Colonizing ability in the *Echinochloa crus-galli* complex (barnyard grass).
II. Seed biology

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Comparisons of some seed parameters of two taxa of barnyard grass (*Echinochloa crus-galli* complex) were made in an effort to understand differences in habitat preference and colonizing ability. The taxa were *E. crus-galli* var. *crus-galli*, a cosmopolitan weed of wet, disturbed ground and *E. crus-galli* var. *oryzicola*, a crop mimic restricted to rice fields. In California, where all seed collections originated, the two taxa are ecologically differentiated within the rice-field ecosystem. *Echinochloa crus-galli* var. *crus-galli* is a weed of paddy banks and shallow water around the periphery of rice fields whereas *E. crus-galli* var. *oryzicola* is found primarily within permanently flooded rice fields. A survey of seed weight in 10 populations of each of the two taxa demonstrated that seeds of *E. crus-galli* var. *oryzicola* were on the average two to three times heavier than those of *E. crus-galli* var. *crus-galli*. Differences in weight were reflected in the buoyancy characteristics of fresh seeds of the two taxa. Approximately 50% of *E. crus-galli* var. *crus-galli* seeds remained afloat after 4–5 days in water whereas during the same period over 95% of the seeds of *E. crus-galli* var. *oryzicola* had sunk. Germination tests on 9- and 18-month-old seeds of 18 populations of *E. crus-galli* var. *crus-galli* and 11 populations of *E. crus-galli* var. *oryzicola* revealed significant differences between the taxa in the number of germinating seeds. The decay of dormancy in *E. crus-galli* var. *oryzicola* was more rapid than in *E. crus-galli* var. *crus-galli* following dry storage and burial in soil. The difference results in the greater germination synchrony of the crop mimic in comparison to the widespread weed. Emergence of seedlings from saturated and flooded soils was compared in the two taxa. In all treatments *E. crus-galli* var. *oryzicola* exhibited significantly greater levels of seedling emergence. The differences may explain changes in abundance of the two taxa in California rice fields, following the introduction of permanent flooding as a weed control practice, as well as their current microdistribution within the rice-field ecosystem.

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Des comparaisons entre certaines caractéristiques des graines de deux taxons de pied-de-coq (complexe de l'*Echinochloa crus-galli*) ont été effectuées dans le but de tenter de comprendre les différences entre ces deux taxons dans leurs habitats et leur pouvoir colonisateur. Les taxons étudiés sont *E. crus-galli* var. *crus-galli*, une mauvaise herbe cosmopolite des terrains perturbés humides, et *E. crus-galli* var. *oryzicola*, une plante mimétique des cultures confinée aux rizières. En Californie, d'où toutes les collections de graines proviennent, les deux taxons sont différenciés écologiquement dans l'écosystème des rizières. *Echinochloa crus-galli* var. *crus-galli* est une mauvaise herbe des berges et des eaux peu profondes à la périphérie des champs de riz, tandis qu'*E. crus-galli* var. *oryzicola* se rencontre surtout à l'intérieur des champs de riz toujours inondés. L'étude du poids des graines dans 10 populations de chacun des deux taxons montre que les graines d'*E. crus-galli* var. *oryzicola* sont en moyenne deux à trois fois plus lourdes que celles d'*E. crus-galli* var. *crus-galli*. Les différences de poids se reflètent dans la flottabilité des graines. Après 4 à 5 jours dans l'eau, environ 50% des graines d'*E. crus-galli* var. *crus-galli* flottent encore, tandis que plus de 95% des graines d'*E. crus-galli* var. *oryzicola* se sont déposées au fond. Des tests de germination ont été effectués sur des graines âgées de 9 et de 18 mois provenant de 18 populations d'*E. crus-galli* var. *crus-galli* et de 11 populations d'*E. crus-galli* var. *oryzicola*; ces tests montrent des différences significatives entre les taxons dans le nombre de graines qui germent. Après l'entreposage des graines à sec et leur enfouissement dans le sol, la diminution de la dormance chez *E. crus-galli* var. *oryzicola* est plus rapide que chez *E. crus-galli* var. *crus-galli*. Cette différence résulte en une plus grande synchronie de la germination chez la plante mimétique que chez la mauvaise herbe. L'émergence des plantules sur des sols saturés et inondés a été comparée. Dans tous les traitements, *E. crus-galli* var. *oryzicola* montre un niveau significativement plus élevé d'émergence des plantules. Cette différence peut expliquer les changements d'abondance des deux taxons dans les rizières californiennes après l'adoption de l'inondation permanente comme technique de répression des mauvaises herbes; elle peut aussi expliquer leur microdistribution actuelle à l'intérieur de l'écosystème des rizières.

Introduction

Colonization of unoccupied habitats by weed species is strongly influenced by events during germination and seedling establishment. Mortality schedules for several annual plants have shown that the highest mortality occurs during the seed and seedling establishment periods (Harper 1977). Baker (1965) proposed that germination strategies of colonizing species frequently involve innate seed dormancy, discontinuous germination, and rapid seedling growth. Harper (1959, 1965), Bunting (1960), Salisbury (1961), and Popay and Roberts (1970) suggested that weeds exhibiting discontinuous germination would be at a selective advantage in the colonization of unpredictable, disturbed sites.

The theoretical models of Cohen (1966, 1967, 1968) suggest that discontinuous germination is selectively advantageous in environments in which the risk of reproductive failure is high. Conversely in predictable environments, where the probability of unsuccessful reproduction is low, dormancy is of less importance and synchronous germination maximizes fitness (Westoby 1981). Similar conclusions on the adaptive significance of dormancy in heterogeneous, unpredictable environments have been reached by Levins (1969). In reviewing the germination behaviour of agricultural weeds, Mulligan (1965) suggested that synchronous germination may be of advantage in predictable cropping systems such as those found in certain cereals.

Following germination, the transition from dependence on seed reserves to independent assimilation usually entails a considerable mortality risk. It has been argued that large-seeded species show greater resistance than small to environmental hazards during establishment (Salisbury 1942; Stebbins 1965, 1971; Harper 1977). These workers also recognized the apparent compromise in fitness between the increased chance of successful establishment and the reduced opportunities for dispersal in heavier-seeded species. Clearly, seed size, dispersal potential, dormancy, and the phenology of seedling emergence are interrelated features of germination (Angevine and Chabot 1979) and may be equally important in determining the colonizing ability of weeds.

In the Central Valley of California several taxa of barnyard grass (*Echinochloa crus-galli* complex) occur which differ in habitat preference and colonizing ability (Barrett and Wilson 1981; Barrett 1983). They include the aliens *E. crus-galli* (L.) Beauv. var. *crus-galli* (hereafter crus-galli), a cosmopolitan weed of open, seasonally wet sites and *E. crus-galli* (L.) Beauv. var. *oryzicola* (Vasing.) Ohwi (hereafter oryzicola), a crop mimic restricted to cultivated rice fields. The two barnyard grasses are ecologically differentiated in Californian rice fields. Crus-galli is abundant on paddy banks and in shallow water around the periphery of rice fields whereas oryzicola occurs primarily within the deep water of flooded fields (Barrett and Seaman 1980). The purpose of this study is to compare various seed and seedling parameters in the two taxa in an effort to understand differences in their distribution within the Californian rice-field ecosystem.

Materials and methods

To compare the average seed (technically a caryopsis) weight of crus-galli and oryzicola a bulk seed sample from 25 seed parents was collected in each of 10 populations of the two taxa from Californian rice fields. Ten replicate weighings, each of 10 oven-dried seeds (70°C to constant weight), were made from all populations. Seeds were stored dry in envelopes at room temperature and mixed thoroughly prior to weighing. Buoyancy of fresh seeds from a single population of the two barnyard grass taxa was compared by recording the numbers of floating seeds at daily intervals in four replicates of 50 seeds in 1000-mL beakers. Seeds were collected from plants of crus-galli growing in shallow water (5 cm) at the periphery of a rice field at Biggs, Butte Co. Seeds of oryzicola were obtained from plants growing within the rice field (water depth 8–20 cm). Distilled water in the beakers was stirred vigorously for 1 min at daily intervals and the experiment was terminated when all seeds had sunk.

Germination levels were compared in the two taxa using seeds collected in 18 populations of crus-galli and 11 populations of oryzicola. The seeds from each population were collected in the manner described above during summer 1976, stored dry at room temperature, and used in two germination tests 9 and 18 months after harvest. Four replicates of 25 seeds from each population were placed in petri dishes on 9-cm Whatman No. 1 qualitative filter paper flooded with 15 mL of distilled water. Dishes were incubated at 30°C, under a 12-h light regime, for 2 weeks. Previous work (Kasahara and Kinoshita 1952; Arai and Miyahara 1964; Brod 1968; S. C. H. Barrett, unpublished data) indicates that 30°C is close to the optimum temperature for seed germination in barnyard grasses although this temperature exceeds that prevailing during the early period of field germination. Differences in levels of germination among populations and taxa were compared by ANOVA following arc sine transformation.

It might be predicted that germination synchrony in oryzicola, the crop mimic, would be greater than in crus-galli. Synchronous germination could be viewed as part of a crop-mimicry syndrome (Barrett 1983). To examine this possibility germination schedules were compared in seed collected from four rice-field sites in Butte Co., Glenn Co., Kern Co., and Sutter Co., California during September 1979. At each site oryzicola plants were in rice fields and crus-galli plants were on open, waste ground next to the rice fields. In each population seeds were collected from 10 seed parents per taxon and kept in separate envelopes. Following collection five replicates of five seeds per family were placed in 5-cm plastic pots (88 cm^3 soil volume) and placed on a glasshouse bench in a fully randomized design. The seeds were covered lightly with soil (0.50 cm) and the pots were positioned in water-filled trays. For the duration of the experiment the glasshouse was maintained at temperatures similar to those prevailing in the Central Valley of California and an attempt was made to provide a moisture regime which paralleled that found in fallow rice fields. No germination occurred from September to March owing to low temperatures (5–15°C) in the glasshouse. Germination began in mid-March when temperatures increased to 15–25°C. The number of emerging seedlings in each pot was recorded at weekly intervals for a 3-month period. Observations of germination phenology under field conditions in California indicate that both taxa begin germination in March–April, so that the differences in germination schedules under field and glasshouse conditions were probably not great. Cumulative percentage germination of the two taxa was compared by Kolmogorov–Smirnov two sample tests.

The striking differences in seed size and weight between crus-galli and oryzicola suggested that they may differ in their capacity for seedling emergence under different conditions. Both varieties occupy habitats which experience flooding and therefore seedling emergence from saturated and submerged soils was examined in a single population of each using nondormant seeds.

In the first experiment, 10 seeds of each taxon were placed at different depths (surface, 0.5, 1.0, and 2.0 cm below the soil surface) in a completely randomized design under uniform glasshouse conditions (25–30°C). Each burial depth treatment was replicated 24 times and seeds were placed in 5-cm plastic pots with approximately 88-cm^3 soil volumes. The soil was kept water saturated by placing pots in flooded trays. The numbers of emerging seedlings were recorded daily during a 21-day period. Ungerminated seeds were then sieved from each replicate and resown on the soil surface as a test of germination ability.

Emergence of crus-galli and oryzicola seedlings from flooded soils was examined in a second experiment conducted at three temperature regimes (10, 18, 26°C) in separate growth chambers. The range of temperatures was chosen to include water temperatures found in Californian rice fields during spring. Four replicates of 50 nondormant seeds per taxon were incorporated at random into the top 2 cm of soil in 15-cm pots which were half-filled with soil. The soil was then flooded to a depth of 8 cm and the emergence of seedlings recorded over a 7-week period.

Results

Seed weight

Oryzicola seeds are significantly heavier (two to three times) than those of crus-galli. The average seed weight of oryzicola populations (n = 10) was 4.95 mg (range of populations means 3.66–6.50 mg) compared with 1.73 mg (range of populations means, 1.66–2.11 mg) in crus-galli. Among the 10 populations of each taxon crus-galli displayed a significantly lower coefficient of variation of mean seed weight (C.V. = 9.82%) compared with oryzicola (C.V. = 20.10%).

The buoyancy and hence dispersal by water of barnyard grass seeds is probably influenced by their weight. The lighter seeds of crus-galli exhibited a greater buoyancy, with approximately 50% of seeds remaining afloat after 4–5 days in water (Fig. 1). In contrast, 50% of the heavier-seeded oryzicola had sunk after 2 days in water and less than 5% of the seeds were still floating after 5 days.

Seed dormancy

Germination tests of 9-month-old seeds of the 29 barnyard grass populations revealed significant variation among populations in levels of germination. Oryzicola populations gave uniformly high germination values whereas crus-galli populations were highly variable in their behaviour (F = 22.97; $P < 0.001$), but in most populations the majority of seeds failed to germinate (Table 1). A single population gave 92.0% germination. Percentage germination was significantly different between crus-galli and oryzicola (F = 66.43; $P < 0.001$). Germination levels after 18 months of dry storage were uniformly high in both crus-galli and oryzicola. The results indicate that the failure of most seeds of crus-galli to germinate in the 9-month test was the result of either innate dormancy or imposed dormancy due to dry storage as opposed to low viability. Under field conditions in California it is possible that the stratification of seeds in or on the soil surface would result in a more rapid decay of dormancy than we observed following dry storage.

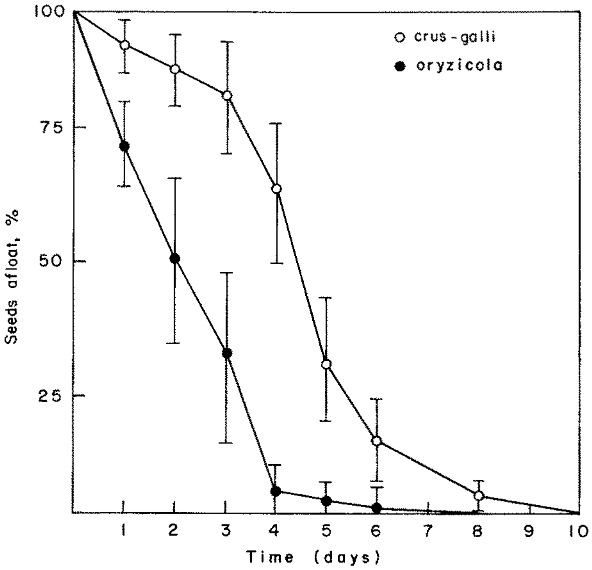

FIG. 1. Buoyancy of seeds of *Echinochloa crus-galli* vars. *crus-galli* and *oryzicola*.

Germination synchrony

Seeds of the two taxa from each of four rice-field locations differed significantly in germination synchrony (Fig. 2). Oryzicola seeds germinated more rapidly. Approximately 75% of all oryzicola seeds had emerged within 4 weeks from the beginning of germination. In three of the four crus-galli populations less than 50% of the seeds had emerged by this time.

Seedling emergence

Average percentage seedling emergence from saturated soil at each burial depth is illustrated in Fig. 3 for crus-galli and oryzicola. Maximum emergence at all burial depths was recorded 13 days after sowing. In both taxa, seed burial caused a reduction in the rate of emergence. Taxa did not differ significantly in the mean percentage germination of surface-sown seeds. Significantly greater ($P < 0.01$) seedling emergence was recorded at all burial depths for oryzicola. No seedling emergence from the 2-cm burial depth was recorded in crus-galli. Seeds recovered at all burial depths and resown on the soil surface gave over 80% germination in both taxa, indicating that burial in saturated soil resulted in the enforced dormancy of seeds.

The average percentage seedling emergence from the

TABLE 1. Percentage germination following 9 and 18 months of dry storage of seeds of *Echinochloa crus-galli* vars. *crus-galli* and *oryzicola*

		9 months					18 months	
		Average germination (%) ± SD	Class of germination (%)				Average germination (%) ± SD	Class of germination (%) 76–100
Taxon	*n* populations		0–25	26–50	51–75	76–100		
Crus-galli	18	25.7±24.9	11	4	2	1	96.7±2.7	18
Oryzicola	11	92.9±7.3	0	0	0	11	94.7±2.8	11

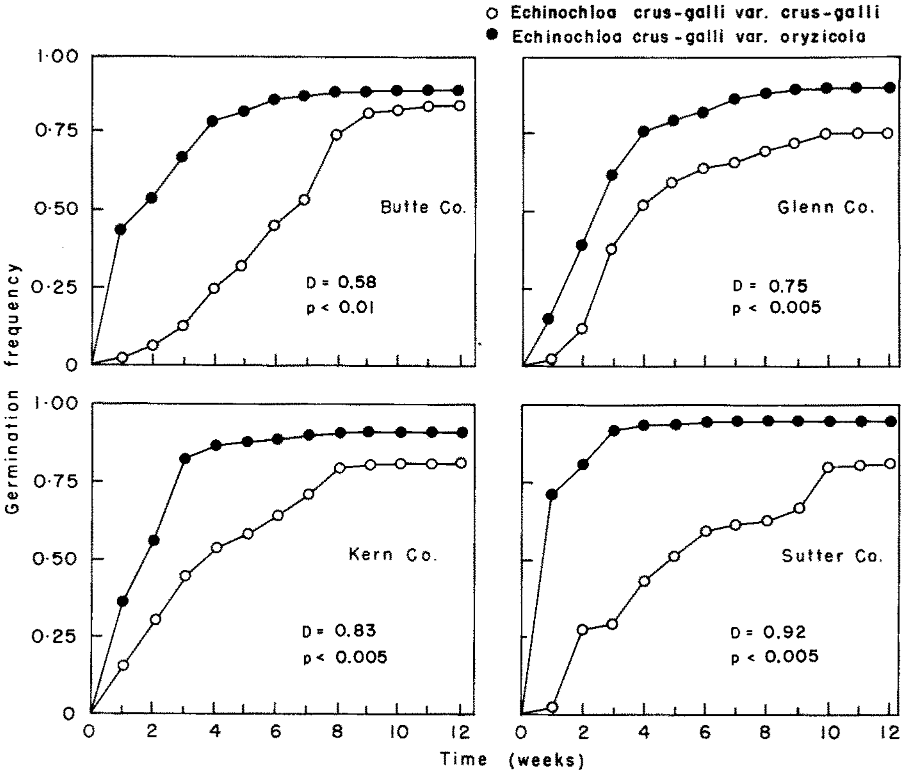

FIG. 2. Germination synchrony under glasshouse conditions of *Echinochloa crus-galli* vars. *crus-galli* and *oryzicola* populations from California.

8-cm water depth at 10°, 18°, and 26°C is presented in Fig. 4. Seedlings of oryzicola exhibited significantly greater levels of emergence than those of crus-galli. At all temperatures approximately 75% of the oryzicola seeds that were sown produced emergent seedlings. The major effect of temperature on the germination and growth of oryzicola seedlings was in regulating the rate of emergence. Seedlings emerged more rapidly at higher water temperatures although after 7 weeks the overall percent emergence among the three temperature regimes was similar. In crus-galli, 13% of the seeds flooded at 26°C produced seedlings which emerged from water after 4 weeks. At 18°C emergence was delayed until after 5 weeks, when approximately twice the number of seedlings emerged than at 26°C. A single crus-galli seedling emerged at 10°C after 6 weeks of immersion.

Discussion

In the Central Valley of California, barnyard grass populations inhabit a mosaic of wetland habitats including open and seasonally moist ruderal sites, closed rice-field communities, freshwater marshes, and naturally disturbed river margins. In these habitats, different taxa often grow in close proximity although they are usually ecologically differentiated (Barrett and Seaman 1980; Barrett and Wilson 1981). The important features of these habitats from the perspectives of colonization and successful establishment concern moisture avail-

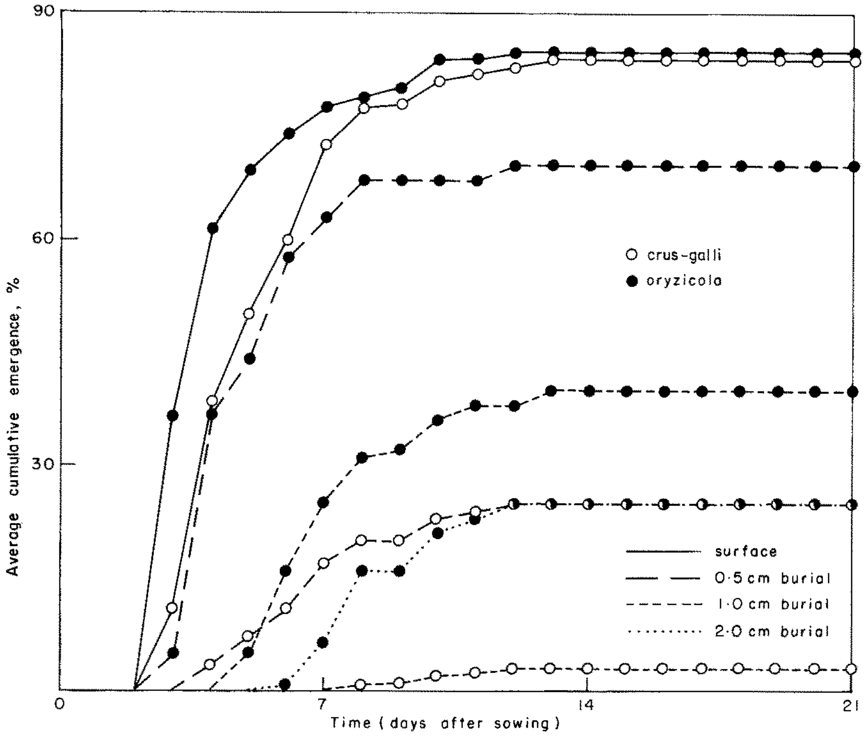

FIG. 3. Seedling establishment of *Echinochloa crus-galli* vars. *crus-galli* and *oryzicola* from different burial depths (surface, 0.5, 1.0, 2.0 cm) in saturated soil under glasshouse conditions.

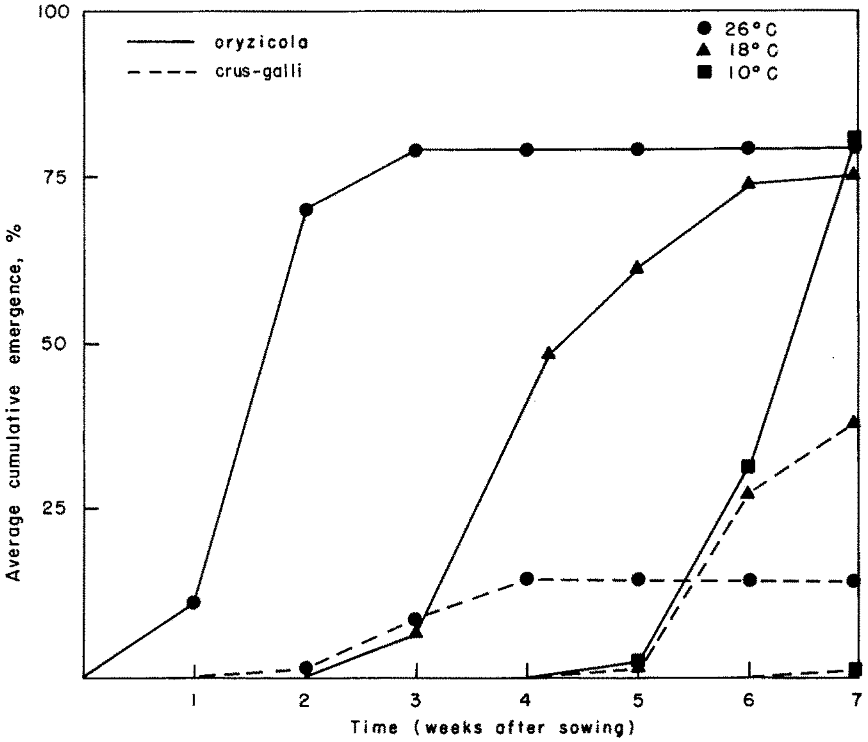

FIG. 4. Seedling emergence of *Echinochloa crus-galli* vars. *crus-galli* and *oryzicola* from soil flooded to a depth of 8 cm at three temperature regimes (10°, 18°, 26°C) in growth chambers.

ability, degree of disturbance, and plant cover and density. In general, the findings of this study are helpful in understanding the adaptive features of seed biology in populations occupying microhabitats within the rice-field ecosystem.

One of the major features which distinguishes crus-galli and oryzicola is the size of their seeds. Salisbury (1942) first considered the importance of seed size in determining the survival of seedlings in different habitats. He observed that seeds of species occurring in open, disturbed sites were on the average smaller than those inhabiting closed communities. Large amounts of food reserves are often required in dense, competitive communities to allow seedlings to compete successfully with neighbours for light and moisture (Black 1957, 1958; Harper *et al.* 1970; Stebbins 1971). Harper and Benton (1966) have also shown that large seeds may be at a disadvantage in open sites where they are more likely to be subject to desiccation. The seed weights of the two barnyard grass taxa conform to Salisbury's observations; the light-seeded crus-galli occurs most frequently in open sites in California and the heavier-seeded oryzicola is confined to the closed rice-field community. While the large seeds of oryzicola probably enhance competitive ability and favour coexistence with rice (see Barrett 1983), they may have originally been selected as an adaptation enabling seedlings to grow and emerge in natural habitats with deep water.

In our experiments with both saturated and flooded soils oryzicola exhibited a greater capacity for emergence in comparison with crus-galli. This behaviour is probably not associated with different capacities for anaerobic germination since both species exhibit germination and limited seedling growth under these conditions (Kennedy *et al.* 1980). It seems more likely that the inability of crus-galli to establish in deep water stems from its small seeds and limited food reserves which must restrict seedling growth in deep water.

The development of 'permanent flooding' techniques in Californian rice fields, in which water is maintained on fields to a depth of 8–20 cm for the duration of rice growth, has helped to reduce infestations of crus-galli in fields (Jones 1923, 1933). Since oryzicola can establish successfully in deep water, it has now replaced crus-galli as California's most economically important weed of rice (Barrett and Seaman 1980; Barrett 1982). Crus-galli persists as a weed of shallow-water areas and paddy banks.

The relatively rapid decay of dormancy and the synchronous germination exhibited by oryzicola are traits predicted by Cohen (1966) and Harper (1977) to be selected in homogeneous environments where the probability of successful reproduction is high. The rice-field ecosystem is an excellent example of a homogeneous environment. In California many areas have been in continuous rice production for several decades. Absence of any well-developed crop rotation practices results from high soil fertility, low pest and disease problems, and the restricted range of alternate crops capable of growing on the heavy clay rice soils (Johnston and Miller 1973). The high predictability from year to year of the rice-field ecosystem enables populations to build up rapidly and has favoured the spread of oryzicola throughout the rice-growing areas of California despite attempts at control by herbicides (Barrett and Seaman 1980).

Despite its widespread distribution and abundance in Californian rice fields, few individuals of oryzicola occur outside the flooded rice-field ecosystem. The failure of oryzicola to establish in open, disturbed sites where risk of reproductive failure is high may thus be a reflection of its inability to develop a significant bank of dormant seeds. Mortality, due to desiccation in habitats with uncertain moisture availability, would be particularly critical in oryzicola since individuals take approximately twice as long to reach reproductive maturity as those of crus-galli (Barrett and Wilson 1981; Barrett 1983). Presumably the heavier, less buoyant, seeds of oryzicola also reduce opportunities for dispersal from the flooded rice-field ecosystem.

The well-developed seed dormancy (and see Rahn *et al.* 1968; Holm *et al.* 1977) and slower rate of dormancy decay in crus-galli are traits predicted by Cohen (1966) to be selected in habitats where the risk of reproductive failure is high. Maintenance of a reservoir of dormant seeds in soil is necessary to ensure survival through transitory periods lethal to seedlings. In open, ruderal habitats heavy mortality of crus-galli seedlings commonly occurs due to desiccation. Since there is virtually no summer rainfall in Central California, ruderal sites become progressively drier as summer continues. Rapid development and seed dormancy are probably important features of life history in these seasonal habitats (Barrett and Wilson 1981). Field studies are requried to test these hypotheses.

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