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An Emerging Constraint to Global Rice Production: Weedy (Red) Rice.

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Abstract. Ongoing increases in the human population necessitate that rice will continue to be an essential aspect of food security for the 21st century. While production must increase in the coming decades to meet demand, such increases will be accompanied by diminished natural resources and rising production costs that will alter how rice is grown and managed. Such resource constraints are the impetus for the current transition from traditional flooding and transplanting to direct-seeded rice (DSR). However, such a transition can result in an increase in pest pressures, especially weeds. Rice production, can be particularly vulnerable to weed competition, with significant yield losses (i.e. >50%) occurring. Among pernicious weeds, weedy (red) rice (Oryza sativa L.) is increasingly recognized as a major constraint in achieving maximum yields in DSR. This is due, in part, to its phenotypic similarity to cultivated rice lines, and its ability to negatively influence qualitative and quantitative aspects of production. As rice will continue to serve as a cornerstone for future food security, a comprehensive assessment of weedy rice impacts associated with increasing adoption of DSR is both timely and critical. In this review, we examine the biological basis for the competitive ability of weedy rice, including its evolution, ecophysiology and genetics; quantify spatial-temporal shifts in its distribution and spread; and emphasize and outline a number of regional and global management strategies for its detection and control. Lastly, we suggest a number of critical research areas that deserve additional scrutiny with respect to weedy rice management.
INTRODUCTION.

Rice production has been described as the world’s single most important economic activity with more than two billion people dependent on rice as their primary source of calories. Accordingly, any factor that negatively impacts rice production is deserving of considerable public concern and scientific scrutiny.

One such factor is a rapid cultural shift from flooded / transplanted rice to direct-seeded rice (DSR). This shift, which appears to be happening globally, is expanding the biological niche of weedy or red rice, a significant and known constraint in rice production systems. In this review we utilize a broad range of international expertise to examine: the basis for the rapid adoption of DSR, the resulting consequences with respect to weedy rice biology, evolution and distribution; and, current / future weed management strategies that can limit weedy rice constraints in rice production. Our overall goal is to provide a scientific basis to enable interested stakeholders to develop weedy rice management options that can maintain---and sustain---DSR cultivation. Given the importance of rice as a basic staple of human consumption, and the increasing risk posed by weedy rice as cultivation practices shift in response to changing resources, such efforts are both judicious and critical to maintaining food security in the 21st century.

BACKGROUND

Weeds and Rice Cultivation. For millennia, rice has been transplanted into standing water to reduce weed competition and maximize yields (Crawford, 2005). This practice reduces weed germination via anaerobic (flooded) conditions, while increasing resource acquisition (e.g. sunlight) from the larger, transplanted seedlings, resulting in an overall competitive advantage for rice in a monocultural system.

The basis for this system is the availability of labor for transplanting and abundant water for flooding. Recent evidence indicates a significant shift in population demographics with more people now residing in urban areas (Grimm et al., 2008). In addition, the number of people experiencing water shortages globally has increased from 9 to 35% (1960-2005, Kummu et al. 2010) due in part, to competitive intensification of water resources between urban and rural populations (Tuong et al. 2005).
Declining water tables, increasing fuel prices needed to transport water and uncertain climate conditions are likely to further exacerbate water availability (Turral et al., 2011).

As the resources needed for flooded, transplanted rice cultivation become scarce, there is increased economic pressure to shift to DSR. Direct-seeded refers to the establishment of a rice crop through seeds directly sown in the field. Dry seeds can be sown on unsaturated soils (dry seeding), or pre-germinated seeds can be sown in wet, puddle soils (wet/flooded seeding). Following germination and seedling establishment, rice can be grown as a dryland crop or kept flooded depending on the soil and climatic conditions. In general, this type of agronomic practice is prevalent in developed countries (e.g. Australia, United States) where labor and water are expensive and mechanization is readily available. Overall, DSR uses less labor, consumes less water, and has fewer methane emissions (Chauhan, 2012).

With demographic shifts and limited water availability, the application of DSR is also gaining prominence in East Asia, where the bulk of rice production (~90%) occurs. Pandey and Velasco (2002) reported that direct seeding was increasing rapidly in Asia, with 21-22% of the total rice area being DSR. This percentage is somewhat higher for India, where the DSR area was estimated at 28% (Rao et al., 2007).

However, the sustainability of DSR with respect to weed management is uncertain as the early competitive advantage of rice seedlings over emerging weeds in a flooded, transplanted system is eliminated. For example, in South Korea, DSR was initiated in the early 1990s, and adopted rapidly reaching a maximum of ~11% of total cultivation by 1995. However, by 2012, DSR had declined to less than 4% (Figure 1) due, in part, to increased weed pressures. Overall, given the ongoing shortages and increasing costs of labor and water, there will be continuing incentive to shift from traditional flooded-transplanting to DSR, but such a shift also brings with it a greater need to understand the stability and sustainability of DSR systems.
Cultivation of DSR (S. Korea)

![Cultivation of DSR (S. Korea)](image)

Figure 1. Changes in cultivated area of DSR for S. Korea since 1991.

**DSR and Weedy Rice.** Although there are clear economic advantages in establishing rice via DSR, Numerous studies have shown that the risk of yield loss from weeds in DSR is greater than transplanted rice (reviewed by Rao et al. 2007). This is significant because among pests in rice, weeds represent the greatest constraint to yield (WARDA, 1996).

Given the importance of weeds in impacting rice yields, there is understandable concern regarding how wide-scale adaptation of DSR could alter weed ecology and fecundity. Changes in management practice are likely to alter selection pressures on existing weed species within an agroecosystem via preadaptation. To date, studies suggest that rice can experience a broader spectrum of weed species under aerobic, non-flooded or partially flooded conditions compared to traditional flooded-transplant conditions (Balasubramanian and Hill, 2002). For tropically grown rice under traditional flooded conditions, average yield losses from weed competition are ca. 35% (Oerke and Dehne, 2004). In contrast, weed-induced yield losses can be as high as 100% under DSR conditions (see Figure 1, Rao et al. 2007). Overall, the implementation of DSR will represent an historical paradigm shift in weed-rice
interactions and potential production losses, potentially threatening the long-term sustainability of rice production.

Although a range of weed species is encountered, in countries where DSR is already practiced (e.g. United States, Brazil), and in countries where DSR is becoming the dominant establishment method (e.g., Vietnam, India), weedy rice is the primary constraint to rice production (Chauhan et al., 2013). For example, in adoption of DSR in S. Korea (Figure 1), weedy rice became the primary weed constraint, and significant populations of weedy rice occurred in the soil within three years, with significant production losses occurring if weedy rice populations exceeded 4 plants per m$^2$ (Tables 1, 2).

Table 1. Occurrence of weedy rice (as %) according to cultivation type from 1995-1997 for S. Korea.

<table>
<thead>
<tr>
<th>Type of Cultivation</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Machine Transplanting</td>
<td>0.0</td>
<td>0.0</td>
<td>0.6</td>
</tr>
<tr>
<td>Direct seeding, dry</td>
<td>0.1</td>
<td>15.1</td>
<td>17.7</td>
</tr>
<tr>
<td>Direct seeding, wet</td>
<td>0.2</td>
<td>10.8</td>
<td>8.2</td>
</tr>
</tbody>
</table>

Table 2. Percent reduction in rice yield as a function of the number of weedy rice individuals (No. m$^{-2}$) for both long and short grain weedy rice.

<table>
<thead>
<tr>
<th>No. Weedy rice individuals</th>
<th>% Reduction (long-grain)</th>
<th>% Reduction (short-grain)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>4</td>
<td>12</td>
<td>11</td>
</tr>
<tr>
<td>7</td>
<td>28</td>
<td>22</td>
</tr>
<tr>
<td>10</td>
<td>47</td>
<td>41</td>
</tr>
<tr>
<td>20</td>
<td>56</td>
<td>53</td>
</tr>
</tbody>
</table>

Weedy rice is characterized as genetically diverse populations of *Oryza* spp. that are similar morphologically to cultivated rice but with greater seed dormancy, longevity and seed shattering (Diarra et al. 1985, Gealy, 2005). Weedy rice often (but not exclusively) is associated with a red pericarp and can be referred to as “red” rice. While weedy rice is often classified as *Oryza sativa*, other *Oryza* species
such as *O. rufipogon*, *O. barthii*, *O. nivara* and *O. longistaminata* have also been proposed as weedy sources. Weedy rice phenotypes occur in rice growing regions globally including Africa, Asia, North and South America. Weedy rice induced production losses can be considerable (Gealy, 2005, Table 2).

**Weedy Rice Impacts.** Close phylogenetic relationships and a long-term sympatric distribution lead to biological and developmental similarities between weedy and cultivated rice through hybridization and introgression (Cao et al. 2006). As a result, weedy rice is a very effective competitor with: (1) a high degree of genetic diversity and phenotypic plasticity induced, in part, by gene flow between wild and cultivated populations, (2) the ability to produce seed with early and heavy shattering, (3) intense and prolonged seed dormancy, and (4) superior vigor and competitiveness from emergence through reproduction relative to cultivated varieties (Delouche et al. 2007). While the degree of competition and impact on rice productivity varies by genotype, soil and climatic factors; the competitive ability of one weedy rice plant can be equivalent to as many as four cultivated rice plants (Pantone and Baker 1991), and large populations of weedy rice can lead to near complete crop failure (Diarra et al. 1985). With the exception of California and Uruguay, weedy rice is the dominant weed species wherever DSR is the primary means of rice establishment (Rao et al. 2007, Chuahan et al. 2013).

**BIology of Weedy Rice.**

Traits that make weedy rice such a troublesome and persistent weed include rapid root and shoot growth, large biomass production potential (either by growing tall or producing numerous tillers), wide diversity in the timing of seed maturation, high amount of seed shattering, variation in seed dormancy, plasticity in seedling emergence, and seed longevity. For example, at cool (25 °C) or warm (30 °C) temperatures, weedy rice germinates faster and develops longer roots than older rice varieties, Maybelle and Lemont, within a week of incubation (Wague 1992). Weedy rice can also emerge from greater depth than cultivated rice (Helpert and Eastin 1978). This indicates high seedling vigor and early-season competitive ability. In the field, current improved rice varieties have higher emergence rates than 83% of weedy rice ecotypes at cooler temperatures (i.e., early April planting in the US mid-south) but the same emergence
rate as the weedy ecotypes at optimum temperatures (Shivrain et al. 2009). Seed dormancy in weedy rice contributes to lower emergence rates under suboptimal temperature. The dormancy trait is universally manifested among weedy rice ecotypes (Noldin 1995; Vidotto and Ferrero 2000; Gianinette and Cohn 2008). Not only is weedy rice generally deeply dormant, it is also reported to last up to 10 years in soil (Goss and Brown 1939). One aspect of dormancy is its impact on uniformity of emergence. Crops are bred to emerge at about the same time, which lends itself to efficient management. Weedy rice, on the other hand, has very low uniformity of emergence compared with cultivated rice at optimum field conditions (Shivrain et al. 2009). This allows weedy rice to escape from unfavorable conditions and ensures overlapping cohorts and extended period of reproduction. Under field conditions this means extended periods of competition and persistence in the soil seed bank.

Not only is the emergence pattern of weedy rice highly variable, its germination capacity (GC) also varies greatly, ranging for instance from 34% to 84% among 215 accessions of blackhull, strawhull, and brownhull ecotypes planted in the field (Burgos et al. 2011). Variability in dormancy expression is higher among blackhull than strawhull ecotypes (Do Lago 1982; Burgos et al. 2011; Tseng et al. 2013); this is supported by the higher gene diversity of dormancy-linked loci than that of strawhull populations (Tseng et al. 2013). Dark coloration of the hull has been associated with more intense seed dormancy, with blackhull generally exhibiting deeper dormancy than strawhull ecotypes (Do Lago 1982; Diarra et al. 1985; Gu et al. 2005; Tseng et al. 2013). In colder climates, the persistence of weedy rice in soil is also promoted by its high overwintering capability. When placed on the soil surface from November to April, 93% of weedy rice seeds remained viable while only 4% of cultivated rice seed survived (Baek and Chung 2012).

Temperature is a major modifier of seed dormancy expression. While the mean GC of 16 blackhull and strawhull weedy rice populations was 98% at 35°C, GC values ranged from 17% to 98% at 15°C, with an overall mean of 78% for blackhull and 87% for strawhull (Tseng et al. 2013). The interaction effect of temperature and genotype on dormancy expression is strong. And while all
accessions were driven into secondary dormancy at 1 °C (i.e., none germinated), dormancy was released when transferred to 30 °C (Tseng et al. 2013). Low temperature effects on dormancy induction and release are highly relevant in subtropical and temperate rice-growing regions. The intensity of dormancy is highest at physiological maturity (De Louche et al. 2007), also called primary dormancy. There is variability in this, but in general <5% of freshly harvested seeds germinate (Gianinetti and Cohn 2008; Tseng et al. 2013). Weedy types also vary widely in seed longevity as indicated by the 27% to 86% loss of dormancy after 6 mo of storage at 10 °C (Do Lago 1982). Overall, the impact of management strategies on reduction of weedy rice in the soil seed bank is expected to be highly variable.

Despite overcoming the seedling vigor advantage with improved cultivars, other weedy advantages prevail in addition to persistence traits. Weedy rice can acquire, and utilize, nutrients from the rhizosphere better than cultivated rice (Burgos et al. 2006; Sales et al. 2011). Weedy rice has finer roots, which are 6 times longer and with about 6 times more root tips than cultivated rice. Therefore, with a much larger root surface area and more absorptive root regions, weedy rice can absorb more nutrients than the rice cultivar. It is not surprising that, whether nitrogen availability is optimum or deficient, the concentration of N in shoot tissue of weedy rice was higher than in the rice cultivar in a non-competitive, hydroponics culture (Sales et al. 2011). In the field, when Stuttgart strawhull weedy rice was grown at 1/3 the density of ‘Drew’ rice, weedy rice continued to respond to added N (in terms of biomass production), up to 200 kg N/ha (the highest rate tested), whereas that of the cultivar already leveled at 100 kg/ha (Burgos et al. 2006). Total N accumulation in weedy rice shoots was linear up to the highest N rate used (Burgos et al. 2006). Thus, weedy rice can continue to remove N from the soil beyond that of the capacity of cultivated rice. Its capability to produce so much biomass is due to high tillering potential, tall stature, or both (Chin et al. 1999; Estorninos et al. 2002; Ferrero and Vidotto, 1999; Fischer and Ramirez 1993; Sales et al. 2011). When planted at 1/19 the density of, and in competition with inbred rice, 12 ecotypes of weedy rice produced 226 – 462 tillers/plant while the cultivar produced 250 tillers (Shivrain et al. 2009). Thus, in at least 9 of 10 cases, weedy rice tillers more than inbred rice. The tillering
The advantage of weedy rice can be overcome with competitive cultivars such as hybrid rice, which can produce the equivalent (or more) tillers than weedy ecotypes in 8 of 10 cases when planted at a density of only 6 times more than the weedy ecotypes. For every additional tiller, weedy rice ecotypes reduce yield of inbred rice by 6% to 12% in contrast to only up to 7% yield loss of hybrid rice for each additional tiller of weedy rice (Shivrain et al. 2009).

The fact that weedy rice has such great diversity not only in morphology but also in phenology and seed shattering ability exacerbates its persistence. A study of 200+ accessions revealed that some weedy rice ecotypes start flowering 56 days after planting (DAP) and some at 126 DAP (Shivrain et al. 2010). All weedy rice in the USA and perhaps worldwide would fall within this range (De Louche et al. 2007). The majority of weedy rice ecotypes flower earlier than cultivated rice. Under non-competitive conditions in Arkansas, USA, the predominant seed yields ranged from 150 – 225 g/plant (Shivrain et al. 2010). These yield potentials can be realized in the field with isolated plants or those growing on the levees and field edges with optimum soil fertility and soil moisture. Because all weedy rice ecotypes exhibit a certain degree of shattering, and shattering occurs early, the majority of weedy rice seeds fall to the ground before rice harvest. Do Lago (1982) determined that shattering starts 17 – 30 days from 50% anthesis across all hull colors. On average, blackhull starts to shatter 3 days later than the strawhull weedy rice in Mississippi, USA and it takes 2 – 9 days to reach the base of the panicle. Across the US rice belt, the onset of shattering of 15 representative ecotypes is 15 days after anthesis on average (Noldin 1995). The degree of seed shattering can vary considerably. In Vietnam, the onset of shattering ranges from 7 to 15 days after flowering and the degree of shattering varies from 19% - 94% (Chin et al. 1999). The majority of recently shattered seeds could not germinate immediately as the after-ripening studies show, but the majority can germinate after separation from the mother plant (Tseng et al. 2013). The wide range in phenological maturation of weedy rice including the early onset of shattering, deep dormancy, high diversity in dormancy expression and longevity of buried seed makes weedy rice very difficult to manage following its introduction.
THE ORIGIN, EVOLUTION AND SEED BIOLOGY OF WEEGY RICE.

With rapid adoption of DSR globally, and the resulting shift in weed demography, there is a clear and present need for increased understanding of the biological characteristics and genetics of weedy rice. Weedy rice’s status as a conspecific weed, i.e., a weed that is closely related to the crop habitat, gives special urgency to two questions about its origin and evolution. First, there is the phylogenetic origin of weedy rice: how many times has weedy rice arisen and which *Oryza* group(s) is/are the direct ancestor(s) of weedy rice? Second, there is the origin of weedy traits: within the framework of weed ancestry, what has been the source of traits and the underlying alleles that have allowed weedy rice to adapt to each agroecosystem? Addressing such questions will be essential in deriving and communicating appropriate management strategies specific to a rice growing region.

**Origins of Weedy Rice.** Because of its broad biogeographical distribution, the occurrence of weedy rice spans regions with varying *Oryza* diversity. This includes regions where different *O. sativa* cultivated varieties predominate, such as *tropical japonica, indica, aus, temperate japonica, and aromatic.* Additionally, weedy rice occurrence encompasses areas that vary in the presence of wild *Oryza* species, in particular the wild ancestor of cultivated Asia rice (*O. rufipogon/O. nivara*) and various other wild *Oryza* species. Three general routes to the origin of agricultural weeds have been proposed and can be hypothesized for weedy rice (De Wet and Harlan 1975, Vigueira et al. 2013b, Kanapecas et al. submitted): (a) de-domestication of cultivated rice giving rise to weedy rice populations; (b) hybridization between wild rice species and cultivated groups; or, (c) direct colonization of wild rice species of rice agricultural fields.

Several morphological and genetic studies have supported hypothesis (a) as more likely in determining weedy rice evolution in different world regions. For example, in regions where the japonica subspecies is predominantly cultivated, weedy rice is phenotypically ‘japonica-like’ (e.g. shorter grains, and plant height); whereas in areas where the indica subspecies is dominate, weedy rice is more ‘indica-like’ (e.g., longer grains, taller) (Bres-Patry et al. 2001, Cao et al., 2006, Cho et al., 1995; Ishikawa et al.,
2005). Likewise, microsatellite, isozyme, or single nucleotide polymorphism (SNP) markers have implicated local crops of japonica (Cao et al. 2006; Zhang et al. 2012; Sun et al. 2012; Akasaka et al. 2009; Kawasaki et al. 2009; Chung & Park 2010) or indica (Zhang et al. 2012; dos Reis Goulart et al. 2012) type in the origin of weedy rice in places ranging from China to Japan, South Korea and Brazil. De-domestication origins of weedy rice have even been demonstrated for cases where the ancestral cultivar is not local or endemic to the continent, such as in the U.S., where weedy populations descend from *aus* and *indica* cultivated varieties (Gealy et al. 2009; Londo & Schaal 2007; Reagon et al. 2010, Lawton-Rauh and Burgos 2010, Kanapeckas et al., submitted). Additionally, interactions between cultivars may have played a role in some weed origins such as Bhutan, where hybridization between *indica* and *japonica* cultivars has been proposed as the source of local weedy rice (Ishikawa et al. 2005) and in California where hybridization between *japonica* varieties has been proposed (Kanapeckas et al., submitted).

Though frequently suggested, wild *Oryza* species have not been often implicated in weedy rice origins. Studies in Thailand have documented hybridization between cultivated rice and wild *O. rufipogon* as a likely source of weedy rice origins (Prathepha 2009; Pusadee et al. 2012), which supports hypothesis (b). Other published genetic evidence of wild *Oryza* involvement in weedy rice origins is rare, giving little support to hypothesis (c) so far. However, this is likely because many studies do not include wild germplasm, or even non-local rice varieties in their sampling, making it difficult to determine shared ancestral mutations and because of reliance on low-resolution markers, which can have rampant homoplasy (independent, parallel evolution of the same mutation), making discernment of true ancestral relationships difficult. Overall, much work still remains to be done to gain an accurate and complete global picture of weedy rice origins and how different origins can relate to local geography, commodity distribution and management practices.

Despite the limited data, studies addressing the origins of weedy rice to date certainly suggest that weedy rice is a case of extreme recurrent evolution leading to independent origins of weedy rice.
genotypes across the globe. It is not surprising that a species group that has been relatively easy to breed for specific traits due to highly effective selection in specific genes leading to strong phenotypic effects can also evolve populations of weedy genotypes that rapidly and independently evolve from many genetic backgrounds and under many cultivation conditions. This makes weedy rice a formidable weed to manage but, from a research perspective, a model system for the study of the processes involved in independent, parallel and convergent evolution.

The Evolution and Biology of Weedy Traits. Weedy rice tends to possess numerous phenotypic traits that differentiate it from cultivated rice. Such traits aid in its identification in situ. It is interesting to note that, given the inferred cultivated ancestry of many weedy rice groups, many of these phenotypic traits are known to have been strongly selected against during the domestication process. A better understanding of how such traits are acquired could facilitate the development and employment of strategies to prevent the spread of existing or independent origins of weedy rice populations. Key questions relevant for such a translation of evolutionary dynamics to weedy rice mitigation include: Which phenotypic traits are common to all weedy rice populations worldwide, and which vary? What is the genetic source of weed adaptive characteristics? Are the numbers and types of genes involved in the most troublesome traits the same? In cases where convergence of weedy traits has occurred among weedy rice populations, are the same genetic mechanisms involved?

Perhaps the most iconic trait of weedy rice is the presence of a red pericarp, a characteristic common in wild Oryza species, and present in some cultivated varieties of O. sativa (Sweeney et al. 2006). Red pericarp can be a critical characteristic that makes weedy rice a more troublesome and costly problem because of its economic impact on post-harvest grain quality (Delouche et al. 2007). Other traits such as hull color, awn presence, flowering time and plant height are easily shown not to converge, as their occurrence varies considerably on a global basis (Arrieta-Espinoza et al., 2005; Gealy et al., 2009; Reagon et al., 2010, 2011).
To date, the seed-shattering trait appears to be truly convergent and may be a consistent trait that is diagnostic of weedy rice. However, quantification of this trait is sporadic with techniques using different measurement conditions making it difficult to assess to what degree weedy rice populations shatter in different regions. Still, the shattering phenotype is found in all wild Oryza species and there is evidence of very strong selection against the trait during domestication of Asian cultivated rice (Li et al., 2006; Zhang et al., 2009). The shattering trait may be necessary and sufficient for weediness, as it leads to efficient dispersal of weed seeds.

Dormancy is sometimes considered to be ubiquitous in weedy rice and is a characteristic that may convey an adaptive temporal advantage to weed groups. Weedy rice grains become developmentally arrested after embryogenesis and are shed dormant into the environment via shattering from the mother plant. The caryopsis develops dormancy before any visual evidence of red pigment formation (Cohn et al., 1984). Both the glumes (lemma and palea) and the pericarp contribute to dormancy maintenance (Cohn and Hughes, 1981; Gu et al., 2003, 2005c); dormancy of isolated embryos is uncommon. While dormancy is tightly associated with the red pericarp genetically, dormancy can also be observed in white grains (Subudhi et al., 2012). Dormancy, in turn, is influenced by: (1) seed moisture content, with <20% moisture facilitating dormancy loss via temperature-dependent dry after-ripening (Cohn and Hughes, 1981; Leopold et al., 1988); (2) the timing and extent of short-term moist chilling that can trigger germination (Gianinetti and Cohn, 2008; Tseng et al. 2013); (3) dormant seed survival under submergence, at 100% relative humidity (Cohn et al. 1984) or buried in soil (Goss and Brown, 1939; Fogliatto et al., 2010, 2011); (4) the presence of secondary dormancy and dormancy cycling among dispersed seeds (Teekachunhatean, 1985; Doherty and Cohn, 2000; Gianinetti and Cohn, 2007, 2008; Tseng et al., 2013).

While photoblastic germination has been observed in some ecotypes (Chung and Paek, 2003) and a wide variety of dormancy-breaking chemicals are effective in laboratory studies (Cohn, 2002), the factors that trigger dormancy-breaking of weedy rice in the field are unknown. The intensity or ‘depth’ of
dormancy can vary greatly among ecotypes (e.g. Tseng et al., 2013), and reports of lack of dormancy in some weedy rice populations have surfaced (Xia et al. 2011). Based upon the wide range of known ecotypic germination behavior and the quantitative genetic nature of the dormancy, it is likely that a number of environmental and genetic factors contributing to dormancy of weedy rice remain to be characterized.

While genetic studies in rice have been conducted for a number of years, the genetics of weedy rice dormancy only began in earnest with the work of Gu et al. (2003). Based on their work and that of others (e.g. Subudhi et al. 2012), up to 10 epistatic (interacting) QTL that contribute to weedy rice dormancy have been identified. Additional dormancy QTL have been found across many Oryza species and cultivars, and every rice chromosome seems to make a QTL contribution (e.g. Gu et al., 2005b; Wan et al., 2006; Jing et al., 2008; Qin et al., 2010; Ye et al., 2010; Xie et al., 2011; Marzougui et al., 2012). Overall, more than 50 putative dormancy/preharvest sprouting-resistance QTL have been found in across various Oryza species, both wild and domesticated (Qin et al., 2010), and many, but not all QTL (e.g. qSD12 for dormancy is an exception) coding for characteristics associated with weedy rice phenotypes (shattering, dormancy, dark hull color, red bran) are clustered together (Gu et al., 2005a, b).

Many years of QTL research are just starting to provide a genetic picture of weedy rice dormancy and its development. The qSD12 and qSD7-1 QTL are associated with elevated immature grain abscisic acid content; genes in the ABA synthesis pathway are upregulated during grain development, but no genes associated directly with ABA synthesis or catabolism seem to be coded within these regions (Gu et al., 2010, 2011). However, while qSD12 can be a major contributor to dormancy (Gu et al., 2004), qSD12 was not detected at all when a highly dormant straw-hulled red rice genotype was evaluated (Subudhi et al., 2012). Somyong et al. (2011) took advantage of the co-linearity of various grass genomes to present evidence suggesting that a network of the Mg-chetalase-like abscisic acid receptor, ABI1, ABI2 and various calcium signaling proteins may be associated with rice dormancy QTL. Several cloned genes of unknown function have also been associated with rice seed dormancy (Sdr4 on chromosome 7, Sugimoto
et al., 2010; DOG1 homologs on chromosomes 1 and 5, Li et al., 2011). Therefore, the complexity of weedy rice dormancy induction and maintenance is well documented at the genetic, as well as the physiological level; not every study reports the same contributing loci, seeming to be variable due to the genetic source materials used in each study and presently undefined environmental interactions.

Overall, given the limitations and lack of uniformity in phenotyping of weedy rice populations around the world, whether there is a single trait or a given combination of traits that universally defines the weedy syndrome of weedy rice remains an open question.

Similarly, we are only just now beginning to make progress in understanding the genetic origins of weedy traits. Standing ancestral variation (current mutations and alleles that existed in the crop progenitors of weedy rice) seem to be implicated in the origin of red pericarp and black hulls in weeds from the U.S. and various parts of Asia, based on studies of Rc and Bh4, the causal genes for these traits (Gross et al. 2010; Gu et al. 2011; Sun et al. 2012; Vigueira et al. 2013a). Introggression has also been found to be involved in the origin of some alleles in weed populations, such as the presence of tropical japonica alleles of the growth-related SD1 gene in some accessions of U.S. weedy rice (Reagon et al. 2011) and introgression of crop alleles of the acetolactate synthase gene (ALS) in weedy rice samples resistant to imidazolinone herbicides (dos Reis Goulart et al. 2012).

An intriguing puzzle is posed by the shattering trait, which is not a trait present in the crop ancestors of many weedy rice populations. Loss of seed shattering in cultivated rice is attributed to a mutation in the Sh4 gene, which is involved in the degradation of the abscission layer between the grain and the pedicel (Li et al. 2006; Lin et al. 2007; Zhang et al. 2009). Surprisingly, despite freely dispersing their seeds, weedy rice populations in the U.S., Japan, China and assorted samples from populations in Europe, Brazil and other countries in Asia have been shown to carry the derived reduced-function alleles present in their crop ancestors (Thurber et al. 2010; Akasaka et al. 2011; Sun et al. 2012; Zhu et al. 2012). This suggests that many weedy rice populations have not re-evolved the shattering trait through reversions to an ancestral functional allele, a conclusion that is supported by developmental differences in
the shattering phenotype between weeds and wild *O. rufipogon* (Thurber *et al.* 2011). Interestingly, mapping results of weed x crop crosses, also suggest that two weedy rice populations in the U.S. have re-evolved the shattering phenotype using different genetic mechanisms (Thurber *et al.* 2013). Taken together, this suggests that genetic convergence is not a necessary feature of weedy trait evolution. This suggests that there are several possible routes to the same result; i.e. highly adaptable *Oryza* genotypes that evolve quickly and lead to co-existence of crop rice and weedy rice from different sources. Thus, stewardship and management of rice cultivation must consider both external and internal sources of weedy rice populations.

**PAST, PRESENT AND FUTURE DISTRIBUTION.**

**Past Trends.** Rice cultivation in the Americas did not rely upon the traditional flooding-transplant culture of Asia and as a result, was among the first systems to experience the negative impacts of weedy rice. After having been grown in Puerto Rico in the Caribbean area as early as 1535 (Lentini and Espinoza, 2005), rice was first grown in the United States in what is now North Carolina and South Carolina at the end of the 17th century (Constantan 1960; Delouche *et al.* 2007). Different red rice biotypes, including “strawhull” and “blackhull”, as well as “crosses” between rice and red rice, had been described in the U.S. by the mid 1800s, but the initial introductions of red rice-contaminated seed, apparently from the Indian subcontinent, probably occurred much earlier (Delouche *et al.* 2007).

Since the inception of cultivated rice, the transplant-flooded culture system has kept weedy rice impacts on yield at acceptable levels for most of Asia. However, as DSR practices replace the transplant culture, the introduction and establishment of weedy rice (as contaminants, or through wild, cultivated crosses) has become a pervasive and serious check on rice yields (Delouche *et al.* 2007). Adaptation of DSR in Asia therefore places greater emphasis on the control of weedy rice as a destructive weed.

In one of the few studies to document changing weed demographics associated in transitioning from transplant-flooded to DSR, Rao *et al.* (2007) relates data from Azmi and Mashor (1995) on changes in weed flora over a 12 year period in Malaysia. In transplanted rice in 1989, a total of 46 weed species
were present, with the flora dominated by *Sagittaria guayenensis*, *Monochoria vaginalis*, *Limnocharis flava* and *Fimbristylis miliacea*. However by 2001, weedy rice was the most dominant weed, followed by *Echinochloa* spp. and *Leptochloa chinensis*. The shift in weed demographics associated with implementation of DSR (e.g. from dicotyledonous to competitive “grassy” weeds from 1989 to 2001) has been associated with the enhanced and continuous use of herbicides for weed control in DSR (Azmi and Baki, 1995; Ho, 1998).

**Current Distribution.**

Presently, the main rice producing areas in the U.S. are in Arkansas (AR, ~49%), Louisiana (LA, ~17%), and California (CA, ~14%), along with Mississippi (MS), Missouri (MO), and Texas (TX). Weedy red rice is a major economic problem in all of these states, except for CA. LA has the greatest red rice problem with essentially 100% of the rice infested, ~70% severely (J. Saichuk, personal communication). In TX 75-80% of the rice is infested with red rice, 50% severely (G. McCauley, personal communication). In AR, a 2006 survey found that >60% of fields were infested (26% severely) with red rice prior to the introduction of herbicide- resistant rice (Burgos et al. 2008).

For Latin America, the extent and severity varies within and between countries with substantial rice cultivation. Weedy rice infestation is a chronic problem in Rio Grande do Sul, an important rice production area in Brazil; whereas in Uruguay, weedy rice impacts can be minimal (Valverde, 2005, Sudianto et al. 2013).

In Southern Europe and the Mediterranean region, weedy rice began to be considered a significant problem with the implementation of direct seeding approximately 50 years ago (Ferrero and Vidotto, 1999). The impact of weedy rice may have been further exacerbated with the adoption of less-competitive semi-dwarf “indica-type” rice lines and rice monoculture about 25-30 years ago (Delouche et al. 2007). Weedy rice induced crop losses can be considerable (>50%) in Portugal, Spain and the Rhone Valley (Barreda et al., 1999; Mouret, 1999).
There has been a recent emphasis on intensification and commercialization of rice culture in West Africa and the sub-Saharan region (Sakurai, 2006). However, introduction and contamination of new varieties, increasing irrigation, mechanization and a greater emphasis on product quality is resulting in greater impacts of weedy rice in African rice systems (Delouche et al. 2007). For example, observations indicate that approximately 50 percent of the rice area in Senegal in infested with weedy rice biotypes (Diallo, 1999).

Globally, Asia remains the primary nexus of rice cultivation. For millennia, the practice of transplant-flooded rice management has kept weed populations at low levels throughout much of Asia. However recent shortages in water and labor have promoted a shift away from transplanting to DSR (Pandey and Velasco, 2002). Major problems associated with infestations of weedy rice in Asia have followed the adoption of direct seeding as an alternative method to transplanting (Rao et al, 2007). Weedy rice is found in rice fields across Asia from Sri Lanka to Korea (Kim and Ha, 2005; Rao et al 2007), and is a particular problem in parts of Thailand, Vietnam, Malaysia (Azmi et al, 2005), Sri Lanka (Abeysekara et al 2010) and Philippines (Rao and Moody, 1994). In addition to weedy rice, the wild rice (Oryza rufipogon) can also be a noxious weed and in some areas of Thailand (Maneechote et al., 2011); invasions in some fields have been so severe that occasionally crops have been abandoned. A weedy form of rice (O. sativa Luolijing) has caused serious problems in cultivated rice in Liaoning Province of China (Yu et al., 2005). For China it is likely that the percentage of direct-seeded rice varies by province; in Tianjin, Hebei, Liaoning and Heilongjiang provinces, rice is transplanted by hand or by machine but in Jiangsu, Shandong, An Hui, and Shn provinces, nearly 80 percent is direct-seeded.

It seems probable that the increase in DSR cultivation for the two principle rice growing countries in Asia, India and China (i.e., ~90% of cultivated rice area), will result in the predominance of weedy rice as the most troublesome weed in Asia. Estimates of the area managed as DSR (ca 28% for India, 5-9% for China) from 2002 indicate that DSR had been implemented on a total of 33 million (out of 150 million) hectares (Pandey and Velasco 2002). More recent estimates from China (Rui, need references
here), indicate that DSR is now practiced in about 15% of all rice planting areas in China. Although flooded-transplanting is still widely practiced, DSR is becoming the dominant method for some provinces (Figure 2).

![Adoption of DSR in China](image)

**Figure 2.** DSR cultivation area (Ha x 1000) for two Chinese provinces, Jiangsu and Zhejiang (1991-2012).

**Future Distribution.** As the rate of DSR adoption in rice cultivation in Asia has not been well quantified, the projected temporal distribution of weedy rice is uncertain. However, it is worthwhile to evaluate the underlying drivers associated with DSR management in order to appreciate its rapid adoption globally.

There can be strong economic incentives for adopting DSR when labor scarcity and wage rates increase. Depending on the production system, DSR can reduce labor requirements by up to 50% (Pandey and Velasco 2002). In addition, the water requirements of transplant flooded rice are high, with 3000-5000 L of water needed to produce 1 kg of rice. DSR in turn, can result in a significant savings and economic cost (e.g. pumping) if implemented. Increasing mechanization and the availability of rapidly maturing rice lines can also lead to double or triple cropping. Consequently, even though DSR can lead
to lower average yields per hectare relative to flooded, transplanted rice, intensification of rice cropping can lead to greater economic benefits. Overall, accurate data on the proportion of the rice area shifting to DSR has not been well-quantified; although preliminary data for China indicate that the land now under DSR cultivation has approximately doubled in the last decade. This shift is likely to continue as ongoing changes in water, labor and mechanization favor a shift in DSR implementation.

**Climate Change and Distribution.** Increased reliance on DSR in rice cultivation is also likely to be altered by, and contribute to, anthropogenic climate change. The rise of carbon dioxide, CO$_2$, and associated “greenhouse” gases could lead to a 3 to 8°C increase in global surface temperatures, with subsequent consequences on weather patterns, particularly precipitation, as well as the occurrence of extreme weather events (IPCC 2007). Mean temperatures are expected to increase with intensification of convective precipitation and acceleration of snowmelt and glacial retreat (Turral et al., 2011). This may further exacerbate both irrigation sources for rice (e.g. river flows from the Himalayas) and availability of surface water for storage and diversion as well as groundwater recharge (Turral et al., 2011). If water availability is low, or uncertain, this would serve to incentivize DSR. However, the implementation of DSR could also lessen greenhouse gas emissions by limiting the anaerobic conditions that foster methanogenesis (Neue et al., 1995). As rice cultivation via transplant-flooding is a known global contributor of methane, DSR could, potentially, result in significant reductions in methane emissions.

The recent anthropogenic driven increase in atmospheric carbon dioxide, in addition to any secondary role in surface warming, represents an upsurge of an essential resource for plants having the C$_3$ photosynthetic pathway. As such, how cultivated and weedy biotypes respond to this change is important in terms of future weed-crop competition. Evaluations of six weedy rice biotypes (RR) and six cultivated rice varieties (VR) indicated a significantly stronger growth and development response to recent and projected changes in atmospheric CO$_2$ for weedy rice (Ziska and McClung 2008); additional experimental data confirmed that rising CO$_2$ enhanced weedy rice competitiveness with greater yield reductions in cultivated rice (Ziska et al. 2010). Experimentally, recent and projected increases in atmospheric CO$_2$
enhanced the flow of genes from wild, weedy rice to a genetically altered, herbicide resistant, cultivated population, with outcrossing increasing from 0.22% to 0.71% (Ziska et al. 2012). The observed differential responses resulted in a subsequent increase in rice dedomestication and a greater number of weedy, herbicide-resistant hybrid progeny.

**MANAGEMENT OF WEEDY RICE IN DSR.**

Clearly, there are a number of short-term advantages to DSR. However, whether or not DSR succeeds as a viable long-term alternative to transplant flooding will be determined by the sustainability of weed management, particularly in regard to weedy rice. Such management, in turn, consists of two overarching strategies: First, to prevent the introduction of weedy rice; and second, to control its spread and economic impact following establishment.

**Detection and Prevention.** We begin by emphasizing that early detection of weedy rice is the best strategy for controlling infestations. To that end, management tools that focus on early detection and population mapping are crucial. Unfortunately, the occurrence and temporal distribution of weedy rice has not been well documented. Such documentation should, theoretically, increase in utilization with the spread of technology, such as mobile phones and/or other social networks that can inform the public of weedy rice distribution both locally and regionally. However, at present, we are unaware of any such effort. Yet, identification of the leading edges of weedy rice infestations and of data gaps in existing distribution maps would be of immense value in DSR and appropriate weed management practices.

It is widely acknowledged that planting certified seed free of weedy rice contamination is the most efficacious means to prevent the introduction and spread of red rice (Gealy et al. 2003). In an interesting case study in Mississippi, the planted rice area more than doubled within a few years in the early 1970s when the federal government relaxed controls on the area planted to rice. This led to a rapid expansion of red rice infestations, which had previously been uncommon in the state, apparently because the demand for seed rice so greatly outpaced the availability of high quality certified seed; consequently, growers were forced to use low quality seed from out-of-state sources that were sometimes contaminated
with red rice (Delouche et al. 2007). Commercial and academic researchers have continued to stress that high-quality assurance standards are essential in producing weed-free seed for DSR cultivation.

Chemical Control, Herbicide-Resistant Rice. Clearfield rice production technology has dramatically changed the control of weedy rice. Because rice and weedy rice are closely related genetically, development of a conventional rice herbicide that will control weedy rice without injuring commercial rice has been difficult. Louisiana State University (LSU) AgCenter Rice Research Station in Crowley, Louisiana employed a process known as induced mutation breeding, subjecting a large number of seed to various agents in order to induce a range of mutations that could be tested for herbicide resistance. After 12 years of this process (and billions of rice seed), a single resistant line 93-AS-3510 used for the transference of the ALS (acetolactate synthase) gene mutation G654E for the cultivars Clearfield 121 and Clearfield 141 in 2002 in the USA and for the cultivar IRGA 422 CL in 2003 in Brazil (Rao et al. 2007; Roso et al. 2010a). This resistance to imidazolinones was developed from a single rice plant that survived a chemically induced mutation trial in 1993 (Sanders et al., 1998). These cultivars are regarded as non-transgenic as they are derived via seed mutagenesis rather than through genetic modification. Two transgenic rice lines were also developed, Liberty Link and Roundup Ready (transgenic with respect to glufosinate and glyphosate, respectively); however, no transgenic rice cultivars have been approved for commercial cultivation for any country. Overall, cultivated rice containing herbicide resistance (currently marketed by BASF as “Clearfield”), is an important facilitator in maintaining production in weed-free DSR cultivation.

However, because weedy rice is the same genus and species as cultivated rice there can be significant gene flow between weedy rice and herbicide resistant rice (Shivrain et al. 2010). The level of herbicide resistance in rice cultivars carrying the ALS mutations S653N and A122T is higher than G654E (Avila et al., 2005, Roso et al. 2010b). For the cultivars carrying the mutation G654E the level of resistance is marginal and is very close to the doses necessary to control weedy rice. Several environmental and application factors could contribute to the spread of these mutations, which, in turn,
facilitate the rapid distribution of herbicide resistance in weedy rice. Onset of herbicide-resistant cultivars should be based on the mutations that provide a higher level of resistance in order to facilitate the use of herbicides in a certain doses that avoid the occurrence of weedy rice escapees. In addition, the use of the imidazolinone herbicides at pre and post-emergence should be preferred instead of only at pre-emergence.

Clearfield lines have been used extensively in Brazil, Europe and the Southern United States. While the rate of natural outcrossing among rice plants is generally low (i.e. <1.0%), once hybrids form they may introgress into weedy rice populations within a few generations (Gealy et al. 2003); furthermore, it does not take much gene flow to spread adaptive mutations (Lawton-Rauh 2008). The ability to survive herbicide applications would not require a very strong selection coefficient, and would, as a consequence, result in a strong selective, competitive advantage for such hybrids. At present, the occurrence of such imazethapyr-resistant hybrids has been observed in almost all areas where Clearfield lines are grown, including the southern the United States (Burgos et al. 2008), Brazil (Rosso et al., 2010a), Italy (Scarabel et al, 2012) and Greece (Kaloumenos et al., 2013).

A paternity exclusion analysis based on SSR (simple sequence repeated) markers indicated that independent evolution and gene flow from the imidazolinone resistant cultivars were the origin of resistance in 1% and 99% of the resistant red rice plants, respectively (Goulart at al., 2012). In addition, weedy rice individuals resulting from gene flow from the herbicide- resistant cultivars had shown fitness advantages related with faster germination (Goulart et al., 2012b) and taller plants (Srivrain et al. 2006). These fitness advantages could result in faster establishment and higher competition of the herbicide resistant individuals in comparison with the susceptible weedy rice or with the cultivated rice. Gene exchange and the spread of herbicide-resistance in weedy rice suggests that wide-scale adoption of transgenic herbicide resistance rice as a means to control weedy rice will be limited unless biotechnological solutions could be used to decrease the occurrence of gene flow.

**Chemical Control, Conventional.** Conventional chemical control, i.e., not based on the application of Clearfield technology, can also be utilized in the control of weedy rice. Such control can be applied in
both monoculture and in rotational cropping systems. Chemical control is primarily utilized pre-planting, usually with application of pre- or post-emergent herbicides applied in combination with stale seed bed practices.

In rice growing regions in Europe, the most versatile pre-emergent herbicide is flufenacet, which is applied to flooded fields about one month before rice planting to avoid crop injuries and planting delays (Maneechote et al., 2006; Vidotto and Ferrero, 2009). Although flufenacet only has a control rate of weedy suppression of 70-80%, it represents a useful means of chemical weed control because it allows the application of routine management techniques without any delay in planting time. The only requirement is that it should be applied at least 25-30 days prior to planting to avoid possible crop damage. Interestingly, recent studies report that the herbicide pretilachlor, commonly used for early post-emergence control of grasses, can be potentially applied on weede-sown DSR for pre-emergence control of weedy rice (Shen et al. 2013). In Latin America a similar system is used in some countries with the herbicides oxyfluorfen and atrazine.

The combination of stale seed beds and herbicide application can be efficacious for control of weeds, including weedy rice. Stale seed bed techniques refer to the preparation of seed beds early in the season followed by flooding/dRAINING to stimulate weed germination. Following emergence, weeds can be eliminated through the application of broad-spectrum herbicides such as propaquizafop, cycloxydim, glufosinate or glyphosate (Ferrero and Vidotto 2007). After herbicide application, the water level can be raised to 15-20 cm to further weaken the weeds. Stale seed bed practices can deplete the weedy rice seed bank, and can be combined with either minimum or no-tillage in the pre-planting period. However since minimum tillage can actually enhance weedy rice seed emergence concurrent with cultivated rice, after the stale seedbed is formed, sowing should be delayed by about 30 days so as to remove any weedy rice seedlings. Because this method delays planting, cultivation is usually restricted to short-season rice varieties.
A variation of the stale seed beds is a very important strategy for weedy rice control in Brazil. The system called “needle-point” is based on minimum tillage where the field is harrowed or receives a burndown application approximately 30 days before drill seeding. A few days after seeding when the weedy rice coleoptiles are visible (but before emergence of the cultivated rice), glyphosate is reapplied. Some variations occur regarding the intensity of tillage, time between glyphosate applications and herbicide used alone or in mixtures (NEED REFERENCE).

If pre-planting treatments are ineffective in controlling weedy rice, additional chemical interventions are sometimes required during rice post-emergence. This can occur by exploiting the height differences between weedy and cultivated rice. A wiping bar, usually a sponge or rope device wetted with systemic herbicides (e.g. glyphosate), is passed over the field as a means to apply the herbicide to the taller weedy rice plants (Ferrero and Vidotto 2007). However, this method can be labor and time consuming and of limited efficacy in highly infested fields.

Non-Chemical Control. The use of tillage (plowing, disking, harrowing, etc.) is indispensable to physical weed removal and in providing a weed-free seedbed for planning. Consequently, the judicious use of tillage (i.e., depth, occurrence, etc.) can be an efficacious means to reduce weedy rice populations over time. For both wet and dry DSR, it has been demonstrated that increasing the number of tillage operations can reduce weed infestation with concomitant increases in rice yield (Sharma 1997). Dry land tillage is commonly practiced in DSR in the United States, southern Australia, most of Latin America, Europe, West Africa and regions in tropical Asia. In general, it can be described as 1-2 diskings to 10-20 cm followed by 2-3 harrowings and, if necessary, a roller-packer to break up big clods followed by land leveling (Anon, 1990). The formation of stale seed beds can also be used with shallow tillage (rather than herbicides) prior to sowing. Care should be taken however, to minimize disturbance so as not avoid exposure of weedy rice seeds to light or other germination stimuli. Additional mechanical control can be utilized either through inter-row cultivation following emergence, or through chopping; where taller weedy rice panicles are removed (chopped) before seed set occurs.
Adoption of zero or no-till conditions can alter weed demographics, with a greater percentage of grassy weeds occurring when compared to dry land tillage (Tuong et al. 2005). Minimum tillage can vary with and without utilization of Clearfield technology. Without Clearfield lines, the use of a cover crop with minimal soil disturbance can be efficient in suppressing weedy rice, but it is very dependent on climatic conditions occurring between drilling and permanent flood (Andres et al. 1997, Marchesan et al. 1998, Avila et al. 2000). If Clearfield is included with minimum tillage practices control of weedy rice can also be achieved (Villa et al., 2006, Sartori et al. 2013). However, control will be dependent on those management practices that affect herbicide efficacy including early sowing and flooding management.

Water management is another cultural alternative for the control of weedy rice. Flooding level fields prior to seeding may help to suppress weedy rice emergence and/or reduce weed seed longevity in the soil. Early flood establishment following crop emergence can also help in suppressing weedy rice (Marchesan et al. 2007, Chauhan et al. 2013). The depth of flooding is also a factor regarding the survival and growth of weedy species in DSR (Kent and Johnson 2001). Shifting back to transplant-flooded after 3-4 years of DSR may also help minimize weedy rice populations and/or reduce the weedy rice seed bank (Chauhan et al. 2013).

Post-harvest management may be another valuable tool to manage weedy rice. If shattered weedy rice seeds are left on the surface, this can promote predation and enhance seed degradation (Marchesan et al. 2003, Fogliatto et al. 2011). Alternatively, post-harvest tillage can reduce the weedy seed bank but only if seed burial is sufficiently deep (Massoni et al. 2013). An additional technique is to maintain flooding during winter months. Flooded rice can increase predation of weedy rice seed by attracting birds as well as through seed degradation (Fogliatto et al. 2010). Such a strategy also can promote wildlife conservation of rice areas (Manley 2008).

Cultivar selection may be another effective management tool. Cultivars with dynamic initial growth can compete better and help to suppress weedy rice emergence. For example, in Malaysia, taller cultivars with greater tillering reduced the weedy rice population (Azmi and Abdullah, 1998). Selection
of cultivars with colored stems or leaves may also help to distinguish cultivated from weedy rice following emergence and thus help in the identification and hand removal of weedy rice (Kaushik et al. 2011).

Practices that influence cultivated rice growth and canopy closure such as seeding rate and row spacing can also reduce weedy rice infestations by promoting rapid canopy closure and reduced light levels. For DSR fields infested with weedy rice, increasing the seeding rate fourfold resulted in an increase in grain yield (Azmi et al. 2000). Similarly, line sowing rather than broadcasting can help in the identification and removal of weedy rice seedlings that emerge between rows (Chauhan et al. 2013).

As with many pest populations, utilizing crop rotation can interrupt the weedy rice life cycle and reduce economic impacts. Effective weed control can be enhanced by rotating rice with other economically viable crops such as soybean, cotton, maize, etc. Although not always practiced in South America, it can be an effective practice. In Uruguay for example, weedy rice populations are low in DSR due to rotations with pastures. (Scavino et al. 2013). For Brazil, two years of non-rice cultivation with soybean, corn or sorghum can reduce weedy rice by ca. 90% (Avila et al. 2000).

Although labor-intensive, and thus unlikely to occur in DSR cultivation, hand weeding or rouging may be a viable alternative for small fields and/or family farms. While tedious and time consuming, it can improve economic benefits by improving quality. Rouging is most effective however, if done prior to seed shattering of weedy rice.

**Integrated Weedy Rice Management.** Different management strategies for keeping weedy rice population(s) in check reflect a range of cultural and physical environments. There is not, and perhaps there never will be, a perfect technology for weedy rice management, particularly given its genetic proximity with cultivated rice. Therefore, while some practices may be more effective than others, sustainable control of weedy rice should include integration of all existing technologies.

Integrated weed management (IWM), is a strategy designed to utilize all management tools in a series of evaluations that begin with monitoring, threat assessment, application of control measures and
follow-up. Population monitoring (e.g. is weedy rice in the region? where is it in relation to my field?) is critical to distinguish significant from routine threats. Secondly, an action threshold must be determined beforehand, i.e. how high can the weedy rice population get before action (control) is required?. Third, prevention is emphasized, so that cultural methods, e.g. exclusive use of weed-free seed, cleaning of farm equipment to prevent dispersion, etc., are routinely practiced. If monitoring, identification and action thresholds indicate that weedy rice is a threat and control is required, then a management decision is made. Such decisions should reflect an understanding of the potential cost, environmental damage and efficacy. Control strategies may include a combination of methods to reduce weedy rice populations to acceptable levels. Following application of control method(s), evaluations of the efficacy of the technique should be incorporated into future management decisions. Such an approach can provide flexibility and continuity to weedy rice management. An integrated strategy may represent an evolving system that could, with proper feedback, provide a useful and effective management tool for control of weedy rice in DSR systems.

**EMERGING MANAGEMENT STRATEGIES.**

Current strategies for limiting the damage of weedy rice are of obvious importance. The adoption of new and innovative approaches to weed management will, however, be necessary if DSR cultivation is to be sustainable on a global basis. As such, this need should be reflected in efforts by the research and extension community to assess innovative and integrative approaches that minimize weed pressures associated with shifts from transplant flooded to DSR.

**Biotechnology and Transgenic Herbicides.** While non-chemical means for control of weedy rice are available, economics will continue as a major driving force for simple and cost-effective means in controlling weedy rice. As such, herbicide-resistant rice should be included as a potential solution to the weedy rice problem in DSR systems.

While gene flow and the transfer of herbicide resistance are of obvious concern, development of new lines of Clearfield is ongoing. Such development is similar to development of new rice varieties in
general with the exception that breeding populations are sprayed with imazethapyr in each generation to eliminate non-resistant segregates. Promising lines are treated with a 3X rate of imazethapyr at the 2-3 leaf stage. After bulk-harvesting to determine yield potential, superior lines are entered into the initial yield testing program, which is typically a small plot between 5-15 m². These small plots are evaluated to determine if any yield differences expressed are a result of true genetic differences and not by environment (e.g., soil type, fertility, etc.). Finally lines that demonstrated superior herbicide resistance and desirable yield characteristics are advanced to multi-location trials. Generally, at least three years of such trials is necessary before an experimental line is considered for release as a new variety.

Transgenic herbicide resistance need not have the same ephemeral fate as herbicide resistance via chemical mutagenesis if failsafe mechanisms are built in that prevent gene flow (i.e. containment), or assure that post facto gene flow does not establish and spread (i.e. mitigation). It was once thought that transforming herbicide-resistance encoding transgenes into chloroplasts would prevent gene flow due to maternal inheritance of chloroplast encoded traits (Lee and Natesan 2006). However, such a concept ignores the fact that the taller weedy rice is a predominant pollen parent in crosses and backcrosses, and chloroplast encoded traits could therefore be easily integrated into weedy rice. Consequently, this leaves mitigation as the best option to prevent herbicide resistance (or other desirable transgenes) from establishing as a major factor in weedy rice populations.

Transgenic mitigation depends on the tandem coupling of a gene that confers unfitness in the weed (but not the crop). Consequently whenever the weed introgresses the herbicide resistance gene, it also introgresses the unfitness gene. This unfitness limits hybrids and their progeny to a minuscule proportion of the overall population (Gressel, 1999). Two types of such unfitness genes have been proposed; genes for biological traits (Gressel, 1999; Gressel and Valverde, 2009) and genes for biochemical traits (Lin et al. 2008).

The biological traits proposed are genes such as dwarfing genes, which will not affect already dwarfed cultivars, but will render the weedy rice less competitive with its weedy cohorts and lower
mitigated rice to the same playing field as the cultivars. This has already been utilized in a model system (tobacco) (Al-Ahmad et al., 2004; 2005), as well as with oilseed rape in confinement (Al-Ahmad and Gressel 2006) and in the field (Rose et al., 2009). A potentially more effective mitigation gene is the incorporation of various anti-seed shattering genes which would prevent the weed from reseeding itself.

As in many cases of de-domestication to feral types, the gene that confers a feral trait may not be the same gene that was selected for during domestication. Thus, there is some evidence that de-domesticated shattering is not controlled by the same gene that mutated to non-shattering during domestication (Thurber et al., 2010; Zhu et al., 2012). Additionally, shattering is likely to have a different genetic basis in different weedy rice populations (Thurber et al., 2013). Thus, globally appropriate anti-shattering genes would first have to be identified to make this a viable option in all weedy rice populations. Transgenically suppressing the yet unknown gene(s) controlling secondary dormancy could also be used as mitigation. If secondary dormancy is abolished, weedy rice can be eliminated prior to planting rice.

Biochemical mitigation is based on introducing a gene that prevents degradation of an herbicide occasionally used in rice (Gressel and Valverde, 2009; Lin et al. 2008). The antisense or RNAi construct is engineered in tandem with a gene for resistance to a previously nonselective herbicide. Transgenic rice containing the tandem construct is rotated with wild type rice, where the herbicide that controls only the weedy rice is used (Lin et al., 2008). This concept was further refined into having a series of rice varieties, each having transgenic metabolic resistance to one herbicide and super-sensitivity to two others (Gressel and Valverde, 2009). By using the appropriate herbicide with each variety, native weedy rice and weedy rice that introgressed the previous varieties transgenes are controlled (Gressel and Valverde, 2009) (Figure 3).

The development of the relevant varieties and their implementation will require considerable industry cooperation and grower training but could facilitate long-term control of weedy rice without the evolution of resistant populations. This would clearly be of benefit to both growers and the chemical and
seed industries. Potentially longer duration sustainability of the system could be obtained by combining biological and biochemical trait mitigation.

A more advanced means of formulating transgenic herbicide resistance is to introduce the mitigator genes in the cultivated rice using a multicopy transposon. This is a derivative of a concept, TAC-TICS (Transposons with Armed Cassette-Targeted Insect Control Strategies) designed to induce a lethal gene (controlled by an inducible promotion) into a transposon and then engineer that transposon into multiple copies within the insect pest (Grigliatti et al. 2001). A parallel modification to this approach would be to put the mitigators for herbicide susceptibility in a transposon in the same domestic rice varieties with herbicide resistance (Figure 3), instead of in tandem. The advantage of multi-copy transposons is that all progeny (backcrossed as well as selfed) contain the transposon and not just a fraction of them; there is no segregation. Thus, the herbicide supersusceptibility will spread to a larger proportion of the weedy rice population than transgenic herbicide resistance per se, facilitating further diminution of the weedy rice population, including weedy rice at paddy borders that are not always sprayed with herbicides. Transposons are typically silenced by small interfering siRNAs that either degrade or methylate transposon transcripts or repress their translation. The siRNAs can also silence transposons by methylation. The countermeasure to prevent such silencing has been elucidated in rice, providing the information for generating transposons that will not be silenced over time (Nosaka et al., 2012) and such technologies will have to be utilized. Such transposon technologies may sound like science fiction at present, but are clearly worthy of consideration and initial experimentation.
Figure 3. A multi-season rotation to preclude the establishment of any herbicide-resistant weedy rice from gene flow as well as prevent establishment of any evolved herbicide-resistant weed from previous rotation cycle. S=susceptible; R=resistant Source: Rotation based on concepts developed by Gressel & Valverde 2009.

Modeling Population Dynamics of Weedy Rice. As software and technology advance, the use of models to predict weedy rice impacts can assist in choosing appropriate weed management programs. Several models have been proposed for different crop-weed combinations (Gonzales-Andujar & Fernandez-Quintanilla, 1991; Colbach & Debaeke, 1998; Kim et al., 2002; Munier-Jolain et al., 2002 inter alia), including some specifically for weedy rice (Fischer & Ramirez, 1993; Vidotto et al., 2001).

The main factors that regulate weedy population dynamics are related either to traits of the weed population itself (e.g., seedbank size, seed germination), to cropping practices (e.g. soil tillage), as well as methods used in weed control (Figure 4).
Figure 4. Main factors influencing weedy rice life-cycle. Symbols: □ = state variables; ↑ = fluxes; × = rates; dashed harrows: seed bank inputs; dotted harrows: seed bank outputs (modified from Vidotto et al. (2001)).

The model proposed by Vidotto et al. (2001) is mainly focused on seedbank dynamics. The main input is seed rain from weedy rice following maturity. The main outputs are emerging seedlings and those that are lost to mortality or predation. Prediction of emergence can be obtained as a simple ratio of the seedbank, considering that seedlings can originate from seeds placed up to 5 cm deep (Vidotto & Ferrero, 2000), but better estimates can be obtained by modeling the consequences of soil tillage on seed movement (Cousens & Moss, 1990; Colbach et al., 2000.) and applying a rate of emergence inversely related to the depth of burial. The number of plants that will reach maturity and eventually produce seeds can be calculated by considering the total number of seedlings per unit area in conjunction with the efficacy of the chemical or mechanical control treatments. Plants originating from weedy rice seeds carried with cultivar seed may also be an important input, in particular if weedy rice is not endemic. It should be emphasized that in the EU, current legislation allows up to about 0.030% of weedy rice grains
in commercial seed lots, which may potentially introduce ca. 2000 weedy rice seeds per hectare (considering a seeding rate of 200 kg/ha and a 1000-seed weight of 30 g).

From the number of mature plants per unit area, it is possible to estimate the number of seeds produced and shattered. This value can be estimated through a linear combination of panicles per plant, seeds per panicle, and percent shattering, assuming that these parameters are constant in the range of infestation density achieved in the field. The seeds that replenish the seedbank and can potentially generate new plants the following season may undergo considerable depletion during intercropping because of ageing, predation from small mammals, birds and arthropods (Clements et al., 1996; Noldin et al., 2006; Raatz et al., 2012). In temperate areas, autumn suicidal germination before winter can also play an important role (Fogliatto et al., 2011).

Scenario Simulation. By modeling the life cycle of weedy rice it is possible to simulate the effects of certain cropping practices on weedy rice populations. Vidotto et al. (2001) used a model of weedy rice seedbank dynamics to test the effect of soil tillage (plowing or minimum tillage) when no specific weed control measures are applied (Figure 5A). With plowing or minimum tillage, the seedbank grows abruptly after the first season. If a stale seed bed is simulated, the two soil tillage systems have an opposite effect, as minimum tillage keeps the seedbank within the initial values (Figure 5B). Temporal changes in weedy rice populations are highly influenced by the efficacy of the control treatments. Even slight changes in this parameter (e.g. from 95 to 98% control efficacy) may have a great influence on the seedbank; and may, in turn, be affected by other conditions (Figure 5C).
Figure 5. Weedy rice seed bank dynamics when A: no specific control measures are adopted; B: stale seedbed and chemical control are used; C: pre-emergence chemical control only is adopted. In A and B seedbed is prepared by plowing (left) or minimum tillage (right). The starting seed bank is 500 and 200 seeds/m² in the layer 0-10 and 10-20 cm, respectively (—), or 2000 and 500 seeds/m² in the layer 0-10 and 10-20 cm, respectively (——). In C, efficacy of the treatment is set to 95% (—) or 98% (——). From Vidotto (2004).

Modeling of weedy rice populations may be also used to compare scenarios in which rice is cultivated either in monoculture or in rotation, alternating the use of imidazolinone-resistant rice varieties (“Clearfield” varieties) with conventional varieties. It should be considered that stewardship guidelines for the use of Clearfield varieties restrict the use of these varieties in the same field for no more than one (in most countries) or two (in Italy and Brazil) consecutive years. However, this recommendation is seldom followed. In Arkansas and Mississippi, 11% of the rice hectares were planted to continuous
Clearfield from 2006 through 2011 and 42% of the rice hectares were treated solely with ALS herbicides in 2011 (Norsworthy et al. 2013).

André (2013) reported that the weedy rice seedbank required up to 17 years for complete depletion, adopting Clearfield every second year in a rice monoculture system. This interval can be reduced to 13 years by adopting the less restrictive guidelines allowed in Italy (2 consecutive years of Clearfield varieties, followed by one year of a conventional variety). Simulations inclusive of rotation with another crop, in which 100% weedy rice control is assumed (Burgos et al., 2008; Davis et al., 2011), showed significant reductions of weedy rice in the soil after 2-4 years (Table 3).

Table 3. Estimated seedbank abundance with different crop rotations (adapted from André, 2013).

<table>
<thead>
<tr>
<th>Time (Year)</th>
<th>Weedy rice abundance in soil seedbank (m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 CL / 1 CR / 1 NCL¹</td>
</tr>
<tr>
<td>0</td>
<td>1105.3</td>
</tr>
<tr>
<td>1</td>
<td>399.7</td>
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<td>2</td>
<td>146.5</td>
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<tr>
<td>3</td>
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<td>4</td>
<td>11.5</td>
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<td>5</td>
<td>4.3</td>
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<td>6</td>
<td>1.6</td>
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<tr>
<td>7</td>
<td>0.1</td>
</tr>
<tr>
<td>8</td>
<td>0.1</td>
</tr>
<tr>
<td>9</td>
<td>1.60E-02</td>
</tr>
<tr>
<td>10</td>
<td>5.56E-04</td>
</tr>
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</table>

¹four-year cycle of 2 years with Clearfield® rice variety (CL) followed by one year of crop rotation (CR), and then by an additional year with no Clearfield® rice (NCL); ²four-year cycle of one year of crop rotation (CR), 2 years with Clearfield® rice (CL), one year with no Clearfield® rice (NCL); ³four-year cycle of 2 years with crop rotation (CR), 2 years with Clearfield® rice (CL). Weedy rice control efficacy was set to 98.5%, 95% and 100% in CL, NCL and CR, respectively.
Models that highlight weedy rice biology in conjunction with land and weed management can be an effective potential tool, one that can expand concurrently with adaptation of new technology. Modeling can identify critical aspects of the weedy rice life cycle associated with soil tillage, water management, efficacy of the chemical or mechanical treatments, presence of weed grains in the commercial rice seed lots, etc. As such, there is an enhanced role for models to serve as integrative tools with respect to identifying management strategies that can, given limited resources, increase the efficacy of weedy rice control.

**FUTURE RESEARCH NEEDS.**

The transition from flooded transplanting to DSR represents a paradigm shift in the control and impact of weeds, particularly weedy rice. Consequently, there is a clear and immediate need to consider those research areas where additional information is needed regarding weed management measures that can sustain and maximize economic returns in DSR cultivation. In areas where DSR has already been adopted, increased intensification of weedy impacts also necessitates new management strategies for sustainable weed control. The following recommendations are meant to be illustrative, but not comprehensive, of those needs.

*Quantifying the spread of DSR globally and characterizing the resulting impact of weed-induced yield losses.* This information, particularly the rate of DSR adoption, is a key first step in determining the potential spread and impact of weeds and their management. Such information is especially relevant to China and India, where ~90% of cultivated rice is grown.

*Increasing our understanding of water management practices on weed population dynamics.* It is clear that globally, water resources are changing rapidly. However, additional information is necessary however to translate these changes into farmer guidelines that expand yield, reduce water use and achieve maximum weed control. This information can include, *inter alia*, the role of alternate wetting and drying on weed establishment, understanding the relationship between water depth and weed recruitment, and improved infrastructure for precision water applications and drainage.
Increasing the competitive ability of rice cultivars. Dynamic early growth is a key characteristic of improved competitiveness, but details regarding specific characteristics that are associated with such vigor and the relative importance of these in different environments and management systems are still unclear. For example, studies have suggested that early root development plays a major role in early competition (Gibson et al. 1999) but the relationship between root growth, resource uptake and utilization in rice-weedy rice competition deserves additional study.

An enhanced understanding of weedy rice evolution, biology and fecundity. More efficacious control is dependent on additional information regarding the basic genetics and biology of weedy rice biotypes/ecotypes. For example, we must identify all possible ancestral sources of weedy rice, to control for the continuing re-evolution of weedy rice groups. Similarly, identification of the genes underlying weedy traits and their origins is necessary to prevent the emergence of these traits and identify possible targets for transgenic mitigation. Additional information on rates of gene flow particularly in regard to the introduction of GM crops is essential for long-term management strategies. Identification of steps within the weedy rice life cycle (e.g. seed dormancy, shattering) that would be susceptible to cultural or chemical control is also needed. Furthermore, such information could be useful for developing models for predicting the risk of herbicide resistance evolving within weedy rice.

Development of specific biotechnological studies based on weedy rice physiology. The high similarity between cultivated and weedy rice should be considered as an advantage. Rice is one of most important plant models used in molecular studies. As such, that information could be used for specifically addressing weedy rice physiology. For example, designing dormancy-breaking chemicals for field application as a means to induce germination in weedy rice (and other weeds) in order to deplete the weedy seedbank is a potential beneficial strategy for weedy rice management. At present, however, there is more of an emphasis on applying knowledge of cultivated rice to weedy rice metabolism.

Effective development and utilization of herbicides in IWM. As DSR becomes more widespread, economic pressures will increase regarding weed management, particularly with respect to herbicide
development and utilization. Such pressures need to be considered in response to environmental regulations and public concerns regarding pesticide residues in food and water. As such, herbicide use, including the potential introduction of transgenic herbicide technologies, should be incorporated into an overall IWM strategy that can sustain profits while safeguarding health and maximizing the sustainability of weed management. However, additional information is needed to increase farmer participation in IWM, including best practice guidelines for cultural and chemical weed control.

*Model development and technological dissemination.* Models that integrate management practices, environmental parameters and plant biology can be indispensable in providing information needed for weed management at the farm level; but also in determining the efficacy of such decisions over the long-term (years). With the rapid acceptance of social media and information technology (e.g., mobile phones), the utility and information sharing possibilities of simple, regionally driven models which could track weedy rice, and provide updated information on management methods is, potentially, enormous.

*Furthering our understanding of rising CO₂ and climate change on weedy rice.* The ongoing disruption in precipitation frequency and accelerated snowmelt will have obvious negative consequences for water availability; additionally, the impetus for reducing methane emissions from rice globally may act as a further incentive for rapid adoption of DSR. However, the role of rising CO₂, temperature and precipitation on the establishment and spread of weedy rice, the possible function of CO₂ on gene transfer between weedy and cultivated rice, and the overall implications of CO₂ and climate change for competition and economic losses in cultivated rice are almost completely unknown.

**CONCLUSIONS.**

The practice of using standing water and transplantation for weedy rice suppression in cultivated rice is declining globally in response to diminishing water resources, increasing energy costs and shifting availability of labor from rural to urban areas. In response, growers have turned to DSR cultivation. DSR has a number of potential advantages; rice is more rapidly and easily planted, is less labor intensive,
consumes less water, produces less methane and matures 7-10 days earlier. Although these benefits are widely acknowledged, the use of DSR comes with a considerable risk: increasing establishment and evolution of weedy rice, a significant constraint on economic production and among the most difficult-to-control weeds in rice cultivation. Whether DSR succeeds as a viable and sustainable means to maintain rice production and by extension, global food security, will be highly dependent on the ability of weed scientists and crop physiologists to assess and develop solutions to the cultural, biological and evolutionary challenges posed by weedy rice.

In this review, we have provided a state-of-the-art assessment of what is known regarding weedy rice biology, its distribution, and the evolutionary and biological basis for its competitive facility in DSR cultivation. With respect to its management, we recognize that chemical control is likely to provide a simple and economically attractive solution and would urge additional research and development directed towards cost-effective, environmentally safe herbicides. However, we would stress that an integrative weed management approach that includes preventive measures (e.g. certified weed free seed), on-site farm management (e.g. rotation, water management), and improved rice cultivars (e.g. early vigor) should also be included in the context of chemical weed management.

Lastly, we would emphasize that any review, no matter how well intentioned, is only a temporary, static assessment. Weeds, particularly weedy rice, will change in an active fashion as rice cultivation itself changes; hence weed science and management must be both diligent and dynamic in response.
Acknowledgements: PLEASE ADD, IN ONE OR TWO SENTENCES, YOUR SPECIFIC CONTRIBUTION TO THE REVIEW AS A WHOLE. For example, LHZ contributed the section on Climate Change, integrated contributor input and led efforts in writing the review.
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