G. (1972) Migrations of Weeds. In: *Taxonomy, Phytogeography and Evolution* (ed. D. H. Valentine) pp. 327-347. Academic Press, London.

Baker H. G. (1974) The evolution of weeds. *Ann. Rev. Ecol. Syst.* **5,** 1-24.

Barbour M. G. & Major J. (1977) *Terrestrial Vegetation of California.* Wiley-Interscience, New York.

Barrett S. C. H. (1983) Crop mimicry in weeds. *Econ. Bot.* **37,** 255-282.

Barrett S. C. H. & Seaman D. E. (1980) The weed flora of Californian ricefields. *Aquatic Botany* **9,** 351-376.

Barrett S. C. H. & Wilson B. F. (1981) Colonizing ability in the *Echinochloa crus-galli* complex (barnyard grass). I. Variation in life history. *Can. J. Bot.* **59,** 1844-1860.

Barrett S. C. H. & Wilson B. F. (1983) Colonizing ability in the *Echinochloa crus-galli* complex (Barnyard grass). II. Seed biology. *Can. J. Bot.* **61,** 556-562.

Beadle N. C. W. (1948) *The Vegetation and Pastures of Western New South Wales.* Department of Conservation of New South Wales.

Beadle N. C. W. (1953) The edaphic factor in plant ecology. *Ecology* **34,** 426-428.

Briggs S. V. (1981) Freshwater wetlands. In: *Australian Vegetation* (ed. R. H. Groves), pp. 335-360. Cambridge University press.

Chirila C. & Melachrinos A. (1976) La flora vascolare delle risaie romene. *Riso* **15,** 83-86.

Clampett W. S. & Clough R. A. (1975) *Weed Control in Rice.* NSW Dept. Agric. Regional Extension Bull., South Western Region.

Clements A. (1983) Suburban development and resultant changes in the vegetation of the bushland of the northern Sydney region. *Aust. J. Ecol.* **8,** 307-319.

Cook C. D. K. (1973) New and noteworthy plants from the northern Italian ricefields. *Ber. Schweiz. Bot. Ges.* **83,** 54-65.

Cornet M. (1971) La culture du riz en France. In: *La Culture du Riz en France* (eds. J. Bethemont, R. Marrot, C. Huguet, J. Horoyan, M. Bonafour, G. Du Cailar, M. Cornet and P. de Montgrand). Payson du Midi, Montpellier.

Davis L. L. (1950) *California rice production.* Circular 163. California Agricultural Extension Service, College of Agriculture, Univ. of California, Berkeley.

Gould F. W., Ali M. A. & Fairbrothers D. E. (1972) A revision of *Echinochloa* in the United States. *Am. Midl. Nat.* **87,** 36-59.

Grime J. P. (1977) Evidence for the existance of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* **111,** 1169-1194.

Grist D. H. (1965) *Rice.* Longmans, London.

Hallsworth E. G., Lemerle T. H. & Rayner H. V. (1952) Studies in pedogenesis in New South Wales. I. The influence of rice cultivation on the grey and brown gilgai soils of the Murrumbidgee Irrigation Areas. *J. Soil Sci* **3,** 89-102.

Harper J. L. (1965) Establishment, aggression and cohabitation in weedy species. In: *The Genetics of Colonizing Species.* (ed. H. G. Baker & G. L. Stebbins), pp. 243-268 Academic Press, New York & London.

Holm L. G., Plucknett D. L., Pancho J. V. & Herberger J. P. (1977) *The World's Worst Weeds: Distribution and Biology.* University Press of Hawaii, Honolulu.

Imam M. & Kosinova J. (1972) Studies on the weed flora of cultivated land in Egypt: weeds of rice fields. *Bot. Jb. Syst.* **92,** 90-107.

Jain S. K. (1976) (ed.). *Vernal Pools — their Ecology and Conservation.* Univ. Calif. Davis Inst. Ecol. Publ. No. 9.

Jacobs S. W. L. & Pickard J. (1981) *Plants of New South Wales.* Government Printer.

Kloot P. M. (1984) The introduced elements of the flora of Southern Australia. *J. Biogeog.* **11,** 63-78.

Leigh J. H. & Noble J. C. (1972) *Riverine Plain of New South Wales: Its Pastoral and Irrigation Development.* CSIRO Division of Plant Industry, Canberra, Australia.

Michael P. W. (1981) Alien plants. In: *Australian Vegetation* (ed. R. H. Groves) pp. 44-64, Cambridge University Press.

Michael P. W. (1983) Taxonomy and distribution of *Echinochloa* species with special reference to their occurrence as weeds of rice. In: *Proceedings of the Conference on Weed Control in Rice* pp. 291-306. International Rice Research Institute, Los Baños, Philippines.

Moore C. W. E. (1953) The vegetation of the south-eastern Riverina, New South Wales. 1. The climax communities. *Aust. J. Bot.* **1,** 485-547.

Pels S. (1964) The present and ancestral Murray river systems. *Aust. Geogr. Stud.* **11,** 111-20.

Pignatti S. (1957) La vegetazione della risaie pavesi. *Arch. Bot. Biogeogr. Ital. Ser. 4.* **33,** 1-68.

Ponnamperuma F. N. (1972) The chemistry of submerged soils *Adv. Agron.* **24,** 29-96.

Sculthorpe C. D. (1967) *The Biology of Aquatic Vascular Plants.* Arnold, London.

Smith R. J., Flinchum W. T. & Seaman D. E. (1977) *Weed Control in U.S. Rice Production.* U.S. Govt. Printing office, Washington, DC, U.S.D.A. Agriculture Handbook No. 497.

Stephens C. G. & Donald C. M. (1958) Australian soils and their responses to fertilizers. *Adv. Agron.* **10,** 167-256.

Swain D. J. (1973) Weeds and weed control in rice in New South Wales, Australia. In: *Proc. 4th Asian-Pacific Weed Sci. Conf.* Rotorua N.Z. pp. 134-139.

Talsma T. & van der Lelij A. (1976) Infiltration and water movement in an *in situ* swelling soil during prolonged ponding. *Aust. J. Soil Res.* **14,** 337-49.

Velthuis R. G. & Amor R. L. (1982) Weed survey of cereal crops in south west Victoria. *Australian Weeds* **2,** 50-52.

Vickery J. W. (1975) *Flora of New South Wales.* No. 19. Graminae Pt. 2. Nat. Herb. of NSW.

Williams O. B. (1955) Studies in the ecology of the Riverine Plain. I. The gilgai microrelief and associated flora. *Aust. J. Bot,* **3,** 99-112.

Williams O. B. (1956) Studies in the ecology of the Riverine Plain. II. Plant-soil relationships in three semi-arid grasslands. *Aust. J. Agric. Res.* **7,** 127-139.

Appendix

Species list of rice weeds in NSW and California.
*Denotes introduced species.

NEW SOUTH WALES

MARSILEACEAE
Marsilea drummondii A.Br.
M. angustifolia R.Br.
Pilularia novae-hollandiae A.Br.

AZOLLACEAE
Azolla filiculoides Lam.

TYPHACEAE
Typha domingensis Pers.
T. orientalis Presl

NAJADACEAE
Najas tenuifolia R.Br.

ALISMATACEAE
* *Alisma lanceolatum* With.
Damasonium minus (R.Br.) Buch.
* *Sagittaria montevidensis* Cham. & Schlecht ssp. *calycina* (Engelm.) Bogin
* *S. graminea* Michx.

HYDROCHARITACEAE
Ottelia ovalifolia (R.Br.) L.C.Rich.

POACEAE
Agrostis avenacea Gmel.
Amphibromus sp. nov.
Diplachne fusca (L.) Beauv.
* *Echinochloa colona* (L.) Link
* *E. crus-galli* (L.) Beauv.
* *E. crus-pavonis* (Kunth) Schult.
* *E. microstachya* (Wieg.) Rydb.
* *E. oryzoides* (Ard.) Fritsch
E. inundata P. Michael & Vickery
Eragrostis parviflora (R.Br.) Trin.
* *Paspalum dilatatum* Poir.
P. paspalodes (Michx.) Scribn.
* *Polypogon monspeliensis* (L.) Desf.

CYPERACEAE
Bolboschoenus caldwellii (V. J. Cook) Sojak
Cyperus difformis L.
* *C. eragrostis* Lamk.
Eleocharis plana S. T. Blake
E. acuta R.Br.
E. pallens S. T. Blake
E. pusilla R.Br.

JUNCACEAE
* *Juncus articulatus* L.
J. aridicola L. A. S. Johnson
J. flavidus L. A. S. Johnson
J. subsecundus N. A. Wakef.

CALIFORNIA

MARSILEACEAE
Marsilea mucronata A.Br.

AZOLLACEAE
Azolla filiculoides Lam.

TYPHACEAE
Typha angustifolia L.
T. domingensis Pers.
T. latifolia L.

POTAMOGETONACEAE
Potamogeton nodosus Poir.
P. pectinatus L.

NAJADACEAE
Najas graminea Raffeneau-Delile
N. guadalupensis (Spreng.) Morong

ZANNICHELLIACEAE
Zannichellia palustris L.

ALISMATACEAE
* *Alisma lanceolatum* With.
A. triviale Pursh
Echinodorus berteroi (Spreng.) Fassett
Sagittaria longiloba Engelm.
S. montevidensis Cham. & Schlecht ssp. *calycina* (Engelm.) Bogin

POACEAE
* *Echinochloa colona* (L.) Link
* *E. crus-galli* (L.) Beauv.
E. microstachya (Wieg.) Rydb.
* *E. oryzoides* (Ard.) Fritsch
Leersia oryzoides (L.) Sw.
Leptochloa fascicularis (Lam.) Gray
L. uninervia (Presl) Hitch. & Chase

* *Oryza rufipogon* Griff.
Paspalum distichum L.
* *Polypogon monspeliensis* (L.) Desf.

CYPERACEAE
* *Cyperus difformis* L.
C. erythrorhizos Muhl.
C. odoratus L.
Eleocharis obtusa (Willd.) Schult.
E. palustris (L.) R.& S.
Scirpus fluviatilis (Torr.) Gray
* *S. mucronatus* L.

J. usitatus L. A. S. Johnson

POLYGONACEAE
* *Polygonum aviculare* L.
* *Rumex crispus* L.
R. tenax Rech. f.

AMARANTHACEAE
Alternanthera sp.

ELATINACEAE
Elatine gratioloides A. Cunn.

HALORAGACEAE
Myriophyllum propinquum A. Cunn.
Myriophyllum sp.

LYTHRACEAE
Ammannia multiflora Roxb.
Lythrum hyssopifolia L.

ONAGRACEAE
Ludwigia peploides (Kunth) Raven

SCROPHULARIACEAE
Glossostigma diandrum (L.) Kuntze
Gratiola pedunculata R.Br.
Limosella australis R.Br.
L. curdieana F. Muell.

ASTERACEAE
Centipeda cunninghamii (DC) A.Br. & Aschers
Eclipta platyglossa F. Muell.
Gnaphalium sphaericum Willd.
* *Aster subulatus* Michx.

S. acutus Muhl.

LEMNACEAE
Lemna minor L.

PONTEDERIACEAE
* *Heteranthera limosa* (Sw.) Willd.

* *Monochoria vaginalis* (Burm. f.) Presl.

POLYGONACEAE
Polygonum coccineum Muhl.
* *P. persicaria* L.
* *P. lapathifolium* L.
* *Rumex crispus* L.

CERATOPHYLLACEAE
Ceratophyllum demersum L.

ELATINACEAE
Elatine californica Gray
* *E. ambigua* Wight
E. rubella Rydb.

LYTHRACEAE
Ammannia auriculata Willd.
A. coccinea Rottb.
Lythrum hyssopifolia L.
* *Rotala indica* (Willd.) Koehne
R. ramosior (L.) Koehne

ONAGRACEAE
Ludwigia peploides (Kunth) Raven
L. repens Forster

SCROPHULARIACEAE
Bacopa eisenii (Kell.) Penn.
* *B. rotundifolia* (Michx.) Wettst.
* *B. repens* (Swartz) Wettst.
* *Dopatrium junceum* (Roxb.) Ham.
Lindernia anagallidea (Michx.) Penn.
* *Limnophila indica* (L.) Druce
x sessiflora Bl.

LENTIBULARIACEAE
Utricularia gibba L.

ASTERACEAE
Aster exilis Ell.
Eclipta alba (L.) Hassk.