

## Review

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**Nomenclature:**

Barnyardgrass, *Echinochloa crus-galli* P. Beauv. or *Echinochloa crus-galli*; P. Beauv. var. *crus-galli*; early watergrass, *Echinochloa crus-galli* P. Beauv. var. *oryzoides* or *Echinochloa oryzoides* Ard. Fritsch; late watergrass, *Echinochloa oryzicola* (Vasinger) Vasinger or *Echinochloa phyllopogon* subsp. *oryzicola* (Vasinger) Kossenko; rice, *Oryza sativa* L.

**Keywords:**

herbicide resistance; species shift; nonchemical weed control; IPM

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# *Echinochloa* in mid-southern U.S. and California rice: What is known and what are the knowledge gaps?

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**Abstract**

Several species of *Echinochloa* P. Beauv., introduced at multiple events, have established themselves as a persistent concern for U.S. rice production. In this review, we highlight the key biological characteristics of economically relevant *Echinochloa* in U.S. rice production, revisit their historical trajectory, and suggest research directions for their management with special reference to barnyardgrass. Ecologically differentiated *Echinochloa* species have a distinct association with rice culture methods that have been practiced for the last few decades, barnyardgrass being historically predominant in drill-seeded rice in the mid-South, and early watergrass and late watergrass in water-seeded California rice. However, the emerging evidence challenges the dogma that other *Echinochloa* species for specific regions are of less importance. Primarily managed by the water-seeding method of rice culture in the early years of the 20th century, *Echinochloa* species have persisted in the sophisticated U.S. rice culture through the evolution of resistance to herbicides in recent decades. Accumulating knowledge, including those of recent genomic insights, suggests the rapid adaptability of *Echinochloa*. The last decade has seen a (re)emergence of nonchemical methods as a key component of sustainable management, among which use of harvest weed seed control (HWSC) methods and cover crops in the mid-South and stale-drill seeding in California are being considered as potential methods for managing *Echinochloa*. In recent years, furrow-irrigated rice has rapidly supplanted a significant proportion of conventionally flooded rice in the mid-South, whereas the propensity for compromised continuous submergence is increasing in California rice. On the cusp of this shift, the question at the forefront is how this will affect *Echinochloa* interference in rice and how this change will dictate the management efforts. Future research will lead to the development of a clear understanding of the impact of the changing agroecosystems on *Echinochloa* species and their response to the prospective integrated control interventions.

**Introduction**

After a decade of commercial rice (*Oryza sativa* L.) production, JW Jones (1926) wrote the following in USDA Bulletin #1387: “Water grass (*Echinochloa crusgalli*) is reported to be in several important rice-producing countries of the world, but apparently in none of these countries has this grass become so troublesome as in California.” Introduced from multiple sources and events, several economically relevant species of *Echinochloa* P. Beauv. have adapted and persisted in the century since U.S. rice culture began, often ranking as the most pressing issue in U.S. rice production (Butts et al. 2022; Fischer et al. 2000a; Norsworthy et al. 2007a, 2013, 2020). *Echinochloa* have ecologically co-evolved with rice for millennia in Asian countries (Yang et al. 2015; Ye et al. 2019), and the species are believed to have invaded U.S. rice primarily as contaminants in rice seed stocks (Barrett 1983; Huelma et al. 1996). *Echinochloa* species, whether one or the other or a composite of them, have been the focal point of weed management interventions ever since the beginning of commercial rice culture in the United States. They are often collectively called “barnyardgrass,” especially in the U.S. mid-South, and “watergrass” or “barnyardgrass” in California. Among the many *Echinochloa* species, barnyardgrass [*E. crus-galli* (L.) P. Beauv.] is a persistent weed of global rice production (Krahemer et al. 2016; Mitich 1990), often ranking among the world’s most serious agricultural weeds receiving unparalleled attention (Barrett and Seaman 1980; Holm et al. 1977; Wu et al. 2022; Yabuno 1966).

Colloquially referred to as barnyardgrass or watergrass, even by stakeholders in its management, the existence of morphologically intergrading types within *Echinochloa* (sometimes referred to as *Echinochloa* complex) is a well-known problem for taxonomists (Danquah et al. 2002; Ruiz-Santaella et al. 2006) and has remained largely esoteric. *Echinochloa* populations that are continuously associated with specific agricultural systems may have evolved phenological patterns that optimize survival within the most favorable growing areas



(Barrett 1983). The differentiation among local ecotypes was probably further encouraged by the self-pollinating reproduction in this genus (Honek and Martinkova 1996). Taxonomists have named numerous intraspecific taxa within the barnyardgrass of their respective regions; however, a comprehensive, worldwide, monographic study is still lacking (Barrett and Wilson 1981; Hoste and Verloove 2022). In the context of North America, multiple introductions from varying sources followed by inbreeding have further complicated the effort to accurately classify them (Barrett and Wilson 1981). We agree with Barrett and Wilson (1981), Holm et al. (1977), and Michael (1983) that until taxa in *Echinochloa* have been correctly identified, interpretation of their biology is greatly hindered. In the last few decades, the rise of molecular studies has greatly improved the identification of these cryptic species of *Echinochloa*. In this review, we integrate the recent delimitation of taxonomic treatment achieved from genomic analysis of the global collection of *Echinochloa* species (Wu et al. 2022), which closely matches the nomenclature and taxonomic concepts reported by Gould et al. (1972).

The genus *Echinochloa* (botanical family Poaceae) includes approximately 250 species, of which only a few are agricultural weeds (Bajwa et al. 2015). On a global scale, barnyardgrass is the most prevalent *Echinochloa* species, followed by junglerice [*Echinochloa colona* (L.) Link] and late watergrass [*Echinochloa oryzicola* (Vasinger) Vasinger] (Krahmer et al. 2016; Yabuno 1966). These *Echinochloa* species evolved adaptive and competitive characteristics to evade removal from rice fields during early rice domestication (Guo et al. 2017; Ye et al. 2019), whereas in modern agriculture, *Echinochloa* species have acquired or evolved resistance to multiple herbicides, making them among the most troublesome herbicide-resistant weeds in the world (Maun and Barrett 1986; Norsworthy et al. 2014).

Owing to the regional and global economic relevance of *Echinochloa*, the basic biology, interference in cropping systems, and management techniques have been thoroughly reviewed since the 1960s (Bajwa et al. 2015; Maun and Barrett 1986; Rahn et al. 1968; Rao 2021). Additionally, molecular analyses have provided recent insights into its evolution as a weed (Guo et al. 2017; Wu et al. 2022). Recently, global cases of herbicide resistance in barnyardgrass were reviewed (Damalas and Koutroubas 2023). With special reference to barnyardgrass, this article aims to 1) highlight the current state of knowledge on economically relevant *Echinochloa* species in U.S. rice production in terms of their introduction and persistence/adaptation in U.S. rice agroecosystems, provide a historical overview of their management and emerging herbicide resistance issues; and 2) identify the research needs for their sustainable management in U.S. rice on the cusp of a paradigm shift in weed management approaches. Sustainability in this context entails enhancing the prospect of sustained, long-term positive outcomes through the implementation of measures to mitigate the risk of rapid herbicide resistance evolution, to curtail the abundance of emerged *Echinochloa* plants and its soil seed banks, and to diminish its interference with rice.

### The “Taxonomic Journey” of North American *Echinochloa*

In 1972, Gould et al. published a strikingly different classification of *Echinochloa* species of North America (seven classes) than those published by Hitchcock (1920) and Wiegand (1921) some 50 yr earlier. In addition to Hitchcock's and Wiegand's classification, a few more conflicting taxonomic treatments of the *Echinochloa* complex and related taxa in North America were described or

defined in the 1950s, 60s, and 70s. The status of native and introduced (adventive) taxa and the intraspecific categories have been the major sources of taxonomic disagreement. Hitchcock and Chase (1950) and most authors who have published studies of the species have combined native and introduced taxa listed under barnyardgrass, whereas Gould et al. (1972), following the ideas published by Wiegand (1921), separate the native populations as rough barnyardgrass [*Echinochloa muricata* (P. Beauv.) Fernald]. Previously, many authors attempted to clarify the phylogenetic/taxonomic problems in *Echinochloa* using seed protein electrophoresis and isozyme analyses (Asins et al. 1999; Gonzalez-Andres et al. 1996), and several other molecular tools available at that time (Aoki and Yamaguchi 2008; Danquah et al. 2002; Roy et al. 2000; Tabacchi et al. 2006). Recently, Wu et al. (2022) have more accurately distinguished *Echinochloa* species and varieties by integrating morphological characteristics with multiple pieces of genomic evidence, including genome size, reads mapping rate, genome coverage, phylogeny, and population structure, providing remarkable insights into the evolutionary trajectory of *Echinochloa* species.

Barnyardgrass is native to Eurasia but is distributed worldwide, principally in a latitudinal zone from 50°N to 40°S (Michael 2003). It is common as an agrestal and as a ruderal weed in more than 60 countries and three dozen different crops (Holm et al. 1991) and is widespread in North America from southern Canada to Mexico, occurring on disturbed, moist, waste ground and as a serious weed of rice and other irrigated crops. Barnyardgrass is highly variable with respect to growth form (Smith et al. 1977), flowering time, inflorescence architecture, anthocyanin pigmentation, and awn length. Several ecological and physiological biotypes varying in sensitivity to herbicides were reported from the northwestern United States in the 1960s (Roché and Muzik 1964). In North America, barnyardgrass is uniformly hexaploid,  $2n = 6x = 54$  (Gould et al. 1972). Although the native species of North America, rough barnyardgrass, closely resembles barnyardgrass morphologically, they are genetically distant (Ruiz-Santaella et al. 2006).

Also native to Eurasia, late watergrass ( $2n = 4x = 36$ ), previously classified as *E. crus-galli* (L.) Beauv. var. *oryzicola* (Vasinger) Ohwi, *E. oryzicola*, *E. oryzoides*, *E. phyllopogon*, and *E. macrocarpa* is an obligate weed of rice fields occurring in rice-growing regions of Asia, Europe, Australia (Michael 1983; Yabuno 1966), and California (Barrett and Seaman 1980). The introduction of late watergrass was primarily as a seed contaminant of rice seed stocks, as indicated by its collections right after the commencement of rice culture in California in 1912 through 1915 (Barrett and Seaman 1980). Late watergrass established in monoculture Californian rice fields in the 1970s and is rarely found outside of the rice agroecosystem (Barrett and Wilson 1981), but this variety is not present in the mid-South rice growing regions (Smith 1970). In California, it is called “late watergrass” because it flowers late in August to September (“late form”) with a close synchrony to rice. This species is an example of a seemingly perfect crop mimic, resembling rice in its morphology and phenology (Vasinger-Alektorova 1931). Yabuno (1966), Gould et al. (1972), Barrett and Seaman (1980), and later followed by Yamasue (2001), were not sure of the ploidy status of this variety, and they identified it as a variety of barnyardgrass, although Crampton (1964) and Yabuno (1966) previously differentiated and elevated this taxon to late watergrass.

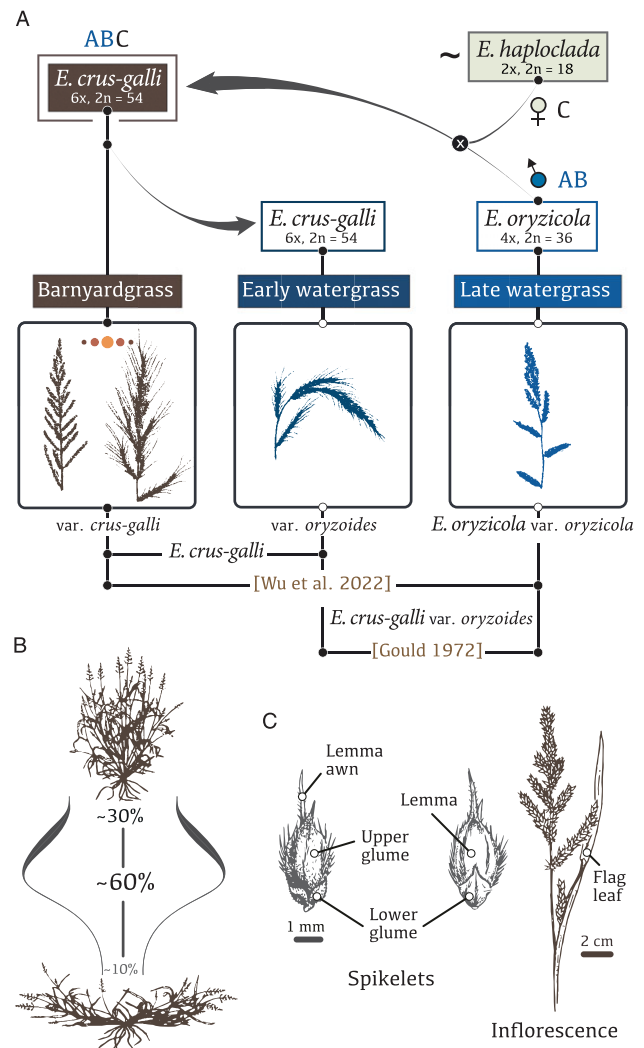
Strikingly different from barnyardgrass and late watergrass is early watergrass,  $2n = 6x = 54$  (sometimes previously identified as *E. crus-galli* var. *oryzicola* or *E. oryzoides*). It has defining features

such as long awns, and lacks visible anthocyanin pigments. Nevertheless, it was considered a part of the variation encompassed within barnyardgrass prior to the 1980s in California, as implied by Barrett and Wilson (1980). This variety is confined to rice fields in California, with its prominent erect plant architecture and drooping inflorescence. There had been some confusion regarding the taxonomic classification of early watergrass and late watergrass. Barrett and Seaman (1980) wrote that two morphologically and phenologically distinct forms of watergrass exist in California (the “early form” and the “late form”), and considered both forms to be under the same variety despite the fact that Yabuno (1984) elucidated, from cytological and morphological studies, that early watergrass is closely related to barnyardgrass, leading to the suggestion that early watergrass be relegated to a variety of barnyardgrass, which was apparently not well received by researchers around the world. However, the recent genome-based global delimitation of *Echinochloa* species by Wu et al. (2022) places the “early form” in a separate variety of *E. crus-galli* (hence, *E. crus-galli* var. *oryzoides*), corroborating the classification reported by Yabuno (1984), and as opposed to earlier classification as *E. oryzoides* (Ard.) Fritsch by Vickery (1975), Chirila and Melachrinou (1976), and Clayton (1980).

Although Yabuno (1966) suggested that barnyardgrass is an allohexaploid produced by natural hybridization between the tetraploid late watergrass with a not-yet-discovered diploid species of *Echinochloa* and subsequent chromosome doubling, it was not clear until Ye et al. (2020) and Wu et al. (2022) revealed the evolutionary trajectory of barnyardgrass and other species and varieties of the genus *Echinochloa* (Figure 1A). Ye et al. (2020) found that the diploid genome of *E. haploclada* (Stapf) Stapf is similar to the unknown diploid progenitor genome of barnyardgrass and used it as a female proxy progenitor. Late watergrass was assumed to be a male donor in the polyploidization of hexaploid barnyardgrass (Akoi and Yamaguchi 2008), but recent chloroplast phylogeny analysis indicated that at least two male donors contributed to the origin of barnyardgrass (Wu et al. 2022). The whole-plant and a typical seed and inflorescence morphology of barnyardgrass are shown in Figure 1B and C, respectively.

### Seed Size and Ecological Differentiation

The four *Echinochloa* species that are of major concern in U.S. rice production, in order of ascending seed size, are junglerice, barnyardgrass, late watergrass, and early watergrass (Costea and Tardif 2002; Wu et al. 2022; Figure 2A). Seed sizes vary to some extent, with barnyardgrass being the most diverse. Barnyardgrass in California generally produces bigger seeds, as heavy as 3 mg (Keeley and Thullen 1989). Junglerice and barnyardgrass seed germination is relatively water intolerant, as explained below, making these weeds common in the predominantly dry-seeded mid-South rice fields (Jones 1952). Conversely, early watergrass and late watergrass seed germination is flood tolerant and found in water-seeded California rice (Kennedy et al. 1980). Seedling emergence generally decreases with increasing depth, and to a greater extent, under flooding conditions (discussed in the *Seed Germination and Seedling Emergence* section). A generalized scheme of their ecological differentiation is shown in Figure 2B. The consequence of flooding (submergence) is anoxia in plant tissues, which in turn, reduces the rate of energy production by 65% to 97% compared with the rate in air (Gibbs and Greenway 2003). Like rice, early watergrass and late watergrass can germinate under the reduced oxygen of submerged conditions (Kennedy et al.



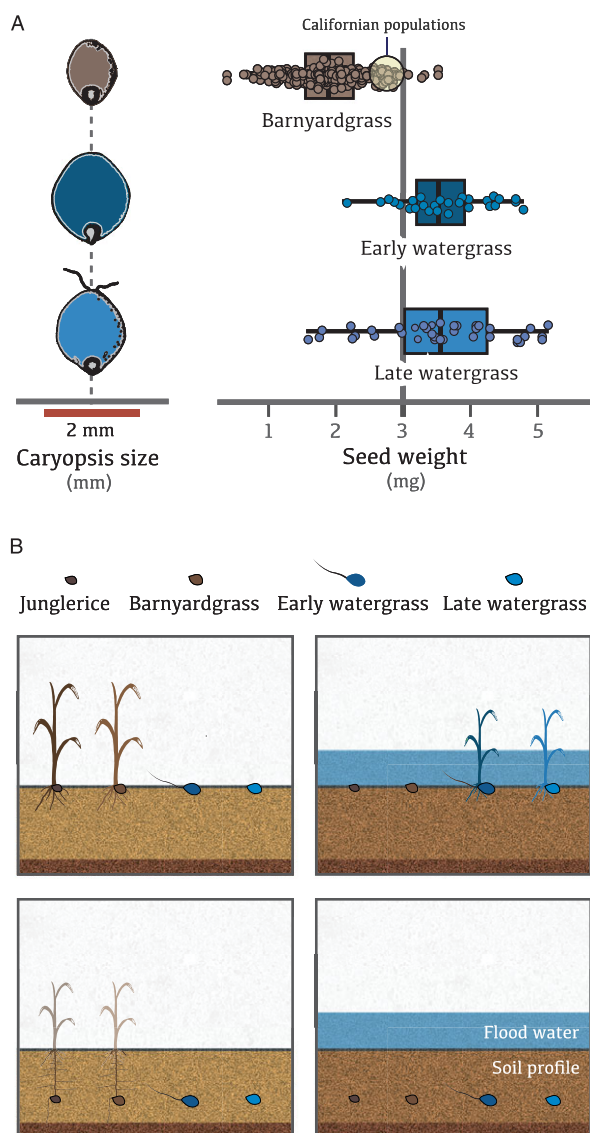
**Figure 1.** Economically most relevant *Echinochloa* in U.S. rice fields. (A) Origin of barnyardgrass (*E. crus-galli* var. *crus-galli*) (adapted from Wu et al. 2022; Ye et al. 2020). (B) Intrapopulation variation in whole plant morphology of a barnyardgrass population from California (adapted from Norris 1996). (C) A typical seed and inflorescence morphology of barnyardgrass (adapted from Jepson Flora Project). Adapted with permission.

1980; Pearce and Jackson 1991; VanderZee and Kennedy 1981) through an array of metabolic adaptations (Kennedy et al. 1992).

### *Echinochloa* Interference and Seed Production

#### Interference with Rice

*Echinochloa* species have co-existed and co-evolved with rice for millennia (Guo et al. 2017), and they have been competitive against both primitive rice and modern, high-yielding rice varieties. Such was probably not the case everywhere; *Echinochloa* once threatened large-scale commercial rice production in California (Chambliss 1915; Jones 1926). Impacts of barnyardgrass interference have been documented in literature from various parts of the world in several crops (reviewed in Bajwa et al. 2015). In the United States, season-long interference from barnyardgrass can reduce rice yield by up to 70% (Smith 1988). Interference by barnyardgrass at 50 plants  $m^{-2}$  reduced rice yields of a short-statured cultivar and a semidwarf cultivar by 28% and 65%, respectively, from



**Figure 2.** Seed size in relation to ecological differentiation in *Echinochloa* species. (A) Caryopsis size of three *Echinochloa* species (left, adapted from Costea and Tardif 2002) and seed size distribution of the global collection of *Echinochloa* species (right, adapted from Wu et al. 2022). (B) Flood as an ecological determinant for the emergence and establishment of *Echinochloa* species along with the effect of seed placement in the soil profile.

season-long competition, and barnyardgrass densities of 5 to 10 plants  $m^{-2}$  were determined to be economic thresholds for short-statured rice cultivars (Stauber et al. 1991). Among semidwarf cultivars, those with a longer maturity period competed more effectively with barnyardgrass (Smith 1974). In a water-seeded culture in California, barnyardgrass at a density of 86 plants  $m^{-2}$  reduced rice grain yields by 50% (Hill et al. 1985). Previously, it was reported that the density of barnyardgrass is more important than the density of rice for the outcome of the competition in terms of rice yield loss and rice panicle number (Smith 1968; Figure 3A). These results were later further supported by Ottis and Talbert (2007) and by Ni et al. (2004) on relatively advanced rice varieties, indicating no or little scope for using crop density as a management strategy for barnyardgrass. It is noteworthy that barnyardgrass has the potential to cause complete yield loss in rice (Johnson et al.

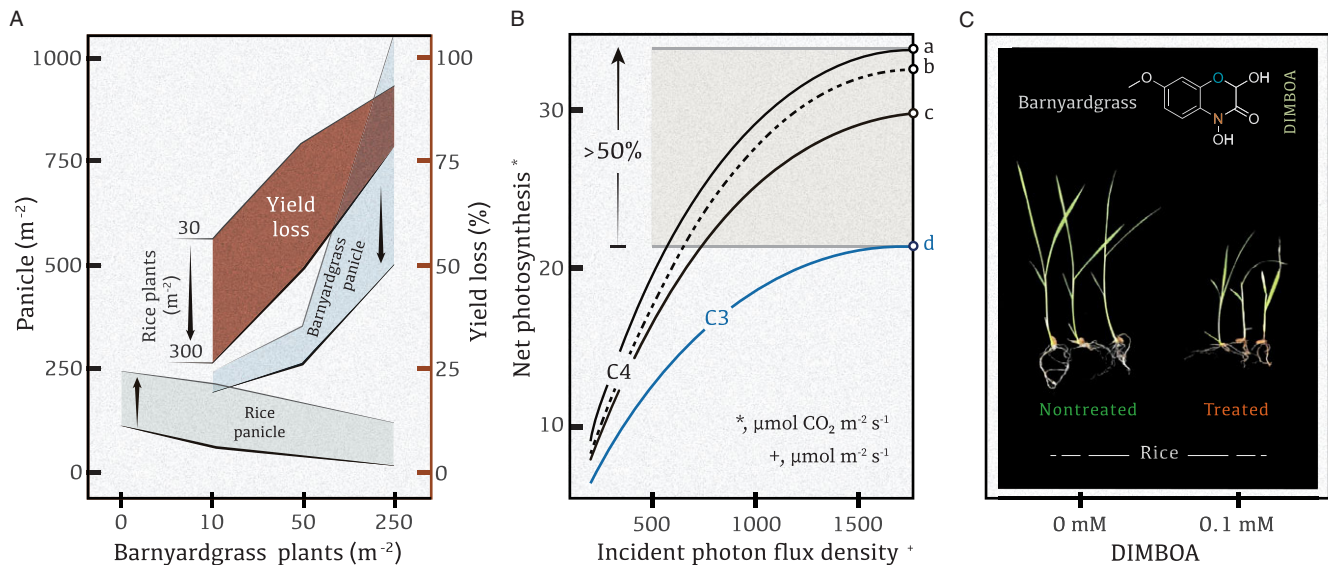
1998) and nearly total crop failure in cotton (*Gossypium hirsutum* L.) (Keeley and Thullen 1991).

Late watergrass, a common *Echinochloa* species in water-seeded California rice, causes up to 50% rice yield losses (Barrett 1983). Interference by one plant of late watergrass with rice in California was 2.3 times greater than intraspecific interference by one rice plant, and the interference was mostly driven by root interactions (Boddy et al. 2012). In that study, late watergrass plants placed their roots deeper and on average produced seven times more root dry weight than a widely used short-stature modern japonica-type rice cultivar, indicating a remarkable niche differentiation between the two species. When plots were kept free of weeds, including *Echinochloa* species, for 30 d or longer during a field experiment in California, rice yields were not affected (Gibson et al. 2002). That finding leads to the suggestion that management strategies that delay the germination or growth of *Echinochloa* species relative to rice may give the crop a significant competitive advantage. Early competition from barnyardgrass for up to 20 d did not cause any rice yield loss in Arkansas (Smith 1974). The interactions between weed and crop could be influenced by several variables, two of which would be maturity of the crop and crop stature.

According to a recent genomic analysis, *Echinochloa* lost a considerable portion of disease-resistance genes during polyploidization, indicating that natural selection may prefer a lower investment in the resistance in this weed to maximize its growth and reproduction (Ye et al. 2020). The next paragraphs highlight the two distinctive characteristics that *Echinochloa* species possess that allow them to successfully compete with rice.

#### C<sub>4</sub> Photosynthesis

*Echinochloa* species possess C<sub>4</sub> photosynthetic cellular machinery. Bouhache and Bayer (1993) studied photosynthetic characteristics of rice (C<sub>3</sub>) and three species of *Echinochloa* to determine how these characteristics vary with changes in light (Figure 3B) and temperature. *Echinochloa* species showed higher photosynthetic activity than rice as indicated by both plants' response to changes in intercellular partial CO<sub>2</sub> pressure, light, and leaf temperature. A C<sub>4</sub>-specific carbon fixation enzyme in conjunction with spatially separated photosynthesis phases with Kranz anatomy ensures high photosynthetic efficiency in C<sub>4</sub> plants (Cui 2021; Sage et al. 2012), providing ostensible competitive advantages such as higher rates of CO<sub>2</sub> fixation, decreased photorespiration, and reduced transpiration (Elmore and Paul 1983). However, the C<sub>4</sub> feature does not confer a universal selective advantage (Elmore and Paul 1983). Rather, a C<sub>4</sub> weed should have a competitive advantage over crop species under many field situations, such as under high light intensities and temperatures, and in dry conditions (Elmore and Paul 1983). Black et al. (1969) also suggested that C<sub>4</sub> photosynthesis may be associated with the more competitive weeds. As is the situation when both weeds and crops are acclimated to the same growth conditions, the C<sub>4</sub> weed frequently overwhelms the crop (Holm et al. 1977) due to its higher net photosynthetic rate, which drives biomass production and reduces environmental stressors in C<sub>4</sub> plants, whereas these stressors are more readily experienced in C<sub>3</sub> species (Elmore and Paul 1983). Estimates suggest that the photosynthetic efficiency of C<sub>3</sub> plants is less than 4.6%, whereas it can reach over 6% in C<sub>4</sub> plants (Zhu et al., 2008). Moreover, C<sub>4</sub> plants are known to use water and nitrogen resources more effectively than C<sub>3</sub> plants (Cui 2021).



**Figure 3.** *Echinochloa* against rice. (A) Competitive outcome of barnyardgrass and rice competition in terms of panicle number and grain yield at varying densities (adapted from Smith 1968). (B) Photosynthetic output of *Echinochloa* species at increasing  $CO_2$  concentration in comparison with rice (a. barnyardgrass, b. early watergrass, c. late watergrass, and d. rice; adapted from Bouhache and Bayer 1993). (C) Inhibition of rice seedlings by 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) extracted from barnyardgrass seedlings (adapted from Guo et al. 2017).

### Allelopathy

Recent studies have shed insight on how barnyardgrass interacts with rice. In response to rice allelopathy, barnyardgrass is thought to respond by inhibiting the signal transduction of plant hormones (Fang et al. 2015). Recently, three functional copies of the 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) synthesis gene cluster have been discovered in barnyardgrass (Guo et al. 2018). DIMBOA or its analogs are the predominant representatives of benzoxazinoids in plants (Frey et al. 2009), which function as allelopathic compounds against rice in the field (Guo et al. 2017). When barnyardgrass was cocultured with rice, transcriptomic analysis showed that expression of genes implicated in metabolic pathways and those associated with cytochrome p450 monooxygenases (CYPs) were enriched and elevated (Guo et al. 2017). Also, the allelochemical DIMBOA gene cluster was activated in response to co-cultivation with rice (Guo et al. 2017), indicating a key role for DIMBOA in competitive interactions with rice (Guo et al. 2018). As low as a 0.08 mM concentration of DIMBOA inhibited rice height and biomass in laboratory conditions (Guo et al. 2017; Figure 3C). Intriguingly, a gene cluster for momilactone A synthesis in barnyardgrass concurrently expressed more after a fungal pathogen infection, indicating that cohabiting with rice benefits barnyardgrass because of enhanced resistance to blast-infection (Guo et al. 2017, 2018).

### Seed Production

Seed production of *Echinochloa* species, specifically barnyardgrass, has been reported to be highly variable across environments (Clay et al. 2005; Holm et al. 1977; Maun and Barrett 1986; Norris 1992b). Barnyardgrass plants produced 7,170 total seeds according to Stevens (1932), whereas Barrett and Wilson (1983) recorded nearly 18,000 seeds, and Holm et al. (1977) reported up to 40,000 seed per plant. Research in California exceeded those numbers and estimated that barnyardgrass growing in sugarbeet (*Beta vulgaris* L.) fields averaged nearly 100,000 seed per plant (Norris 1992a).

According to Mitich (1990), barnyardgrass has the potential to produce up to 1 million seeds per plant in California. Seed production in barnyardgrass can be highly variable depending on local growing conditions, nutrient availability, and day length (Maun and Barrett 1986), the associated crop (Clay et al. 2005; Gibson et al. 2003; Lindquist and Kropff 1996), and time of emergence relative to the crop (Bagavathiannan et al. 2012; Bosnic and Swanton 1997). In Ontario, Canada, Bosnic and Swanton (1997) investigated the seed production of barnyardgrass in corn (*Zea mays* L.) crops and reported that at a density of 10 plants  $m^{-2}$ , barnyardgrass produced up to 34,600 seeds  $m^{-2}$  when it emerged by the 3-leaf stage of the crop, whereas the seed production drastically decreased to 2,800 seeds  $m^{-2}$  when it emerged after the 4-leaf stage. In Greece, at a similar density (5 to 10 plants  $m^{-1}$  of crop row), barnyardgrass produced many fewer seeds per plant (1,300) when it emerged with corn, and only 170 seeds per plant when emergence was delayed until the 6-leaf stage (Travlos et al. 2011). Likewise, in South Dakota, barnyardgrass at a density 1.3 of plants  $m^{-2}$  among corn plants produced seed ranging from 3,385 seeds per plant when planted prior to crop emergence to 158 seeds per plant when planted at the 2-leaf stage (Clay et al. 2005). With soybean [*Glycine max* (L.) Merr.], however, Clay et al. (2005) reported that barnyardgrass failed to produce any mature seeds. With rice, barnyardgrass seed production ranged from 2,800 seeds per plant when it emerged with the crop to 100 seeds per plant when it emerged 45 d after rice emergence (Chauhan and Johnson 2010). When emerging with the crop, barnyardgrass produced 16,500 to 35,500 seeds per plant with cotton and 2,900 to 39,000 seeds per plant with rice in Arkansas, and the seed production drastically decreased when barnyardgrass emerged 5 wk or more later (Bagavathiannan et al. 2012). Similarly, Tahir and Romaburgos (2021) reported variable seed production among barnyardgrass accessions collected from rice fields in Arkansas in a common garden study. In the same study, few accessions of *E. colona* produced as much as a three-fold greater number of seed (>200,000 seeds per plant) compared to barnyardgrass.

Collectively, these data suggest that seed production by *Echinochloa* is highly variable across crops and environments, and ecotype differences likely play a significant role in its fecundity.

## Seed Dormancy, Germination, and Seedling Emergence

### Seed Dormancy

Seed dormancy is crucial for plant ecology because it enables seeds to endure conditions that are unfavorable for seedling emergence. Seed longevity and seed dormancy characteristics are also attributed to the persistence and weediness of *Echinochloa* species. It has long been known that fresh seeds of barnyardgrass exhibit innate dormancy, the duration of which varies considerably (Barrett and Wilson 1983; Rahn et al. 1968), and the dormancy is attributed to the pericarp and epidermis (Arai and Miyahara 1963). Even more pronounced is the variability among accessions as reported by Barrett and Wilson (1983), for which germination capacity ranged from 0% to >75%. The duration of dormancy is partly determined by the size of caryopses (Honek and Martinkova 1996). As a result, a fraction of early produced large caryopses may germinate shortly after they ripen, and a new cohort of seedlings may be established in the same year. In a common garden experiment, three out of nine accessions of barnyardgrass from Arkansas that were after-ripened at room temperature for 6 mo remained dormant, whereas only two accessions of junglerice out of 77 accessions were dormant (Tahir and Roma-Burgos 2021). The other larger-seeded types (early watergrass and late watergrass) are known to have minimal dormancy. Barrett and Wilson (1983) compared germination of 18 populations of barnyardgrass and 11 populations of late watergrass with 9- or 15-mo-old seeds and found that the decay of dormancy in barnyardgrass was less rapid than it was in late watergrass following dry storage and burial in soil. Dormancy is generally greater in barnyardgrass than in junglerice seeds (Chul and Moody 1989).

Most research on dormancy has occurred in *ex situ* environments involving a single population. A better comprehension of the dormancy and germination behavior of varieties of *Echinochloa* species and populations as affected by tillage and seed depth in situ would aid in the more accurate prediction of seedbank dynamics of *Echinochloa* species. Despite the fact that seed dormancy is the single most important feature of weed seedbank dynamics and periodicity, it has been customary to avoid addressing dormancy directly within predictive models due to its complexity (Grundy 2003).

### Seed Germination and Seedling Emergence

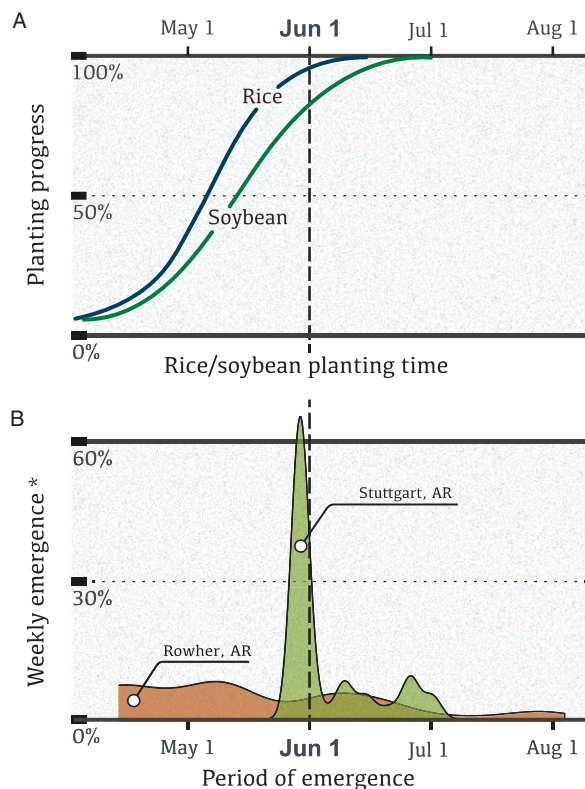
Seedling emergence is a manifestation of the dormancy status, germination requirements, and growth of seedlings to the surface (Vleeshouwers and Kropff 2000). It is one of the most important demographic events in the life cycle of an annual plant species because the emergence timing determines its survival and reproductive success (Forcella et al. 2000), and this is especially true for agricultural weeds. Much research has occurred since the 1930s to understand the effect of manipulation of moisture and seeding depth on *Echinochloa* emergence. Important research findings on aspects that have shaped today's rice production practices and been the major determinant of the population dynamics of *Echinochloa* species are highlighted below.

Common varieties of Californian barnyardgrass populations seeded on puddled soil emerged to a 100% stand, but those submerged 5, 10, 15, 20, and 25 cm emerged to a 10%, 5%, 1%, 0%,

and 0% stand, respectively (Jones 1933). Later, in the 1960s, it became apparent that some *Echinochloa* plants were emerging through the water-flooded rice fields. Barrett and Wilson (1983) studied the effects of soil moisture and seed burial depth on two *Echinochloa* species, barnyardgrass and late watergrass. When soil moisture was at field capacity, the seeds of both types germinated equally well at all depths, but the maximum number of seedlings emerged from 1- to 2-cm depths. Seedling emergence decreased with the depth below 2 cm, reaching zero at 10-cm depth. The emergence occurred first at shallower depths. Most of the surface-lying seeds that germinated failed to produce seedlings, probably because of a lack of moisture. In saturated soils, however, seed burial caused a reduction in the rate of emergence even at 0.5- to 2-cm depths; seedling emergence was significantly greater at all burial depths in late watergrass as compared to barnyardgrass; and no seedling emergence in barnyardgrass occurred from 2 cm or deeper depths.

In another study, seedling emergence of late watergrass was also greater than barnyardgrass from soil flooded to 9- and 18-cm water depths (Barrett 1983). Anaerobically grown late watergrass seeds are metabolically active, which may explain their ability to emerge from flooded rice fields (Kennedy et al. 1980). In a pot culture experiment with Crowley silt loam soil in Stuttgart, Arkansas, seedling emergence of barnyardgrass decreased by 90% with flooding to 1.3 cm (Smith and Fox 1973). Arai and Matsunaka (1966) reported that when the soil moisture content was 70% to 80% of field capacity, a Japanese population of barnyardgrass seed germinated as deep as 10 cm in the soil. But when the soil was submerged, the seeds germinated only in the top 2 cm of soil. The seedling emergence of barnyardgrass was greatest from shallow depths of 1 to 2 cm in a fine, sandy loam soil (Dawson and Bruns 1962), and the best germination occurred at 70% to 90% field capacity (Arai and Miyahara 1963; Brod 1968). The relatively large seeds of Californian barnyardgrass (weighing up to 3 mg) have been reported to emerge (up to 16%) from 10.1 cm or deeper depths under nonflooded conditions (Keeley and Thullen 1989). Collectively, these results give insight into how moisture and seeding depth affects emergence of *Echinochloa* species (Figure 2B).

Several other factors have been shown to affect *Echinochloa* emergence. Seeds in which dormancy had been broken (1 yr old) germinated best with continued exposure to light (60%) as compared with continuous darkness (6%) (Rahn et al. 1968). More mature (dark gray, brownish, and shiny) seeds produced significantly greater germination than immature (light gray) seeds (Rahn et al. 1968). The seeds may germinate at a wide soil pH range of 4.1 to 8.3 (Arai and Miyahara 1963), but the optimal pH for germination is around neutral (Brod 1968). *Echinochloa* species seeded 30 d after rice in a field experiment in California did not survive (Gibson et al. 2002). No reduction in germination of seeds buried in submerged soil for 30 mo was observed by Roché and Muzik (1964); however, seeds buried at 10- and 20-cm depths under nonflooded soil conditions for the same period lost considerable viability. Dawson and Bruns (1975) buried seeds of barnyardgrass at 2.5-, 10-, and 20-cm depths in irrigated and nonirrigated sandy loam soil, and they showed that seeds exhumed from 10- to 20-cm depths had highest germination rates in the second year after burial. The seeds buried for 13 yr had 3% viability but those buried for 15 yr were nonviable. Seeds buried at a 20-cm depth remained viable for a longer period than at 10 cm probably because of greater induced dormancy (Roché and Muzik 1964). Germination was more rapid in sandy loam rather than loam soil,



**Figure 4.** Emergence of barnyardgrass in relation to rice/soybean planting time in Arkansas. (A) Rice/soybean planting progress in 2022 (adapted from USDA-NAAS 2022). (B) Barnyardgrass weekly emergence at two sites in Arkansas in 2008 (adapted from Bagavathiannan et al. 2011). \*Percentage of total seasonal emergence.

and soil compacted by tamping and surface watering in a greenhouse produced a higher germination rate (Rahn et al. 1968). Robert et al. (1983) showed thermal adaptation and acclimation of barnyardgrass at the enzyme level, especially in populations collected from warmer locations. A recent report from Europe indicates that adaptation to local environmental conditions leads to interpopulation differences in base temperature, which affects the emergence process in barnyardgrass (Royo-Esnal et al. 2022). Barnyardgrass seeds were found to germinate in a wide soil pH range of 4.7 to 8.3 (Maun and Barrett 1986). Laboratory studies on junglerice in the Philippines determined that temperature, light, salt, osmotic stress, soil pH, seed burial depth, and rice residue influenced its germination and emergence (Chauhan and Johnson 2009).

In a study on naturally occurring seedbanks in Arkansas, barnyardgrass exhibited an extended period of emergence, with emergence varying widely in the initiation time and the duration across sites and years (Bagavathiannan et al. 2011). Such variation was attributed to corresponding rainfall events; however, the vertical distribution of seed in the soil profile was not considered, which is one of the key components to be considered for emergence modeling (Grundy et al. 2003). The two contrasting emergence patterns along with relative crop planting time in Arkansas are shown in Figure 4 A and B. Nonetheless, seedling emergence patterns may also be strongly affected by differences in seed dormancy and burial depth and may vary among populations (reviewed in Grundy 2003). Accurate prediction of barnyardgrass emergence, however, will require experiments that adequately

control the sources of such variations (Bagavathiannan et al. 2011). In California, late watergrass populations emerge in a biphasic pattern, and the ability to model the second phase of the biphasic emergence curve is necessary (Brim-DeForest et al. 2022).

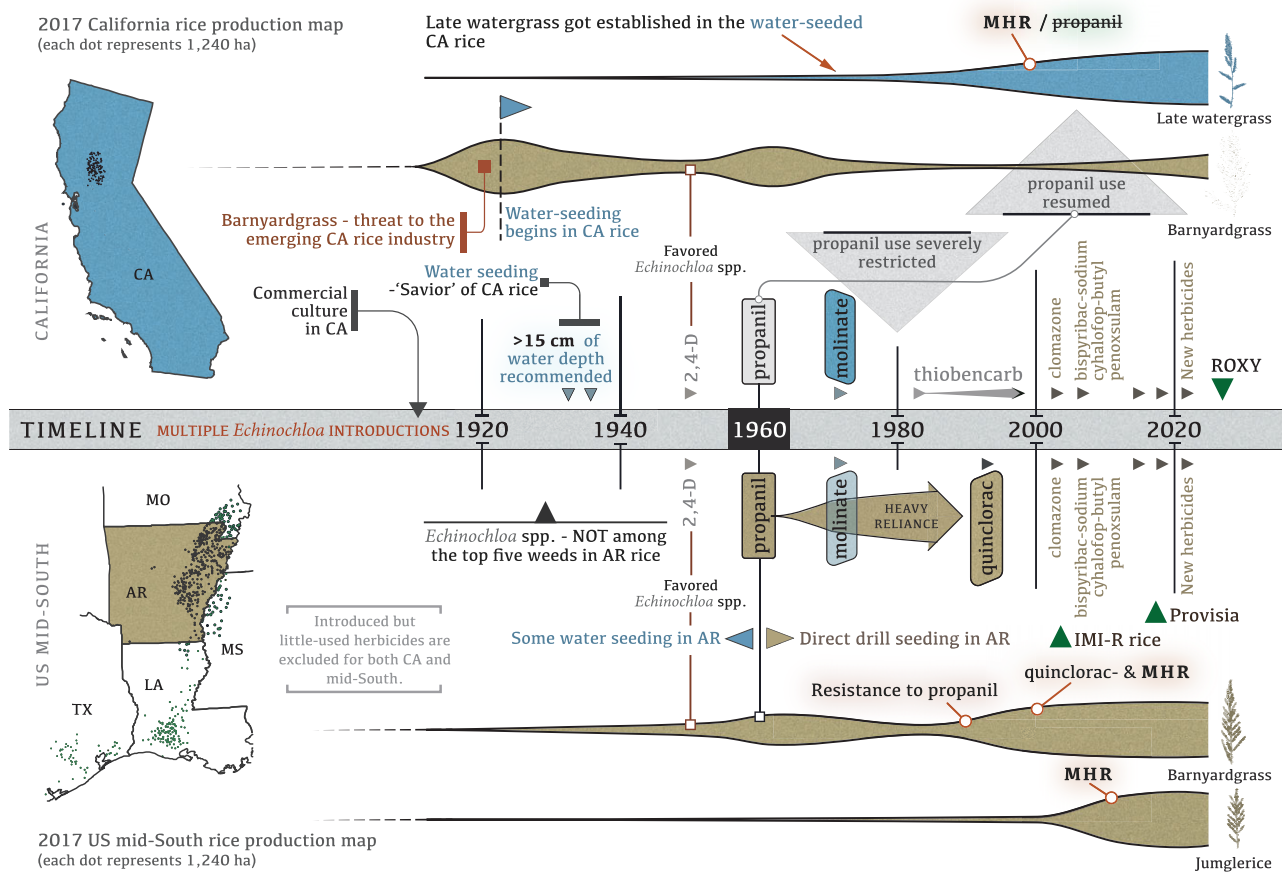
### *Echinochloa* – A Persistent Issue in US Rice

Considering that all the economically relevant *Echinochloa* in U.S. rice production are introduced species and have persisted through the most advanced weed management tools at our disposal, revisiting the historical trajectory of their agroecology is important. Broadly, water management and the use of herbicides that shaped the agroecosystem can be attributed as the determinants driving their population dynamics over the course of the century-long history of U.S. rice production (Figure 5).

In the USDA Farmer's Bulletin (#688), published within 3 yr of commencement of rice culture in California, CE Chambliss (1915) wrote "In three seasons, this weed has become a menace to the rice crop of Sacramento Valley, and unless serious action is taken for its control or eradication its presence may seriously affect the normal development of the rice industry of the state. This may be effectively done through county or community organizations with police power." In the same bulletin Chambliss mentioned that some farmers spent more than 25% of the total cost of rice production just to manually control the weed. However, according to the reports from the 1930s and 1950s (Jones 1938, 1952), *Echinochloa* was not among the top five weeds in the early years of commercial rice cultivation in the mid-South. The water-seeding and continuously flooded rice culture that was developed in 1920s was the savior of the young California rice industry that was threatened by barnyardgrass. This method, in which water is maintained on the fields to a depth of 8 to 20 cm for the duration of rice growth, helped to reduce infestations of barnyardgrass in rice fields (Jones 1923, 1933).

Because rice grew and yielded well in a water-seeding culture, this method became popular in California in the 1920s (Jones 1933) and later spread to the southern rice-growing area to control *Echinochloa* species (Smith and Fox 1973). Right before the introduction of propanil, the widespread use of 2,4-D to control dicotyledonous weeds in the 1950s favored *Echinochloa* (Holm et al. 1977) in U.S. rice fields, by creating an opportunity for, and an aggressive population shift to, grassy weeds; like the proliferation of *Setaria* species in U.S. corn and soybean fields (Oliver and Schreiber 1971; Warwick 1990). California rice remained predominantly water-seeded; however, mid-South rice producers shifted to dry-seeding after propanil became available to control a broad spectrum of weeds.

Since then, it was apparent that *Echinochloa* species, particularly barnyardgrass, became the keystone species in the mid-South (Smith 1970). A well-developed seed dormancy, as noted earliest by Rahn et al. (1968) and Holm et al. (1977), as well as the slower rate of dormancy decay in barnyardgrass, according to Cohen's prediction (Cohen 1966) are the traits to be selected in habitats where the risk of failure is high from propanil use (Barrett and Wilson 1981). In contrast, the relatively rapid decay of dormancy and the synchronous germination in early watergrass and late watergrass are traits that Cohen (1966) and Harper (1977) both predicted to be selected in a homogeneous environment where the probability of successful reproduction is high (Barrett and Seaman 1980). The water-seeded monoculture Californian rice agroecosystem is an excellent example of a homogeneous environment.



**Figure 5.** Historical trajectory of *Echinochloa* establishment in U.S. rice crops with milestones in its management. Following multiple introductions, the population dynamics of *Echinochloa* in U.S. rice have been primarily driven by water management and the use of herbicides. Water-seeding rice culture was developed in the 1920s to reduce infestations of barnyardgrass in rice fields. The widespread use of 2,4-D to control broadleaf weeds in the 1950s favored *Echinochloa*. Producers in the mid-South shifted to dry-seeding rice after propanil became available in the early 1960s, when barnyardgrass became the keystone rice weed. The long-established water-seeded monoculture of California rice was selected for large-seeded, water-tolerant late watergrass. For the past 50 yr, these species have prevailed in their respective regions with the evolution of resistance to almost all major herbicides that were deployed through the decades, leading to the increased abundance of *Echinochloa* in U.S. rice. Recent reports indicate an increase in barnyardgrass in California and junglerice in mid-South rice in the last two decades. MHR, multiple herbicide resistance.

The predictability of the rice field ecosystem from year to year enabled these water-tolerant species to build up rapidly and favored their spread throughout the rice-growing areas of California, where they persisted in most rice fields despite attempts at control by herbicides (Barrett and Seaman 1980). Additionally, the large seeds of late watergrass probably enhanced their competitive ability and favored coexistence with rice; they may have originally been selected as an adaptation that enabled seedlings to grow and emerge in a natural habitat with deep water (Barrett 1983). Since late watergrass can establish successfully in deep water, it replaced barnyardgrass as California's most economically important weed of rice (Barrett 1983; Barrett and Seaman 1980). However, as noted by Smith and Fox (1973), barnyardgrass persisted in shallow-water areas and field borders thereafter. For the past 50 yr, species of *Echinochloa*, particularly early watergrass and late watergrass in California and barnyardgrass in the mid-South, have prevailed. With the evolution, spread, and prevalence of resistance to almost all the major herbicides deployed, simultaneously or in sequence, as discussed in the later section, it can be assumed that the abundance of *Echinochloa* in U.S. rice fields has increased compared to that of the era prior to the 1990s.

### Outstanding Question: Are Barnyardgrass in California and Junglerice in the Mid-South on the Rise?

Several anomalous reports in recent years (Lui et al. 2021, 2022; Rouse et al. 2018; Tahir and Roma-Burgos 2021; Wu et al. 2022) raise the question of whether junglerice has become more established than was previously believed in mid-South rice fields, even to the extent that it has indeed surpassed barnyardgrass. The greater representation of junglerice than barnyardgrass in the samples analyzed does not necessarily indicate the greater relative abundance of junglerice. Nonetheless, it is well recognized that in glyphosate-based cropping systems weed spectrums will adapt or vary in response to changes in production methods or new technologies, especially in crop fields where yearly monoculture is frequently the goal (Reddy and Norsworthy 2010; Webster and Coble 1997; Webster and Sosnoskie 2010), favoring the perpetuation of one or several weed species, including those that have evolved the ability to escape herbicide applications (Norsworthy et al. 2013). This observation in mid-South rice may be attributed to the higher prevalence of herbicide resistance in junglerice, as reported by Rouse et al. (2018) in Arkansas and by Lui et al. (2021) in Texas. It may also reflect its proliferation in the continuous dry



seeding and delayed flooding rice culture, as well as the rice-soybean production system practiced in the region, or a combination of all these factors. Unlike barnyardgrass, junglerice is intolerant of anaerobiosis, and hence cannot germinate in the absence of oxygen (Mujer et al. 1993; Rumpho and Kennedy 1983).

Counterintuitively, a majority of *Echinochloa* seed samples submitted to the University of California–Davis Weed Science Program for resistance screening from 2015 to 2020 were identified as barnyardgrass. It is widely accepted that late watergrass is the most prevalent species in water-seeded California rice crops and that barnyardgrass is not a relevant weed in many fields (Marchesi 2009). In flooded rice fields in Japan, Yamasue (2001) observed that the dominant species of *Echinochloa* weeds is changing from late watergrass to barnyardgrass because of the shift from manual to herbicidal weed management. Ironically, early watergrass and late watergrass have greater concentrations of antioxidants in their leaves, which may be attributed to greater tolerance to herbicides compared to barnyardgrass (Damalas et al. 2008). Thus, it may not be the relative sensitivity to herbicide among the species, but rather, due to compromised deep water in rice fields. Soon after the introduction of propanil, Oelke (1966) reported that a deep flood inhibits growth of young rice seedlings, reduces tillering, and lowers grain yield, whereas Smith et al. (1977) reported that a shallow flood of 2.5 cm to 10 cm, combined with the use of effective herbicides, resulted in weed species control and increases in rice yields compared with a deep flood culture. In the last two decades, most rice fields in California have been treated postemergence with herbicides, including propanil, and in almost all cases, the water depth is lowered so as to expose weed foliage to the herbicide. It is likely that such practices have favored relatively flood-intolerant species such as barnyardgrass. These observations also provoke us to question the extent of hybridization among *Echinochloa* forms as we discussed in the previous section. This necessitates more efforts to differentiate between established and emerging biotypes of *Echinochloa* in the California rice agroecosystem. Furthermore, there have been reports of *Echinochloa* in some rice fields that have yet to be properly identified (WB Brim-DeForest, personal communication). Additionally, a recent study showed genomic evidence of admixtures in some *Echinochloa* samples, leading to unresolved taxonomic classification for those samples (Wu et al. 2022).

### Insights From Recent Genomic Studies

Three recent genomic studies have shed light on how *Echinochloa* have evolved as a weed, made adaptations, and interacted with rice. Pertinent information from these studies to a varying extent has been mentioned throughout this article. Guo et al. (2017) for the first time generated a draft genome of barnyardgrass and provided novel insights into the adaptive molecular mechanisms for its survival and invasiveness in rice fields. The study specifically revealed biosynthetic gene clusters responsible for allelopathic compounds and phytoalexin (DIMBOA and momilactones) in the barnyardgrass genome and decoded evolutionary trajectory of coevolution with rice. Ye et al. (2020) improved the genome assembly quality by generating PacBio long reads representing ~86× coverage of the genome with contig and scaffold N50 sizes of 1.57 Mb and 4.09 Mb, respectively. One of the significant discoveries of the genome research was that *Echinochloa* may have lowered disease resistance in favor of aggressive growth and development. The other study by Wu et al. (2022) unprecedentedly distinguished a global collection of *Echinochloa* species and varieties (a total of 596 samples) by integrating morphological characteristics

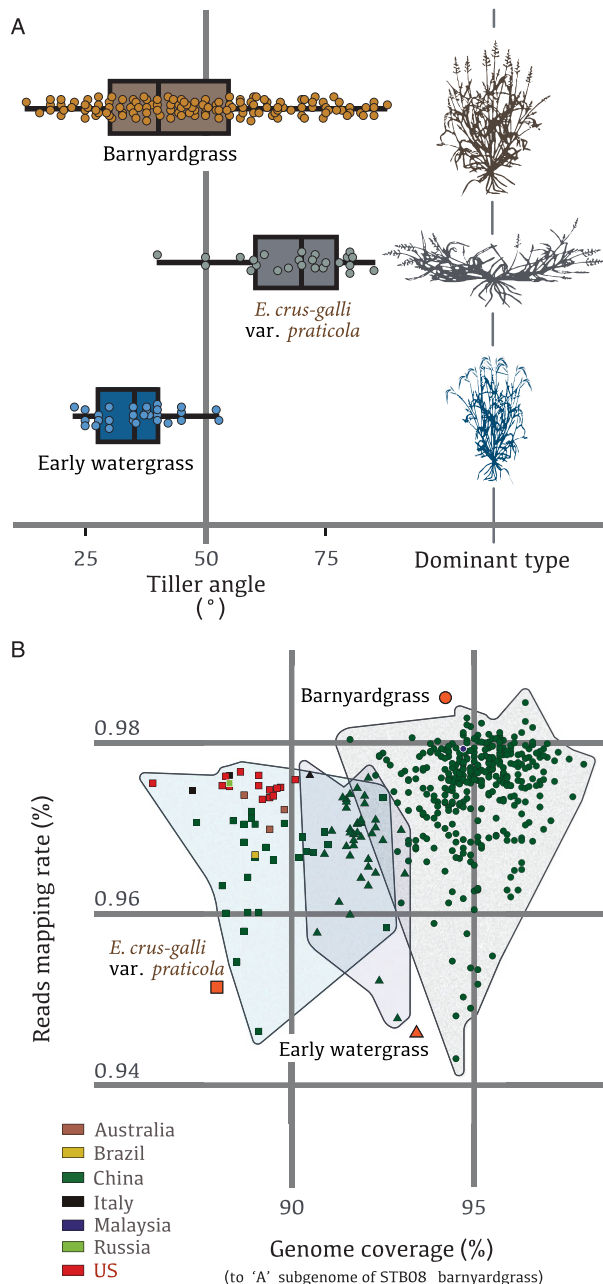
with multiple pieces of genomic evidence. As highlighted by Wu et al. (2022), genomic resources made accessible will accelerate research in *Echinochloa* evolutionary biology, evolution of resistance to herbicides, interaction between the crop and the weed, and the development of novel weed control strategies. These two studies discovered that this hexaploid genome, yet compact (~1.4 Gb), contains an incredibly large repertoire of genes for enzymes involved in xenobiotic detoxification, including ABC transporters, CYPs, and glutathione S-transferases (GSTs). These genes in barnyardgrass outnumber those typically found in other grass species. These are the major genetic components that are known to contribute to increased capacity to detoxify herbicides (Yu and Powles 2014); hence, the widespread occurrence of herbicide resistance in barnyardgrass is not surprising.

Of particular interest from the study by Wu et al. (2022) is that the *Echinochloa* samples collected from U.S. rice fields were more diverse than *Echinochloa* from other countries, albeit the U.S. samples were collected from a narrow geographic area. The study did not represent any samples from California. Of the 39 samples from the United States, more than one-third were *E. crus-galli* var. *praticola* and none of them were barnyardgrass. Such a large representation of a less-known *Echinochloa* is likely due to the site of collection being far from rice fields. Of the six samples collected from Arkansas, which appeared to be from the same rice field based on GPS coordinates, all were junglerice. Further research with a wide pool of *Echinochloa* samples from U.S. rice fields is necessary to address this apparent shortcoming. Genomic proximity, tiller angle, and dominant types of three varieties of *E. crus-galli* are shown in Figure 6 (adapted from Wu et al. 2022). Although the varieties show little differentiation at the genomic level, their plant architecture is quite different. The seed size of *E. crus-galli* var. *praticola* is on the lower side of barnyardgrass and it has a very prostrate morphology (Wu et al. 2022).

### Herbicide Resistance in *Echinochloa*: An Increasingly Serious Issue

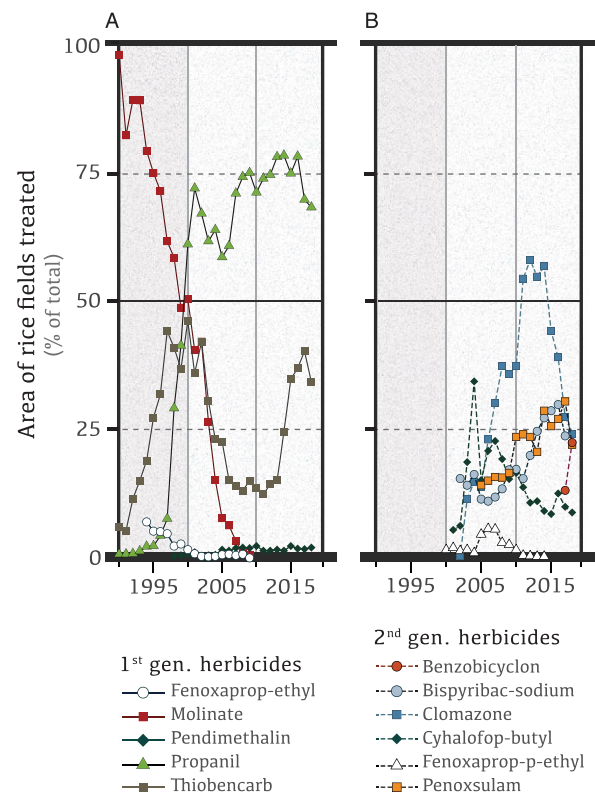
For the past three decades, the U.S. rice industry has been experiencing the predicament of an emerging number of herbicide-resistant *Echinochloa* species, even for those herbicides that have never been used or are rarely used. Several reports of increased abundance of barnyardgrass populations in response to triazine and thiocarbamate herbicides started to appear in the 1970s and 1980s (reviewed in Maun and Barrett 1986). That it could evolve resistance to herbicides was realized as early as the 1980s (Maun and Barrett 1986; Mitich 1990), and since then this fact has been implicated in its remarkable persistence in modern rice cropping systems. Most cases of herbicide resistance in *Echinochloa* in U.S. rice crops have been documented in the International Herbicide Resistant Weed Database (Heap 2023).

The first cases of herbicide resistance in two *Echinochloa* species, early watergrass and late watergrass, came from water-seeded Californian rice in 2000 (Fischer et al. 2000a). For reference, herbicide use history from 1990 through 2018 in California rice crops is shown in Figure 7 (California Department of Pesticide Regulation 2022). Despite the fact that molinate was the only major grass herbicide used in California, those populations of late watergrass were reported to have resistance to multiple herbicides from different chemical classes and modes of action (MOAs) including molinate, thiobencarb (thiocarbamates), cyhalofop-butyl, fenoxaprop-ethyl (aryloxyphenoxy propionate), bispyribac-sodium (pyrimidinyl benzoate), penoxsulam



**Figure 6.** Tiller and genomic proximity of three *E. crus-galli* varieties. (A) Distribution of tiller angle, and (B) genomic proximity as defined by reads mapping rates and genome coverage of reads mapped to a reference genome of a barnyardgrass population from China (both A and B adapted from Wu et al. 2022).

(triazolopyrimidine sulfonamide), and clomazone (isoxazolidinone) (Fischer et al. 2000a, 2000b; Osuna et al. 2002; Ruiz-Santella et al. 2006; Yasuor et al. 2008, 2009). Besides thiocarbamates, all other herbicides were under development at that time. None of the populations were resistant to the less-used herbicide propanil, although they were found to be less sensitive compared to susceptible populations (Fischer et al. 2000b; Yasuor et al. 2012). Quite surprisingly, the same populations were later found to be resistant to another herbicide that had also never been used, quinclorac (Yasuor et al. 2012). A single, introduced



**Figure 7.** Herbicide use history in California rice fields from 1990 to 2018 (data compiled from the California Department of Pesticide Regulation). (A) First-generation rice herbicides (introduced before 2000), and (B) second-generation rice herbicides (introduced after 2000).

multiple-resistant biotype (“the founder effect,” as termed by Gressel and Segel 1990) dispersed throughout California under continued use of molinate and/or thiobencarb (Tsuji et al. 2003). Recent results from herbicide resistance testing on grower-submitted samples from California rice fields from 2015 to 2020 indicated the presence of multiple resistance in the vast majority of the *Echinochloa* samples and the occurrence of multiple resistance up to five MOAs (Becerra-Alvarez et al. 2022).

Earlier work suggested that the resistance had primarily endowed by enhanced CYP degradation in late watergrass (Osuna et al. 2002; Yun et al. 2005; Yasuor et al. 2009), with some role of GST in conjugating herbicides (Bakkali et al. 2007). More recently, Fang (2019) and Iwakami et al. (2014, 2019) further uncovered the role of two cytochrome P450 enzyme (CYP) genes, *CYP81A12* and *CYP81A21*, in imparting resistance to these herbicides from a wide range of classes. Recent studies on the resistant late watergrass by Dimaano et al. (2022) demonstrated that resistance to thiobencarb is independent from these CYP genes. In California rice, flooded conditions in the late watergrass populations induces metabolic adaptations (Boddy et al. 2012) that might lead to the selection of the CYP genes that enable survival after an application of thiobencarb. Additionally, the herbicide bensulfuron-methyl (sulfonylurea) was widely used for controlling broadleaf and sedges in California rice in the 1980s and 1990s; however, it also partially controlled *Echinochloa*, indicating a sublethal selection from this herbicide (Fischer et al. 2000b). Most herbicide resistance mechanism studies in California *Echinochloa* have been conducted primarily on early watergrass and

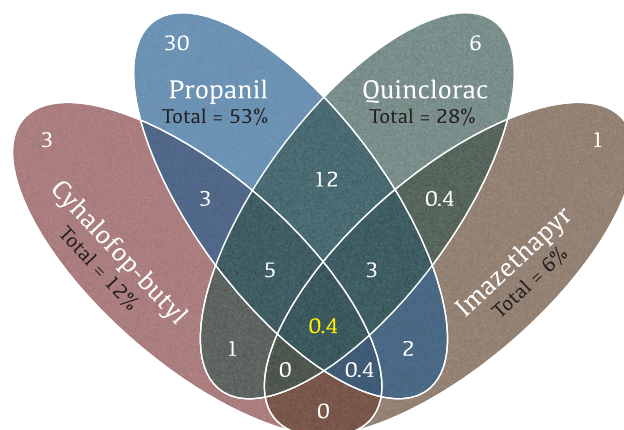
late watergrass. Hybridization among *Echinochloa* species has been suggested or experimentally shown, including recent genomic investigations that show some degree of gene flow (Bagavathiannan and Norsworthy 2014; Marchesi 2009; Wu et al. 2022; Yabuno 1981).

Herbicide resistance by *Echinochloa* species in Arkansas has been well documented via routine screening or surveys; for example, by Riar et al. (2013b), Norsworthy et al. (2013), Rouse et al. (2018), and Butts et al. (2022), and the early cases of resistance were reviewed by Talbert and Burgos (2007). Resistance to the extensively used acylanilide herbicide propanil in U.S. rice production (Hoagland et al. 2004) was reported in *Echinochloa* populations from several mid-southern regions in the early 1990s (Baltazar and Smith 1994; Carey et al. 1995a, 1995b). Since its commercialization in the 1960s, propanil had remained the primary herbicide for controlling *Echinochloa* in mid-southern rice for more than three decades (Carey et al. 1995b). Introduced in 1992, quinclorac controlled propanil-resistant barnyardgrass effectively when mixed with propanil (Baltazar and Smith 1994; Talbert and Burgos 2007); however, several biotypes with multiple resistances to propanil and quinclorac had evolved by the early 2000s (Malik et al. 2010), portending evolution of resistance to the next tool, clomazone (Norsworthy et al. 2007b), essentially threatening the economic viability of rice production in the U.S. mid-South (Malik et al. 2010). Thereafter, clomazone was widely used to control propanil- and quinclorac-resistant barnyardgrass (Norsworthy 2007a), and still today remains the major herbicide in mid-southern rice because resistance to this herbicide is not widespread (Norsworthy et al. 2014; USDA-NAAS 2022). Following the commercialization of imidazolinone-resistant rice, imazethapyr was another option for controlling barnyardgrass (Norsworthy et al. 2007a). However, the instances of overuse of the herbicide, especially without crop rotation and the use of multiple effective herbicide modes of action, led to selection for the acetolactate synthase-resistant barnyardgrass (Norsworthy et al. 2013; Riar et al. 2013a, 2013b) in a short time. Once used in nearly half of the rice fields, imazethapyr use has decreased drastically in recent years (USDA-NAAS 2014, 2022).

Herbicide resistance in Arkansas rice fields has continuously increased in frequency and complexity with additional resistance to aryloxyphenoxy propionate herbicides (cyhalofop-butyl, quizalofop-ethyl) among *Echinochloa* populations, including junglerice (Rouse et al. 2018, Figure 8). The evolution is apparently a consequence of sequential selection with different major herbicide MOAs, starting with propanil followed by quinclorac and others (Rouse et al. 2018), unlike in California rice where simultaneous resistance to multiple MOAs occurred. Recently, resistance to the newly registered rice herbicide, floryprauxifen-benzyl, has been reported in barnyardgrass (Hwang et al. 2022). The mechanism is nontarget site-based and involves hydrolysis of a methoxy group followed by glucose conjugation (Hwang et al. 2022; Takano et al. 2023), and it is believed to have evolved under the selection of an older rice herbicide, penoxsulam (Takano et al. 2023). Earlier, a similar case was reported in a population of barnyardgrass from China that had been under penoxsulam selection for several years (Fang et al. 2019).

### Research Efforts in the Nonchemical Weed Management Space

In a recent survey on weed management concerns in Arkansas rice, effective, nonchemical weed management strategies were rated as



**Figure 8.** Resistance profile of *Echinochloa* species submitted for resistance testing in Arkansas (2010 to 2016) to four commonly used rice herbicides (adapted from Rouse et al. 2018).

only moderately important as current research or an educational effort, even though 78% of the respondents reported high concern with herbicide-resistant weeds (Butts et al. 2022). This finding indicates an inadequate appreciation of the fundamental importance of nonchemical approaches for sustainable weed management and indeed suggests that the views of rice producers on weed control need to change considering the expanding herbicide resistance profile in *Echinochloa* species. It is a fact that the commercialization of highly effective herbicides has de-escalated the scope, opportunities, and advancement of nonchemical approaches to weed management. Nonetheless, research in the 1970s and 1980s reported successful management of barnyardgrass under certain crop production practices, particularly with the use of tillage and crop rotation (reviewed in Maun and Barrett 1986). Although the greater need for integrated weed management (IWM) has been realized by some researchers (Hill et al. 1994), widespread recognition of herbicide resistance as an inevitable consequence has emerged only in the past two decades, and significant research and extension efforts are being placed on nonchemical methods of weed control as a fundamental element of an IWM strategy. Specifically for rice, the use of harvest weed seed control (HWSC) methods and cover crops in the mid-South and alternate dry and wet seeding in California are being considered as potential IWM components of sustainable management of *Echinochloa*.

### Harvest Weed Seed Control

The HWSC method effectively expands the number of nonchemical strategies for weed management, but it has been underused until recently. Originating in Australia (Walsh et al. 2013) and deemed an effective tool for managing multiple herbicide-resistant Italian ryegrass in cereal crops (Walsh et al. 2017), HWSC strategies are currently being evaluated for use in U.S. field crops (Norsworthy et al. 2020). As a potent weed seed recruitment preventer (Walsh et al. 2017), this technique is seen as a vital component of sustainable weed management because it directly targets the weed soil seedbank (Norsworthy et al. 2012, 2020). In order for *Echinochloa* to continue interfering with rice, its seedbank must replenish. In a survey on the adoption of best management practices for herbicide-resistant weeds in the mid-southern United States, prevention of crop weed seed production

was perceived as one of the most important practices in rice (Riar et al. 2013b). HWSC techniques have the potential to efficiently disrupt the seedbank replenishment process. Previous research on barnyardgrass has shown that each plant retains approximately 43% of the total seed produced at the time of soybean maturity (Schwartz-Lazaro et al. 2017), but information on seed retention of *Echinochloa* species in rice is lacking. Seed shattering is well known in *Echinochloa* species, yet some benefit to using the HWSC method for barnyardgrass can be expected. Variations in seed shattering/retention may exist among different forms of barnyardgrass, and it should be considered in future research. In the context of rice-soybean cropping systems of the U.S. mid-South and a significant proportion under furrow-irrigated rice, another problematic weed, Palmer amaranth (*Amaranthus palmeri* S. Watson), is likely to drive HWSC adoption as encouraging results are being reported regarding its effectiveness on this weed (Norsworthy et al. 2020; Schwartz-Lazaro et al. 2017).

Unlike in the mid-South, the HWSC method has not yet gained much interest in Californian rice. Earlier studies in California reported that late watergrass flowered simultaneously with rice, but most seeds were shed during the period of rice harvest (Barrett 1983; Barrett and Seaman 1980; Boddy et al. 2012), and compared with susceptible plants, those that were resistant to multiple herbicides tended to mature even earlier and shattered greater proportions of their seed before rice harvest (Boddy et al. 2012; Tsuji et al. 2003). Yabuno (1966) and Yamasue (2001) noted similar observations for this type of *Echinochloa* in Japan. In a wild form of *E. oryzicola* from China, Hirose et al. (2000) reported that the spikelet shattering percentage was 99.8% 80 d after heading. Regarding barnyardgrass, several phenological and morphological forms were reported in the 1920s, with varying seed shattering characteristics (Jones 1923; Kennedy 1923), and even more forms are apparent now. Seed shattering from barnyardgrass plants that germinated in mid-May begin to appear by late July or early August (Norris 1992a), whereas rice harvest in California does not begin until October or November. However, barnyardgrass that has once gone through the domestication process has a relatively less seed shattering attribute (Wu et al. 2022) and could be a good target for the HWSC method. Contrary to the results reported by Wu et al. (2022), Costea and Tardif (2002) reported that spikelets persist in the panicle longer in late watergrass than in early watergrass. Even though the effectiveness of HWSC on a broad range of *Echinochloa* species remains a question, research and analysis need to be initiated to evaluate whether this strategy can yet be a significant component of sustainable management of *Echinochloa* in California rice.

### Cover Crops

Cover crops historically have been adopted on a limited acreage to protect highly erodible lands. However, they are becoming increasingly popular due to the various benefits they offer for soil health, crop productivity, and weed management, as well as the incentives provided by government programs. Cover crops are one of the cultural tools that aid in herbicide resistance management, and their effectiveness in suppressing the initial flush of weeds with various crops has been demonstrated by a recent meta-analysis (Osipitan et al. 2019). Weeds that thrive in current agroecosystems are generally susceptible to the negative effects of shade (Fenner 1978). These weeds are at one extreme of the adaptive continuum in which their inherent physiological trade-offs prevent them from fully adapting to low light (Givnish 1988). Cover crops create a type

of agriculture that is diametrically opposed to conventional systems; one that disfavors weeds that have adapted to emerge and prosper in disturbed habitats over time. Given this, it is worthwhile to develop cover crop techniques that can successfully smother *Echinochloa* in rice and effectively reduce their short- and long-term population dynamics. Even though cover crops might not be immediately compatible with all rice cropping systems in the United States, they can be successfully integrated into dry-seeded rice culture, which is common in mid-southern states. Although cover crop adoption is still limited by several factors such as cost, availability, knowledge, and management challenges, as the benefits of cover crops converge, conjoined with greater efforts to promote grower awareness and support, it is highly promising that the adoption of cover crops will be elevated.

### Alternating Dry and Wet Seeding

Water-seeding (wet seeding) has been the predominant method of rice cultivation in California since the 1920s (Hill et al. 1994) and has been used to suppress competitive *Echinochloa* species (Adair and Engler 1955), but this has led to the establishment of water-tolerant introduced *Echinochloa* species (Hill et al. 1994). As herbicide resistance by *Echinochloa* species emerged as a major economic issue in California rice production (Fischer et al. 2000a; Hill et al. 1994; Peterson et al. 2018), some growers began to modify the dominant water-seeded system they had practiced (Hill et al. 1994). For example, rice seedbeds are prepared as usual and flushed with water to promote weed germination, and then broad-spectrum herbicides are used as a burndown treatment (Hill et al. 2006). Currently, drill-seeding (dry seeding) is practiced on a limited number of fields in California. The use of alternate dry and wet seeding has the potential to disrupt the ecological cycle and, as a result, restrict the proliferation of *Echinochloa* species in the rice cropping system since these species have a niche that is ecologically distinct in terms of moisture regimes. Because frequent drought has increased concerns about water management in California rice, there may be an increase in the number of farmers who practice dry seeding instead of the traditional continuously flooded system (Brim-DeForest et al. 2022). Studies on the impact of dry seeding on weed dynamics, its ecological fitness, or its role in managing herbicide resistance have received some attention in recent years (Brim-DeForest et al. 2017b, 2022; Ceseski et al. 2022; Pittelkow et al. 2012). Brim-DeForest et al. (2017a) evaluated weed community dynamics under various water management regimes in California rice and found a greater abundance of *Echinochloa* species occurred in a dry-seeded alternate wet and dry water management regime compared to continuously flooded conditions. However, the study did not consider the relative composition of seedbanks of water-tolerant and water-intolerant *Echinochloa* species or varieties.

### *Echinochloa* in Furrow-Irrigated Rice

Furrow-irrigated rice has rapidly supplanted a significant acreage of conventional rice in recent years in Arkansas (Hardke et al. 2022) and Missouri, driven by its potential benefits in terms of simplifying crop rotations, decreasing expenses, providing more options in crop management, and conserving water. This system creates more temporal and spatial variability in moisture within the field compared to conventional practices. Furrow irrigation is expected to modulate several key factors in *Echinochloa* such as emergence, interference with rice and other weeds, response to

management interventions, and seedbank renewal. This type of irrigation is generally practiced when crops are planted in rotation, such as with soybean. To better comprehend how this production system influences *Echinochloa* population dynamics, a relatively longer-term study is required, and the ongoing research efforts should also take junglerice as a potential invader of furrow-irrigated fields into consideration.

### Future Directions for Research and its Management

In protecting yield loss from weeds, particularly from *Echinochloa* species, exciting and depressing moments have both occurred over the course of commercial rice production in the United States. While deep water-seeding saved the growing rice industry in the early 20th century, the discovery of chemicals that selectively killed *Echinochloa* and other weeds in U.S. rice fields has played a vital role in realizing the monumental gain in rice productivity made possible by improved production practices and the use of advanced genotypes in the last six decades. The U.S. rice industry experienced a “golden period” of weed control in the 1980s when just two herbicides, often only one of which was active against *Echinochloa*, would keep all the weeds in rice fields at bay. In just six decades of chemical weed management, rice growers today have options for more than a half dozen different MOAs to choose from to target *Echinochloa* (Barber et al. 2022). However, as indicated by the recent herbicide screening assays, many populations of *Echinochloa* possess resistance to multiple MOAs of herbicides. The selection of multiple herbicide resistance in *Echinochloa* species has promoted the development or usage of already available herbicides, but they afford only a partial answer to the weed problem. It might seem intuitive that many herbicides are available or becoming available to target *Echinochloa*, yet herbicides overlap in their target sites, the mechanism that determines their fate within the plant system, and the way that cellular machinery protects against suffering damage from them. Hence, the selection of mechanisms, especially those that confer the ability to metabolize a broad range of chemical classes, has the potential to render multiple herbicides ineffective. Because the number of herbicide options for *Echinochloa* control is limited, rice production in the U.S. is becoming more vulnerable to losses from these weeds. The need for an IWM strategy to address *Echinochloa* issues in US rice is evident. For a more *Echinochloa*-resistant agroecosystem that dilutes selection from chemical intervention measures, dynamic integration of nonchemical components is important and an apparent future direction. Research efforts into nonchemical practices must gain momentum in the United States as well as globally, especially in light of *Echinochloa* resistance to herbicides, even those recently introduced. As we enter new endeavors for *Echinochloa* management, a greater understanding is needed of the adaptive features of the seed biology of such ecologically differentiated *Echinochloa* types/varieties in varying agroecosystems. Effective management of *Echinochloa* should rely on knowledge of its population dynamics, including its reproductive potential as affected by chemical and nonchemical intervention efforts. Such knowledge will be useful for manipulating several crop production practices as valuable tools in IWM practices.

Our experience with introduced *Echinochloa* species clearly indicates that spread and local adaptation are continuous, ongoing processes. Fifty years ago, some water-tolerant *Echinochloa* species were unknown in U.S. rice fields, and for the last four decades, they have been serious concerns in Californian rice fields. Seemingly,

some *Echinochloa* species have been highly adapted to exploit new opportunities provided by changes in management practices in rice fields. It is to be expected that their response to fundamental selection forces such as changes in crop management practices and the consequential evolution to herbicides will continue to determine the future of the *Echinochloa* species in U.S. rice fields. The features and adaptations that the surviving *Echinochloa* plants pick up in this fight will continue to be the immediate issues that U.S. rice producers will face. Therefore, *Echinochloa* management, as with other weeds, involves the management of selection pressures. The past and present of *Echinochloa* weeds in U.S. rice crops emphasize the need for understanding its future behavior. From a weed management and overall crop production perspective, the biggest needs for *Echinochloa* management are the prediction of seed dormancy behavior and seedling emergence pattern, identification, and development; and discovering the most effective use of chemical and nonchemical interventions. Finally, *Echinochloa* seeds must be prevented from returning to the soil. A modeling study suggests that highly effective herbicide applications and any other efforts that minimize seedbank size are vital for preventing herbicide resistance in barnyardgrass (Bagavathiannan et al. 2014). As highlighted by Bagavathiannan and Norsworthy (2012), such efforts should take late-season seed production into account. It is also crucial that effective control interventions reflect how they affect weed fecundity (Norsworthy et al. 2018).

Research on the diversity in *Echinochloa* species driven by management practices in recent decades should continue. Properly construed, the apparent increase in abundance of some species/types acknowledges the need to distinguish and respond to them. Studies on a wider selection of samples is needed so as to elucidate the extent of the diversity in the *Echinochloa* species, which will lead to the development of prudent management strategies. Using genomics, researchers might study how genetic changes, particularly those that associate with their persistence mechanisms in agroecosystems, have occurred after the multiple introductions of *Echinochloa* species into U.S. rice and how many resulted from hybridizations among them. A comprehensive genome analysis of *Echinochloa* that have adapted to U.S. rice fields would probably enable the reconstruction of the evolutionary trajectory of *Echinochloa* species/varieties, shed light on the developmental origins of diversity in morphological and physiological traits since introduction, and pinpoint the scope and significance of gene flow in the diversification of adaptive mechanisms under various cultural and herbicide interventional regimes.

Obvious historical factors that have determined the persistence and abundance of *Echinochloa* species, varieties, or ecotypes in U.S. rice crops are the seeding method, water management, land preparation, type and use pattern of herbicides, and their interactions. Those are the ecological or crop production factors that matter most, as they can determine whether, when, and where one or the other *Echinochloa* species fail or prosper; which production systems are resistant or liable to infestation by a particular species or variety; the impacts that they cause; and the approaches through which they can be managed. Long-term studies comparing the reproductive success of a wide pool of *Echinochloa* species under varying production systems, taking shifting production practices into account, would provide insight for actions that need to be taken to sustainably manage *Echinochloa*. Recognizing and implementing ecological and evolutionary principles being the central priority, future research and the efforts should, therefore, lead to its sustainable management through 1) a better understanding of their biology

and ecology pertinent to their persistence in the rice agroecosystems of the respective regions; 2) reproductive and genetic mechanisms that drive herbicide resistance evolution, especially that of multiple herbicide resistance; and 3) innovations or new approaches that expand the number of control strategies and effectively disrupt the process of their adaptations, including evolution of resistance to herbicides.

## Summary

1. The discovery of chemicals that selectively killed *Echinochloa* and other weeds in U.S. rice fields has played a vital role in protecting yield from the monumentally improved productivity of rice in the past several decades. Yet *Echinochloa* species have been a constant concern and immediate issue for U.S. rice production.
2. The spread and regional adaptation of *Echinochloa* species in U.S. rice fields have been a rapid, continuous, and ongoing process. The trajectory of adaptations that the survivors will pick up in the future rice agroecosystems needs to be curtailed with a greater variety of selective forces.
3. The major adaptation—resistance to multiple MOAs—has promoted the development of new or usage of already available herbicides, affording only a partial answer to the weed problem.
4. As new herbicides are not effectively expanding the diversity of selective forces for *Echinochloa* control, rice production in the United States is becoming more vulnerable to weed losses. Henceforth, “dynamic” integration of nonchemical components into the weed management to a potential level is evidently important.
5. *Echinochloa* management should rely on knowledge of its population dynamics, including its reproductive potential as affected by chemical and nonchemical intervention efforts.
6. The changing relative abundance and increasing complexities in forms in *Echinochloa* species in recent decades indicate an urgent need to reduce the ambiguities regarding its extent.
7. A comprehensive analysis of genomes of *Echinochloa* species/types that have adapted in U.S. rice fields could shed light on the developmental origins of diversity in morphological and physiological traits and pinpoint the scope and significance of gene flow.
8. The seeding method, water management, land preparation, weed control technology, and their interactions are the major determinants of the persistence and abundance of *Echinochloa* species in U.S. rice production. Future research should lead to sustainable management of *Echinochloa* through a better understanding of its adaptation and persistence mechanisms, as well as identifying ways to intensify chemical and nonchemical selective forces.

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