

Chapter 4

Seed shattering and dormancy in weedy rices

EARLY AND HEAVY SEED SHATTERING

The shattering of seeds as they mature in the inflorescence is the naturally selected trait of plant species that produce dry fruits and seeds and is one of the most important of the seed dispersal and distribution mechanisms in plants. Shattering increases not only the survivability but also the area distribution of the species. Retention of seeds in the inflorescence at least until they all reach maturity is the opposing trait selected at first unconsciously and later consciously by humans in the domestication and improvement of plants to permit and/or facilitate the gathering of the desired plant products: food and feed grains, oilseeds, grain legumes. The selection was at first unconscious as the early human gatherers collected grains retained on the plants for food or seed in preference to those dispersed on the ground. Conscious selection for the non-shattering trait in wheat, barley and rice 6 000–10 000 years ago was probably the first major human “improvement” in plants (Diamond, 1999).

Early and heavy seed shattering, the red pericarp and seed dormancy are the constant traits among all the diverse types and other variants of the red rices. If the reference is broadened to include all weedy rices, then seed shattering becomes the invariable trait because some weedy rices, especially in Asia and Africa, have white pericarps, and the seeds of some weedy types are not any more dormant than those of some cultivated varieties. The seeds of Nato, an older-type medium-grain variety, are as dormant as those of many red rice phenotypes for a time after harvest but dormancy is released sooner. Constantin (1960) determined seed shattering for the 1 084 red rice panicles he collected from rice fields in the southwest Louisiana rice area and stated: “No red rice panicles were found that had non-shattering spikelets characteristic of cultivated rice. All had shattering spikelets and no variation among plants was detected.” The older literature on weedy rices in Asia (Graham, 1913; Roy, 1921; Chatterjee, 1947), and red rices in North America (Nelson, 1908; Quereau, 1920; Hodges, 1957; Williams, 1956), and, generally (Grist, 1955), always emphasized the importance of the “shattering”, “shedding” or “deciduous” nature of the spikelets in the persistence and spread of weedy rices.

Seed shattering – weedy trait

The early and heavy shattering of seeds as they mature in the inflorescence is an important mechanism for their dispersal and distribution. It increases the probability that a substantial portion of the seeds produced by a plant are scattered to the surface of the soil where they can be spread further by wind and water before being consumed by animals, harvested with the grain, or eventually falling to the ground in a clump along with the plant. Shattering is the naturally selected trait of plants but, as mentioned above, it was a very inconvenient trait in plants that produced food grains desired by early humans in the gathering stage of human development. Thus, since the dawn of crop husbandry, non-shattering has been a prized trait in the selection and improvement of varieties of crops. The non-shattering trait has not been disadvantageous to the



Plate 15

Top: seed shattering of four RR phenotypes compared with the non-shattering variety Starbonnet (left). Bottom: vigour of RR manifested in tillering as compared with the Starbonnet variety (middle).

of shattering for 28 red rice phenotypes collected in Mississippi, the United States of America, in 1980 and found that the mean time of the onset of shattering was 24 days past 50-percent anthesis for all phenotypes, 23 days for the SHR group and 27 days for the BHR group. In 1981, he studied the onset of shattering for 14 selected phenotypes and also determined seed moisture content at the time of shattering (Table 9).

The mean shattering time for the BHR types was 3 days later than for the SHR types, but there was much less variation in the onset of shattering (4 days vs 13 days for

TABLE 9
Shattering time and seed moisture content of 14 rice phenotypes

Type	Hull colour	Shattering time from 50% anthesis		Seed moisture content at start of shattering	
		Mean (days)	Range	Mean (%)	Range
Com. var.	STW	NS		NS	
All reds (13)	SH & BH	24	17–30	29.4	23.0–44.2
SHR (9) *	STW	24	17–30	27.7	23.0–35.7
BHR (3)	BLK	27	25–29	27.6	24.5–31.1
BrHR red (1) *	BRN	17		44.2	

*Anthesis, shattering and maturation were quite random and irregular in the panicles of two strawhull reds (SHR) and the brownhull red (BrHR).

Source: Do Lago, 1982.

crops cultivated because their survival is dependent on human activities and not nature. However, the non-shattering trait would be disadvantageous to "wild" plants that grow in association with crops, i.e. weeds. Most of the seeds produced would be removed and destroyed by farmers or mixed in with the harvest and consumed. Farmers plant seeds of crops but not knowingly of weeds. Modern cultural practices and technologies, such as specialized seed production, mechanical harvesting, and grain and seed cleaning, have increased considerably the disadvantages of even relative non-shattering in annual wild plants or weeds growing with crops. Plate 15 compares shattering in panicles from four red rice phenotypes with the non-shattering panicle of the Starbonnet variety.

Onset of seed shattering in red rice

While seed shattering is apparently a characteristic of all weedy rices, there is considerable variation in the time and degree of shattering among the phenotypes or ecotypes. Do Lago (1982) determined the onset

the SHR group). Similarly, the mean seed moisture content at the onset of shattering was the same for the SHR and BHR groups but there was less variation among the BHR phenotypes (6.6 percent vs 12.2 percent for the SHR). These data were influenced strongly by two very atypical strawhull phenotypes and the unique brownhull red (BrHR). When they are excluded, the mean seed moisture contents and the ranges at the start of shattering are 26.4 percent, 23–31.1 percent, and 25.8 percent, 23–27.9 percent, for the remaining 10 red rice phenotypes and the 7 SHR types, respectively.

In 1981, Do Lago made a more detailed study of the time-course of shattering along the panicle for 6 red rice phenotypes, 4 SHR types and 2 BHR types. Shattering began in the tip of the panicle, as expected, as early as 16 days past 50-percent anthesis for the SHA+ phenotype and as late as 26 days for the 79/11 SHR, but shattering for the latter then progressed to the bottom of the panicle in 2 days (Table 10). The mean times for shattering to begin in the top, middle and bottom third of the panicle for 5 of the 6 phenotypes were 21, 23.4 and 26.4 days, respectively. Seed moisture content of seeds in the upper third of the panicle at the first evidence of shattering ranged from 23.5 to 31.2 percent with a mean of 27.0 percent for the 5 phenotypes. As noted in Table 10, the 79/5 BHR flowered more-or-less randomly rather than from tip to bottom of the panicle so that shattering and maturation were very non-uniform. Thus, the exceptionally high seed moisture content (42.2 percent) at the onset of shattering reflects the mixture of “drier” and “moister” seeds collected in the top third of the plant for the moisture content determination. The 27.0-percent mean moisture for the 5 phenotypes in Table 10 is 2.4 percent lower than that of the 13 phenotypes in Table 9. The difference probably reflects the greater care taken in the detailed study but mostly the inclusion of the brownhull red, coded 78/8, in the mean for the 13 phenotypes. As noted above, it exhibited the same random flowering habit as the 79/5 BHR red excluded from the means in Table 10.

Noldin (1995) examined some of the properties associated with seed shattering in 18 red rice ecotypes obtained from four different rice-producing states in the south of the United States of America. Five of the 6 ecotypes from Mississippi had been collected more than 15 years earlier for the studies of Do Lago (1982), Teekachunhatean (1985), Garcia-Quiroga (1987) and others. Noldin found that:

- The mean time of the onset of shattering for the 15 ecotypes that exhibited shattering was 15 days after anthesis with a range of 11–18 days.
- The mean seed moisture content at the onset of shattering for the 15 ecotypes was 25 percent with a range of 16–30 percent.
- The mean shattering index for 17 of the ecotypes on a scale of 1 (very low, < 1 percent) to 5 (moderate, 6–25 percent) to 9 (high, > 50 percent) was 6+ with a range from 1 (3 ecotypes) to 9 (7 ecotypes).

TABLE 10
Time-course of seed shattering in selected red rice phenotypes and moisture content of seed in the upper third of the panicle at the first evidence of shattering

Phenotype	Hull colour	Shattering from panicle area			Time to reach bottom of panicle (days)	Seed moisture at top of panicle (%)
		Top	Middle	Bottom		
		(days from 50% anthesis)				
SHA+	STW	16	18	21	5	31.2
79/1	STW	22	23	25	3	23.5
79/11	STW	26	27	28	2	24.3
79-15	BLK	24	29	33	9	28.3
79/5	BLK	19	20	21	2	42.2 ¹
80/1	STW	17	20	25	8	27.9
Mean (less 79/5)		21	23.4	26.4	5.4	27.0

¹Anthesis, shattering and maturation were not uniform along the panicle axis.

Source: Do Lago, 1982.

Two of the two ecotypes classified as essentially non-shattering by Noldin were from Mississippi and had previously been classified as a heavy and a moderate shatterer by Do Lago. While Do Lago did not use a shattering index, it is difficult to reconcile the very different observations of the two investigators regarding the phenotype coded BLKH in Do Lago's studies and MS 3 in Noldin's studies. This phenotype was the most common blackhull red in Mississippi in the period 1977–1990 and was observed to shatter rather easily and heavily by many workers involved in the red rice studies. The other Mississippi phenotype recorded as resistant to shattering by Noldin (MS 5) had been recorded as a moderate shatterer by Do Lago (80/1). There were also differences between the two researchers regarding the time of the onset of shattering and, to a lesser extent, the moisture content of the seeds at the time of shattering. Noldin reported 15 days past 50-percent anthesis as the mean time for the onset of shattering for 15 ecotypes while, as indicated above, Do Lago reported a mean time of 24 days for both the 28 phenotypes in his 1980 studies and the 13 phenotypes in his 1981 studies. However, the mean seed moisture contents for seeds at the time of shattering reported by the two workers were rather close, 25 percent by Noldin and 28 percent by Do Lago for 12 phenotypes and 27 percent for the 5 phenotypes in the more critical studies in Table 10. The differences in time of onset of shattering between the two researchers appears to be related to differences in the criteria and procedures used to determine the 50-percent anthesis baseline. Do Lago stated that his method of determining 50-percent anthesis, i.e. 50 percent of the plants in rows of 22 or 44 plants exhibiting anthesis, probably prolonged unduly the period from 50-percent anthesis to the beginning of shattering. Do Lago's studies were also carried out at a location more than 300 km further north than those of Noldin.

The parameter of greatest ecological significance is seed moisture content at the time of shattering. The mean percentages determined by the two researchers (25 and 27 percent) are just below the 28–30 percent seed moisture content determined at physiological maturity, i.e. maximum dry weight, for the Bluebonnet 50 variety by Rajanna and Andrews (1970) and for several other varieties and red rice phenotypes by Larinde (1979). Do Lago (1982) also determined the changes in seed dry weight and moisture content for the two most common red rice phenotypes in Mississippi and the variety Starbonnet beginning on the 12th day after anthesis. The data obtained for the three types were very similar: seed dry weight increased steadily reaching a maximum at about 22 days past anthesis. Seed moisture content at 22 days was 26–28 percent. Do Lago also noted that all of the 13 red phenotypes in the study summarized above started shattering before the varieties Starbonnet and Lebonnet reached "harvest" maturity, defined as 20 percent seed moisture or less, but none were shattering when the earlier maturing Labelle variety reached the harvest maturity stage.

Chin *et al.* (1999) studied the seed shattering characteristics of ten typical weedy rice lines in Viet Nam, all with the red pericarp. The mean percentage of seeds shattered

for the ten lines was 25.7 percent. In a more detailed study, they determined the time and degree (percent) of shattering for five of the weedy rice lines as compared with the variety IR 64 (Table 11).

TABLE 11
Time and degree of shattering of five weedy rice lines compared with variety IR 64

Weedy rice line	Time of shattering (days after flowering)	Shattered seeds (%)
Latta 10	15	19.3
Latta 11	14	94.3
Latta 18	10	38.0
Latta 20	8	56.4
Latta 23	7	24.6
Cultivar IR 64	Non-shattering	0.0

Source: Chin *et al.*, 1999.

Shattering commenced very early for two of the weedy rice lines. There did not appear to be any relationship between the time of shattering and the percentage of seeds shattered.

Viability of shattered seeds

On average, the main flux of seed shattering in red rices appears to be about the time the seeds attain physiological maturity and, thus, are fully capable of germination when dormancy is released. However, the seeds of some ecotypes begin to shatter considerably before they attain physiological maturity, even sooner than 10 days after anthesis. While the amount of seeds shattering at such an early stage is quite small, it could be significant in replenishing the soil seed bank if the seeds are capable of germination.

Ferrero and Vidotto (1999) and FAO (2003) studied the development of the germinative capacity and time of shattering of red rice (*Oryza sativa* var. *sylvatica*) seeds in Italy in order to establish the most appropriate time during the flowering and maturation period for applying control measures, such as panicle cutting, and application of herbicides with brush or wiping bar. They determined that:

- About 20 percent of the hand-harvested developing red rice seeds were capable of germination at 9 days past flowering and 85 percent were germinable by 12 days.
- Seed shattering was evident at 9–12 days after flowering, but seeds shattered before 15 days were very low in viability (about 5 percent). Shattering increased gradually from 15 days to complete development of the panicle at about 30 days, at which time 65 percent of the seeds had shattered in the 1996 study, but only 15 percent in the 1997 study.
- Panicle cutting and crushing with a roller as a post-planting control measure has to commence within 9 days after flowering in order to prevent escape of shattered seeds into the soil seed bank.

Rajanna and Andrews (1970) studied seed development and maturation in Bluebonnet 50, a long-grain variety. Seed moisture decreased gradually from a high of about 60 percent while seed dry weight increased rather dramatically up to about 25 days past anthesis. Thereafter, dry weight remained constant as seed moisture content further declined to 15 percent at 40 days. Seeds exhibited maximum germination at about 25 days regardless of the date of planting within a three-week period. A small percentage of the seeds were capable of producing obviously weak seedlings under laboratory conditions at 10 days. The percentage of seeds capable of germination increased up to 20 days although the most vigorous seedlings were not produced until a few days later (24–25 days). Larinde (1979) determined that, for the seeds of the common BHR and SHR red rices in Mississippi, moisture content decreased from almost 60 percent at 4 days past anthesis to about 20 percent at 26–30 days. Seed dry weight increased rapidly reaching a maximum at about 20 and 24 days, respectively, for the SHR and BHR. Although some seeds (fewer than 5 percent) were capable of germination at 10 days, the germinability of the seeds began to increase rapidly only after 14–16 days and reached full capability at 22–24 days.

“Panicle exsertion” and “heading” are terms for essentially the same stage in reproductive development in rice on an individual plant basis (Stansel, 1975). Some of the earlier studies on the development of the germinative capacity in red rices used “panicle exsertion”, “heading” or “flowering” as the baseline and, thus, cannot be related directly to those that used days past anthesis or days past 50-percent anthesis as the baseline. Nevertheless, they provide additional evidence that the seeds are fully germinable at about the time shattering begins although seedling vigour does not reach a maximum until the seeds attain physiological maturity, i.e. accumulate maximum dry weight. Sonnier (1963, 1965) harvested seeds of SHR and BHR types in September in Louisiana at daily intervals beginning 4 days after full exsertion of the panicle until 23 days. The seeds were dried at room temperature, threshed and stored until germination tests were made in April (seven months storage). A few seeds (fewer than

5 percent) were capable of germination, i.e. produced normal seedlings, at 6 days after panicle exertion. Germination then increased rapidly to about 70 percent at 23 days. Although the seeds had been stored for 7 months at room temperature, the percentage of dormant seeds increased from about 5 percent at 7 days to about 70 percent at 14 days, and then decreased to less than 20 percent at 23 days. When the germination and dormant seed percentages were added to obtain the total viable seeds, the 80-percent level was reached between 12 and 15 days. Sonnier noted that dormancy was much more persistent in seeds produced in 1964 than in 1962 and 1963. In related date-of-seeding studies, Sonnier determined that SHR matured a few days earlier than BHR but that both types shattered viable seeds before harvest of Nato, an early variety, and Bluebonnet 50, a mid-season variety.

Helpert and Eastin (1976, 1978) reported similar studies on the development of the capacity for germination by seeds of SHR and BHR ecotypes compared with the variety Labelle, an early-maturing, long-grain variety. Panicles were tagged at heading and harvested at three-day intervals. Seeds of the SHR and BHR tested immediately after harvest were essentially all dormant until 27–33 days after heading, while those of Labelle were less dormant and germinated 25 percent at 27 days. Seeds of the BHR stored for two weeks at 30 °C to break dormancy before testing, germinated 40, 70, 80 and 90 percent for the 21, 24, 27 and 30-day harvests, respectively, while those of the SHR germinated 70, 85, 90 and 95 percent for the same periods. Seeds of Labelle stored for two weeks at 30 °C before testing germinated at least 50 percent at 15 days and almost 80 percent at 21 days. The authors concluded that seeds of Labelle, SHR and BHR types were viable 12, 15 and 18 days after heading, respectively. However, this conclusion apparently confounds viability, germinability and dormancy. It is probable that seed development followed the same time-course for the three lines but that dormancy was more intense and persisted longer for the two red rice types.

Importance of seed-shattering trait for weedy habit of red rice

The importance of the early and heavy seed-shattering trait to the very successful weedy habit of red rices cannot be overemphasized. In their review of Asian rice and weedy rice, Vaughan *et al.* (2005) stated that seed shattering is the single characteristic of all weedy rices in the rice field. Similarly, after examining and characterizing 1 084 panicles of red rices collected in the southwest Louisiana rice area in the late 1950s, Constantin (1960) noted that shattering and hull pubescence were the only two traits that did not vary among the plants represented by the panicles and concluded: “The two main factors involved in the survival and spread of red rice are grain shattering, and the ability of the grain to remain viable in the soil during long adverse periods.”

The seed-shattering trait contributes to the persistence and spread of red rice in several critical ways. First, red rice is an annual that is dependent entirely on seed for survival during adverse seasons until conditions become favourable again for the start-up and completion of its annual life cycle. Shattering ensures that a substantial portion of the seeds produced are distributed to the surface of the soil before and during harvesting rather than gathered with the grain and removed from the field. Second, the main flux of seed shattering in most red rice types appears at the time or a few days before the seeds reach physiological maturity, say 24–28 percent seed moisture content. This is very significant in terms of retention of dormancy during the post-maturation (and post-harvest) period when the temperature and soil moisture levels are often favourable for germination of rice seed in contact with the soil surface. Seedlings developed from seeds that germinate would be killed by freezing temperatures in temperate climates or by drought or land preparation for sowing and weeding in the succeeding crop in subtropical and tropical wet and dry season

climates (Teekachunhatean, 1985; Teekachunhatean and Delouche, 1986). Chapter 6 examines the ecological relationships between seed moisture content at the time of shattering, dormancy and survival of a significant portion of the seeds shattered onto and eventually into the soil for germination and emergence in the next rice production season and in succeeding years.

INTENSE AND PERSISTENT SEED DORMANCY

Seed dormancy also evolved as a survival mechanism in annual plant species. When the vegetative and reproductive stages of the annual cycle have been completed, the species survives as seed, the most resistant stage, until conditions again become favourable for start-up of the annual cycle. Simpson (1990) noted that while seed dormancy is of great adaptive significance for most plant species, it is one of the main reasons why grass species constitute the most serious weed problem in crops worldwide. Seed dormancy is an inconvenient trait in crop agriculture based on annual species. Relatively intense and persistent dormancy only interferes with the timely sowing of crops. In addition, even a moderately persistent level of seed dormancy complicates and increases the difficulty of post-sowing operations, e.g. weeding and harvest, because of non-uniformity in emergence, plant growth and development. On the other hand, the absence of dormancy or a very low level thereof (ephemeral dormancy) can lead to preharvest sprouting, often termed “germination-on-the-ear” or “germination-in-the-head”. This condition can occur where rice plants lodge into water or, more generally, where there is frequent rain and high humidity during the maturation and harvesting period. For example, a relatively low-intensity, short-term dormancy can complicate multicropping in rice where there is a relatively short period between crops and the seeds of the first crop are used to sow the second crop. Germination-on-the ear is a rather common problem for some types of wheat grown in Northern Europe and a serious but infrequent problem in cotton, sorghum and wheat in the southeast of the United States of America.

Since the beginning of crop husbandry, farmers have unconsciously and consciously selected annual crop varieties for limited but varying levels of dormancy in order to adapt them to the prevailing climate conditions and cropping intensity. Simpson (1990) viewed the success in reducing dormancy to a level that permitted timely sowing as one of the great achievements of humans in the Neolithic Age. In the past century, scientific plant breeders have successfully crafted varieties with the most appropriate incidence and intensity of seed dormancy. Therefore, seeds of most modern rice varieties have a short dormancy period that persists until harvest maturity and a few days beyond, rather than no dormancy as frequently claimed by researchers comparing them with weedy rices.

As discussed above, many early rice farmers in the United States of America believed that white rice grains left on the soil after harvest were transmuted by exposure to adverse winter weather so that they germinated and developed weedy-type plants that produced red-pericarp grain (seeds) that then continued to produce red rice in subsequent generations. However, the pioneering students of the red rice problem in the United States of America did not accept the transmutation explanations for the origin and spread of red rices (Allston, 1846; Austin, 1893; Dodson, 1898, 1900; Knapp, 1899). They suggested that the initial entry of red rice types into a rice field was usually through contaminated seeds and that their subsequent persistence and spread were a result of early and heavy shattering, which left most of the red rice seeds on the soil, and the maintenance of viability of many of them over the winter season and for several years in soil. Dodson (1898) undertook field experiments in Louisiana and demonstrated that a much higher percentage of red rice seeds survived the adverse

field conditions during the winter season than did those of white (cultivated) rices, and, thus, germinated and produced red rice plants the following season. The very few cultivated rice seeds that survived the winter produced “white rice” plants. Dodson concluded that: “From long cultivation the white rice has (sic) largely lost its power of self preservation. If they are on the ground, the fall rains with warm days that come in November and the early part of December, cause the seeds to germinate, and then they are killed by winter’s cold. On the other hand, the red rice is dependent upon self-preservation for the continuation of the species, and under the same conditions as above stated, hardly a grain can be found that shows evidence of germination. In the following spring, of the seeds that had remained on the field, a large per cent of the red rice would grow, and (only) a small per cent of the white rice would (germinate), and it is not hard to understand why the idea should become prevalent that the white seeds had developed plants that bore red seeds.”

While Dodson’s conclusions were correct, his explanation of why this was the case was necessarily cast almost wholly in Darwinian terms because Mendelian genetics was just being rediscovered. The survival and spread of the red rice populations are indeed totally dependent on the maintenance of viability of a significant portion of the seeds shattered to the soil surface until conditions become favourable again for initiation and completion of the annual cycle of growth, development and reproduction.

Seed dormancy is an effective survival mechanism for wild, native and weedy annual and perennial seed-propagated plants because it fulfils several critical conditions.

- Dormancy blocks (delays) germination so that the species survive as seeds, the most resistant stage, until conditions are again favourable for growth, development and reproduction.
- The intensity of dormancy varies among individual seeds in the population in order to distribute germination over time and increase the probability that some of the seeds will germinate when conditions are favourable for establishment and completion of the life cycle of the species.
- Dormancy inhibits and/or ameliorates physiological deteriorative processes so that seeds retain their viability during the dormancy period.
- Dormancy, in nature, is released by some natural event or condition, the most common of which is time but also light, low temperatures, high temperatures, soil acidity, soil nitrates, etc.

Many studies have demonstrated that dormancy in weedy rices (including red rices) meets all of these conditions in full.

Effectiveness of dormancy in delaying germination

Dormancy inhibits the germination of seeds when all environmental requirements for germination are met fully. Germination is delayed for a few days to more than a year depending on the intensity of dormancy in the individual seeds of the population. Dormancy is manifestly very effective in accomplishing the function it evolved to accomplish, i.e. the distribution of germination over time and space in order to maximize the probability of survival for species and populations. Chapter 6 presents the results and some of the data from studies on the effectiveness of dormancy in distributing germination over time to increase survivability in red rice populations

Variation in the intensity and persistence of dormancy

The persistence or intensity of dormancy varies among the seeds in a population. Dormancy would be a much less effective survival mechanism if it persisted for the same period in all of the seeds in the population. Germination of all the seeds would

occur at the same time, which might not be favourable for establishment, growth and reproduction. In rice, the initial level and intensity of seed dormancy varies among both weedy types and cultivated varieties. In 1980, Do Lago (1982) did a preliminary survey of the variability in intensity of dormancy in red rice phenotypes in Mississippi. The percentage of dormant seeds was usually determined as the percentage “firm, ungerminated seeds” remaining at the end of the germination period. Their viability was confirmed periodically by the tetrazolium test or dormancy-releasing treatments. The intensity or initial level of dormancy was determined for 4 cultivated varieties and 28 uniform red rice phenotypes by making standard germination tests on seeds, “collected at harvest maturity, dried at room temperature for 7-12 days, (and) stored at 10 °C. for a few weeks.” As expected from the lack of rigorous control of the survey, i.e. the imprecision of the words italicized in the quotation, the results were variable but suggestive:

- Seed dormancy for the four cultivated varieties ranged from 26 to 77 percent with an average of 52 percent. The medium-grain, mid-season variety Nato exhibited the most intense dormancy.
- The level of dormancy for seeds of the 18 SHRs ranged from 26 to 100 percent with an average of 50 percent while that of the 10 BHRs ranged from 94 to 98 percent with an average of 97 percent. The average level of dormancy for the combined 28 red rices was 66 percent.

Do Lago emphasized the preliminary nature of the study, acknowledged its lack of adequate controls and attributed the rather low average level of dormancy of the SHRs (50 percent) compared with the very high level for the BHRs (97 percent) to the later maturity of the latter (Table 2), which resulted in later harvest and less drying time at room temperature and storage at 10 °C than for the “typical” SHRs. In 1981, he repeated the study with more rigorous controls using the same 4 cultivated varieties and 20 red rices, many being the same phenotypes used in the earlier study. After the initial determinations, the seeds were stored at 10 °C (50 percent relative humidity storage) and re-tested for germination and dormancy after six months. The results are summarized in Table 12.

In another survey, Do Lago transplanted 22 seedlings each for 14 of the segregates from the heterozygous 78/21 red rice described in Table 4, and randomly harvested panicles from 54 plants for determination of pericarp colour and germination/dormancy within a few days after harvest and drying to below 15 percent moisture in a 10 °C low-humidity room. Ten of the plants produced grain with a white pericarp while 44 had a red pericarp. Table 13 shows how the initial level of dormancy varied among the 54 randomly selected segregates, all SHR types.

Although this survey indicated that red-pericarp segregates were more dormant on average than those with a white pericarp, it is only suggestive because the study was designed only for observation and not to determine whether pericarp colour and dormancy were associated. However, further observations of more than 2 000

TABLE 12
Intensity of seed dormancy for cultivated varieties and RR phenotypes harvested at 24 days past anthesis and dried for 9 days at 22–24 °C and after 6 months storage

Variety or phenotype	Hull colour	Months storage at 10 °C – 50% relative humidity	
		0	6
Variety		(% dormant seed)	
Labelle	Straw	83	1
Lebonnet	Straw	90	4
Starbonnet	Straw	75	3
Nato	Straw	96	40
Red rice (RR)			
BLKH	Black (BH)	100	14
SHA-	Straw (SH)	100	15
SHA+	Straw	99	37
78-5	Black	100	38
78-8	Brown	100	73
9 SH-RR	Straw	r = 100–94; x = 98	r = 35–3; x = 11
6 BH-RR	Black	r = 100–95; x = 99	r = 61–5; x = 33

Note: r = range; x = mean.

Source: Do Lago, 1982.

TABLE 13
Initial level of dormancy in 54 randomly selected SHR segregates

Dormant seeds (%)	White phenotypes (no.)	Red phenotypes	Total phenotypes
< 30	1	1	2
30–39	3	0	3
40–49	0	0	0
50–59	2	2	4
60–69	1	2	3
70–79	1	0	1
80–89	0	8	8
90–100	2	31	33
Total no.	10	44	54
Mean dormancy	45%	90%	

Source: Do Lago, 1982.

TABLE 14
Variation in the persistence of dormancy in seeds of two cultivated varieties and five red rice phenotypes in open storage at 30 °C

Variety or phenotype	Storage period (days)					
	0	3	5	10	20	25
	Germination (%)					
Labelle	8	88	94	98	100	100
Nato	4	8	9	14	39	57
BLKH	5	68	79	91	97	99
SHA-	7	73	81	93	96	98
SHA+	1	2	6	10	69	91
79/1	5	10	36	65	90	96
78/8	0	0	2	12	45	78

Source: Moreno (1990).

25–30 percent moisture content) and dried to about 14 percent or less with cool air (20–22 °C) approaches 100 percent for most RRs and can be very high even for many cultivated varieties. However, as noted above, the persistence of dormancy varies among the individual seeds in populations. This variation is evident in the data presented in Table 12. If the dormancy periods were the same in all seeds in a population, the percentage of dormant seeds after six months' storage would have been either the same as at zero months or 0 percent. The variation in persistence of dormancy among and within populations of two cultivated varieties and five red rice phenotypes in open storage at the relatively warm temperature of 30 °C for periods up to 25 days is evident in the germination data in Table 14.

Protective role of dormancy

Dormancy would not be very effective in ensuring the survival of plant populations if dormant seeds succumbed to the most common environmental factors involved in seed deterioration, i.e. high seed moisture, high humidity, and high and low temperature. In their studies of methods for overcoming dormancy in rice seed, Delouche and Nguyen (1964) observed that many seeds of the Nato variety that did not germinate under standard test conditions during an 80-day period were still firm, i.e. dormant, and viable as established by tetrazolium test. These remnant, fully imbibed dormant seeds were collected, sealed in glass bottles without drying and stored at room

plants from segregating populations in the period 1982–83 indicated that dormancy in white-pericarp segregates was generally less intense and less persistent than for the red-pericarp segregates. Further critical studies are needed of the association of white or non-pigmented pericarp (the recessive trait) with the intensity and persistence of dormancy in segregating populations from red and cultivated rice crosses.

Noldin (1995) determined germination and dormancy at harvest for 19 red rice ecotypes from 4 states and 3 cultivated varieties in 1993. He found that the level of dormancy varied among the 19 red rice ecotypes: 13 exhibited a level of dormancy in excess of 90 percent, 2 between 80 and 89 percent, 3 between 70 and 79 percent, and 1 had a level of dormancy of 63 percent. Dormancy in the three cultivated varieties was less than 10 percent, which is low compared with the findings of Do Lago (above) and others reviewed below.

The intensity or level of dormancy in seeds harvested when about physiologically mature (circa

temperature (about 25 °C) for an additional 90 days. At the end of the 90-day period, the seeds were removed from the bottle in order to determine seed moisture content and germination. Seed moisture content was about 27 percent, germination without special treatment was 30 percent, and germination after a soak treatment to release dormancy was 98 percent. Non-dormant seeds of rice at 27-percent moisture content and 25 °C would have either germinated within 10 days or decayed within a couple of weeks, but dormant seeds under the same conditions were protected so that full viability was maintained for almost six months (170 days). These observations were confirmed about 20 years later in a specifically designed study by Teekachunhatean (1985). Dormant and non-dormant seeds of the BLKH and SHA+ red rices were placed between moist germination blotters at 15 °C for 30 hours in order to condition them to full imbibition, circa 30-percent moisture content. The fully imbibed seeds were allowed to dry down briefly to about 27-percent moisture content (which is below the minimum moisture content for germination of rice). They were then divided into 24 portions of 125 seeds for each genotype and dormancy status, sealed in 2-mm-thick polyethylene envelopes and placed in several large glass containers with sealed closures for storage at 30 °C. Two envelopes for each genotype and dormancy status were removed at monthly intervals over a 12-month period for germination under standard test conditions. Dormancy-release treatments were applied randomly on seeds classified as “dormant”, i.e. firm, clean, no evidence of decay or germination at the end of the test period, in order to confirm that they were viable and germinable. Table 15 presents the results of the study for the bimonthly sampling periods. The non-dormant seeds of BLKH were all dead after about two months while nearly 50 percent of those of SHA+ survived for the 12-month period – apparently because dormancy was induced at the warm temperature (30 °C) between the second and fourth months. More than 75 percent of the dormant seeds survived the year-long storage period, most of them still in the dormant condition.

Noldin (1995) subjected dormant and non-dormant seeds of 11 red rice ecotypes from 4 states to accelerated ageing conditions of 45 °C and 100-percent relative humidity for periods up to 24 days before testing for germination. Noldin considered seeds lots as non-dormant if they germinated 80 percent or higher; lots that germinated less than 80 percent were considered dormant. Table 16 presents selected results from this study. The accelerated ageing treatment released dormancy during the first 4 days, but the initially dormant seeds survived from 4 to more than 8 days longer under the very adverse accelerated ageing conditions than did those classified as non-dormant. These various studies demonstrate that dormant rice seeds are much more resistant to

TABLE 15
Effects of storage of fully imbibed non-dormant and dormant seeds (circa 28-percent moisture content) of two red rice types at 30 °C on dormancy and germination

Red rice phenotype	Seed response	Storage period (months)						
		Non-dormant seeds						
		0	2	4	6	8	10	12
BLKH	% dormancy	0	0	0	0	0	0	0
	% germination	100	54	2	0	0	0	0
SHA+	% dormancy	3	6	45	37	48	44	36
	% germination	90	78	9	15	11	13	2
Dormant seeds								
BLKH	% dormancy	99	80	92	57	92	87	84
	% germination	1	28	5	37	4	10	4
SHA+	% dormancy	99	100	89	89	86	85	76
	% germination	0	0	8	10	6	0	0

Source: Teekachunhatean, 1985.

TABLE 16

Differential germinative responses of non-dormant and dormant seeds of red rice ecotypes after accelerating ageing for periods up to 24 days

Ecotype / condition	Hull colour	Accelerated ageing at 45 °C – 100% relative humidity (days)							
		0	4	8	12	16	20	24	
		Germination (%)							
AR 2	ND	FBL	91	89	87	62	17	1	0
	D		61	90	93	82	68	33	6
LA 4	ND	BLK	99	99	95	52	24	5	0
	D		74	98	92	78	58	7	8
MS 2	ND	STW	97	98	91	72	40	7	0
	D		75	99	100	99	57	7	3
MS 5	ND	STW	98	98	84	54	9	1	0
	D		90	98	98	87	73	50	19
TX 4	ND	BLK	90	65	13	1	0	0	0
	D		56	95	95	86	24	4	0

Note: ND = non-dormant; D = dormant; FBL = faded black; BLK = black; STW = straw.

Source: Noldin, 1995.

the combination of high temperatures and moisture content than those in which the dormant condition has been released, i.e. non-dormant seeds.

In another study, Teekachunhatean (1985) determined the relative resistance of fully imbibed dormant and non-dormant seeds of the Nato variety and the BLKH and SHA+ red rices to low temperatures of 5, 0 and -15 °C for periods up to four weeks. The seeds were actually between moist germination blotters during the exposure periods, as if for germination testing. Selected results are presented in Table 17. Non-dormant seeds maintained germination at high levels at 5 and 0 °C for the four-week period, especially the Nato variety, but there was no evidence of induced dormancy and the seeds that did not germinate decayed. Dormancy was mostly released in Nato seeds after two weeks at 5 and 0 °C, while those of the two red rice phenotypes remained mostly in the dormant condition. These data show that dormant rice seeds are relatively more

TABLE 17

Effects of low temperatures and period of exposure on germination responses of fully imbibed non-dormant and dormant seeds (27–30-percent moisture content) of the Nato variety and the BLKH and SHA+ red rice phenotypes

Variety / phenotype	Seed response	Initial values 0 weeks	Temperature					
			5 °C		0 °C		-15 °C	
			Weeks	Weeks	Weeks	Weeks	Weeks	Weeks
Non-dormant seed								
Nato	Germination %	98	92	72	74	65	1	0
	Dormancy %	0	0	0	0	0	0	0
BLKH	Germination %	100	82	43	18	18	0	0
	Dormancy %	0	0	0	0	0	0	0
SHA+	Germination %	99	81	36	40	23	2	0
	Dormancy %	0	0	0	0	0	0	0
Dormant seed								
Nato	Germination %	21	73	75	64	70	2	0
	Dormancy %	78	22	7	20	8	0	0
BLKH	Germination %	3	4	9	13	24	0	0
	Dormancy %	96	90	82	49	41	0	0
SHA+	Germination %	3	5	5	2	9	0	0
	Dormancy %	96	94	92	81	78	0	0

Note: BLKH = black hull genotype; SHA+ = strawhull short awns.

Source: Teekachunhatean, 1985.

resistant to low temperatures than are non-dormant seeds. Both non-dormant and dormant seeds succumbed to the very low -15 °C.

Dormant rice seeds are relatively more resistant to adverse combinations of temperature and internal moisture content than are non-dormant seeds. Dormancy provides substantial protection against the common conditions that cause seeds to deteriorate and lose viability. Thus, it fulfils one of the four conditions for an effective survival mechanism set forth above. Chapter 6 presents additional evidence on the protective role of dormancy in the survival of red rice populations.

Release of dormancy

The fourth and final criterion for dormancy as an effective survival mechanism set forth at the beginning of this chapter is that dormancy must be released by natural events and/or conditions. This criterion is met in full in the case of rice seed dormancy. After-ripening, or the release of dormancy, takes place in naturally dried rice seeds over time. The length of time required for after-ripening is determined by:

- inheritance, which sets the potential depth of the dormant condition;
- climate conditions during seed maturation, which influence its expression;
- seed moisture content and temperature, which influence the rate of dormancy release.

The intensity of dormancy is greatest at the time the seeds attain physiological maturity, circa 28–30-percent moisture content. Shattering begins at about this time for the weedy red rices (the significance of which is considered in Chapter 6) but not for the non-shattering cultivated varieties. The release of dormancy probably commences as the seeds dry-down to below 15-percent moisture, at which time it is controlled largely by temperature – the higher the temperature (up to about 50 °C), the more rapid the release of dormancy. Researchers studying dormancy in both cultivated and weedy red rices need to appreciate how rapidly dormancy can be released by warm temperatures. Seeds harvested at relatively high moisture contents in order to maximize dormancy should be dried at cool temperatures to 8–12-percent moisture and stored at or below freezing temperatures (-10 to -20 °C) until needed for experiments (Roberts, 1963; Cohn, 1980; Teekachunhatean, 1985.)

The effects of time, temperature and seed moisture content on the period of dormancy in rice have long been known and taken advantage of in overcoming dormancy problems in cultivated varieties. Umali, Parker and Dumla (1960) exposed seeds of the variety Peta to wood smoke for 84 hours in order to overcome dormancy. They attributed the dormancy-releasing effect of the smoke to some chemical that counteracted an inhibitor in the seed coverings. However, Jennings and de Jesus (1964) re-interpreted these results and concluded that the effective agent in the smoke was its temperature, as a temperature of about 49 °C was maintained throughout the 84-hour smoking treatment. They tested and recommended the exposure of fresh but naturally dried seeds to 50 °C in open containers for 4–5 days for overcoming dormancy in small experimental lots of rice seeds. Earlier, Roberts (1962) had made a detailed analysis of the effect of temperature on the dormancy periods of a cultivated variety of rice. He determined that the temperature coefficient for breaking dormancy was 3.38. He interpreted the result as ruling out the idea that a temperature-dependent diffusion process is involved in rice seed dormancy, as temperature coefficients for most diffusion processes are typically only about 1.3. He speculated that some non-enzymic oxidation reaction essential for germination was promoted by the warm temperatures. Even earlier, Weir (1959) observed that seed dormancy in rice grown in Arkansas, principally the Bluebonnet 50 and Nato varieties, was related to: time of harvest,

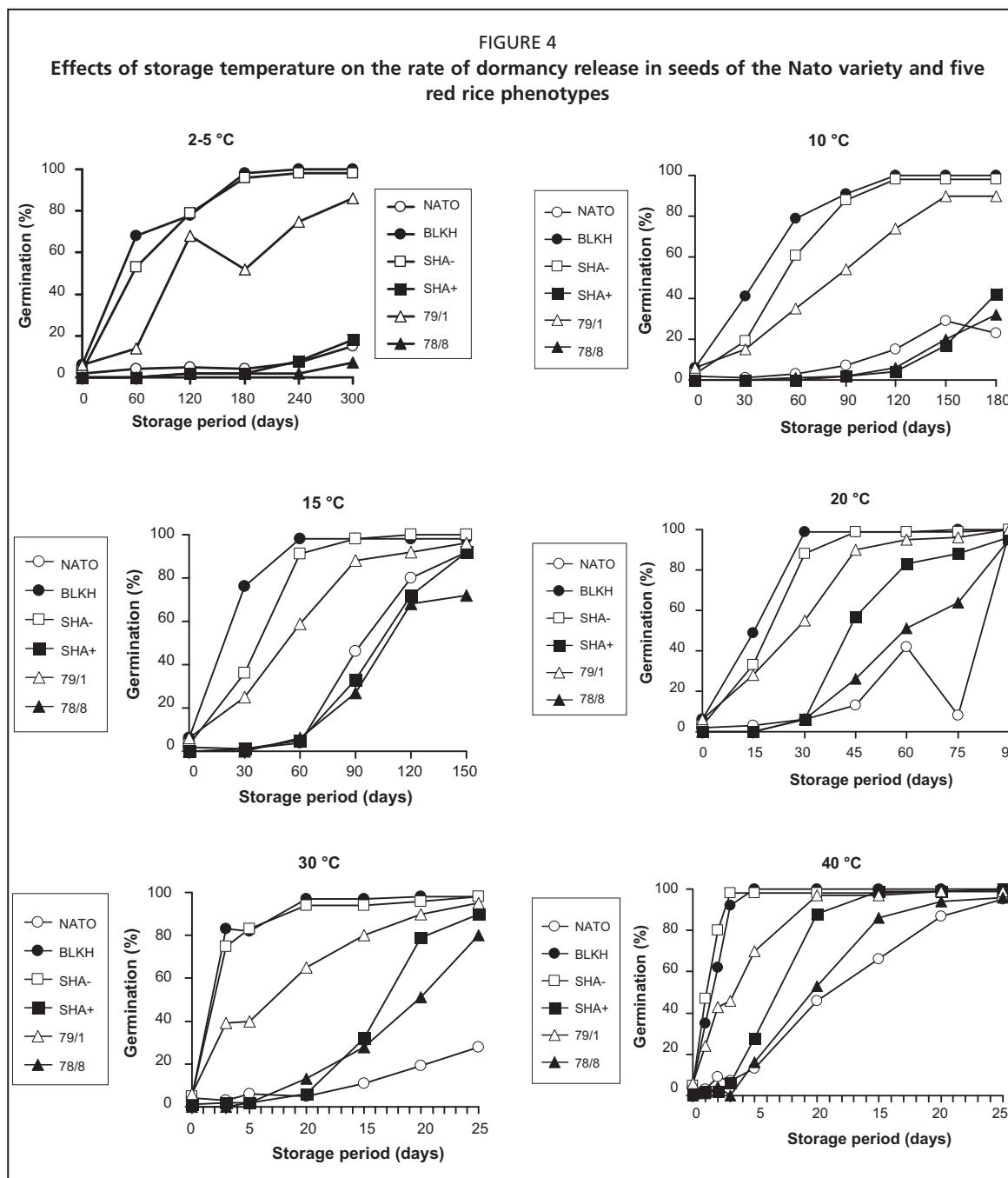
moisture content at harvest, and drying method. Seed harvested at relatively high moisture levels and dried with natural, i.e. non-heated, air exhibited the greatest degree of dormancy. Drying the seeds at 40 °C for four days before testing for germination overcame dormancy for most seed lots, except for some of the most dormant lots of the Nato variety. There have been many other reports on the dormancy-releasing effects of high temperatures for cultivated rices since the early 1960s, as heating became established as the preferred method of overcoming dormancy (Delouche and Nguyen, 1964; Pili, 1968; Nugraha and Soejadi, 1991). Because there was no breeding or testing interest in the weedy red rices, the dormancy-breaking effect of heating for red rices was not demonstrated until some 20 years after Weir's observations by Larinde (1979), Do Lago (1982), Moreno (1990) and others.

The data in Table 12 that illustrate the variations in the intensity of dormancy among red rice phenotypes also illustrate very well the dormancy-releasing effect of time, even at a very cool temperature (10 °C). The initial level of dormancy in the cultivated varieties ranged from 75 percent for Starbonnet to 96 percent for deeply dormant Nato and from 94 to 100 percent for the 20 red rice phenotypes. Dormancy was essentially completely released for 3 of the 4 varieties and decreased to less than 40 percent for 4 of the 5 identified red rices during the 6-month storage at 10 °C. The Nato variety maintained a higher level of dormancy, 40 percent, during the 6-month period than any of the group of 9 SHR types and all of the identified red rice types, except 78/8, the most persistently dormant (73 percent after 6 months) of the 20 red rices and 4 cultivated varieties evaluated. The group of 6 BHR types was more persistently dormant than the group of 9 SHR types. The effect of temperature on the dormancy period is also evident in the results of studies by Moreno (1990). Dormancy of seeds of the Labelle variety was essentially released in three days, i.e. dormancy decreased from more than 90 percent to about 10 percent (Table 14), while the five identified red rices varied considerably in the rate of dormancy release at 30 °C. Dormancy in BLKH and SHA-, two of the most common red rices in Mississippi, was released rather rapidly with germination increasing from less than 10 percent at 0 days to about 70 percent after just 3 days and more than 90 percent after 10 days. Dormancy was released more rapidly in 78/8, the most deeply dormant red rice, than in Nato, the deeply dormant variety. Dormancy in SHA+, a third common red rice phenotype, was released at about the same rate as for Nato and 78/8 through 10 days but then reached an essentially non-dormant condition at 25 days, at which time substantial percentages of the Nato and 78/8 seeds were still dormant.

Additional data from studies by Moreno (1990) on the interacting effects of time and temperature on the release of dormancy in the variety Nato and five red rice phenotypes are presented graphically in Figure 4. The BLKH, SHA- and 79/1 phenotypes lost dormancy at a relatively rapid rate at all temperatures from 2–5 °C to 40 °C. For example, BLKH and SHA- reached more than 90-percent germination in 180 days at 2–5 °C and in about 3 days at 40 °C, whereas Nato and 78/8 did not even reach 20-percent germination at 2–5 °C in 300 days and 90-percent germination at 40 °C until 20 days.

Nature of rice seed dormancy and responses

There is a large and expanding literature on the nature of rice seed dormancy and responses of seeds to a wide variety of treatments effective to varying degrees in breaking or releasing dormancy. While most of the research has been on the cultivated rices, the weedy red rices have also received some attention, especially in the last 25 years. The information accumulated thus far suggests that while the intensity and persistence



Source: Adapted from Moreno (1990).

of dormancy varies widely among species, *Oryza sativa* and *O. glaberrima*, the *O. sativa indica*, *japonica* and *javanica* types, and among their weedy red rice ecotypes or biotypes, the essential nature of dormancy is similar if not the same. Generally, the database indicates that *O. glaberrima* populations have the most deeply dormant seeds followed by those of *indica*, *javanica* and *japonica* (Dore, 1955; Tang and Chiang, 1958; Ikeda, 1963; Nakamura, 1963; Hayashi and Himeno, 1974; Ellis, Hong and Roberts, 1983). The intensity and period of dormancy in cultivated populations appears to be controlled by genetic/environment interactions. Deep and persistent dormancy is considered to be dominant over the very short dormancy periods characteristic of most cultivated varieties.

Plant type and climate conditions

Relatively photo-insensitive and short-maturity genotypes generally have the shortest and least intense dormancy (Chandraratna, Fernando and Wattegedera, 1952; Dore, 1955; Agrawal, 1981; Deore and Solomon, 1983), but the relationship between maturity and dormancy is not very consistent. Seeds that mature during periods of rainy weather and high humidity are generally more intensely and persistently dormant than those that mature during drier periods (Ghosh, 1962; Jennings and de Jesus, 1964; Nair, Ponnaiya and Raman, 1965). Dormancy is also more intense in seeds that mature under warmer temperatures, e.g. 30 °C, than at lower temperatures (Ikehashi, 1972, 1975). Buenaventura (1956) observed that the post-harvest dormancy period of Philippine rice varieties ranged from 0 to 11 weeks and that its intensity and persistence were greatest when the seeds were harvested at a relatively high moisture content. Weir (1959) also noted that, in Arkansas, dormancy was most intense in seeds harvested at “high” seed moisture and dried naturally or with non-heated air.

Chemical treatments

Many different chemical treatments have been shown to stimulate germination of dormant rice seed. However, the results obtained by different researchers have been relatively inconsistent except for a few of the chemicals. Nitrates and nitrites generally stimulate germination of varying portions of the dormant seeds, especially if the seeds are hulled (Roberts, 1963; Agrawal, 1981; Cohn, Butera and Hughes, 1983; Howard-Kandakai, 1983). Roberts (1964a, 1964b) tested the idea that dormancy release in rice involves blocks to conventional respiration by applying the common inhibitors of cytochrome oxidase that should prolong dormancy, but they did not. Instead, most of them, especially sodium azide, promoted germination of dormant seeds to varying degrees. Roberts (1964 b) speculated that cytochrome oxidase is a strong competitor for available oxygen and that its inhibition makes more oxygen available for the non-enzymic oxidation reaction he assumed was involved in the release of dormancy. Soaks in water at 40 °C are effective in promoting germination of slightly dormant seeds, while soaking in 0.25-percent sodium hypochlorite worked well in stimulating germination of more dormant seeds (Delouche and Nguyen, 1964). Dormancy in rice was released by soaks in sulphuric, nitric and hydrochloric acids, for various periods, i.e. acid scarification (Lin and Tseng, 1959; Roberts, 1963; Murty and Roghavaiah, 1966; Sikder, 1967; Agrawal, 1981; Paquiot, 1992). Roberts found that nitric acid scarification was more effective than the other acids for cultivated varieties and attributed this to the additive effects of nitrate. Paquiot, working with the very dormant Nato variety and three red rice phenotypes, found that nitric acid was most effective in terms of soaking time (relatively good results were obtained in five minutes), while sulphuric acid was the most effective and safest in terms of stimulating complete germination during longer soaking periods up to 30 minutes. The effects of acid scarification cannot be separated from mechanical scarification, such as hulling, scratching of the pericarp, and excising portions of the spikelet. The two types of scarification probably act on both the hulls and pericarp-testa.

The data on the effects of hormones, such as gibberellic acid (GA), ethylene and the cytokinins on release of dormancy are also rather inconsistent. Cohn and Butera (1982) found that various cytokinins effectively broke dormancy in red rice, but in some years only when the hulls were removed. Several workers reported that gibberellin promoted germination of some but not all of the dormant seeds in genotypes evaluated (Roberts, 1963b; Nakamura, 1963; Roberts and Smith, 1977; Ellis, Hong and Roberts, 1983; Paquiot, 1992). However, Eastin (1978b), failed to stimulate germination of dormant red rice seeds with GA and several other phytohormones. Ethylene chlorohydrin, a

chemical with hormonal-like activity, applied as a 1 000-ppm soak for 24–48 hours at 40 °C was consistently effective in releasing dormancy in both cultivated and red rices (Delouche and Nguyen, 1964; Do Lago, 1982; Teekachunhatean, 1985; Garcia-Quiroga, 1987; Paquiot, 1992).

Seed coverings

Removal of the hulls and rupture of the pericarp-testa complex are the two most effective treatments for releasing dormancy in rice and many other *Poaceae* species (Simpson, 1990). Permeability of the hulls to water is not a factor as dormant and non-dormant seeds absorb water at about equal rates (Roberts, 1961; Larinde, 1979). Nguyen and Delouche (1964) contended that for rice the beneficial effects of hull removal reported by others (Mikkelsen and Sinah, 1961; Roberts, 1961) were probably the result of hull removal combined with abrasions and scratches of the pericarp-testa incidental to hulling. They found that careful removal of the hulls increased germination of a population of dormant seeds of the Nato variety only from 5 to 35 percent over a 30-day period, while hulling and scratching the pericarp along the scutellar margin induced 98-percent germination in 6 days. In addition, they found that nicking the pericarp along the margin of the scutellum through a very small opening cut into the lemma over the embryo was equally effective. Similar results have been reported by Pili (1968), Larinde (1979), Paquiot (1992), and Nugraha and Soejadi (1991). These data and others did not support the view of Mikkelsen and Sinah (1961) that dormancy in rice seed is caused by the leaching of an inhibitor or inhibitors from the hulls into the pericarp-testa and embryo. Although the specific or even general mechanisms remain unknown, it is certain that both the hulls and pericarp-testa of rice seeds are involved in the establishment and release of dormancy in rice.

Causes of seed dormancy in rice

Several theories on the mechanisms of dormancy in rice have emerged from the voluminous database. Those that have already been mentioned and others include:

- the migration of inhibitors from the lemma and palea into the caryopsis;
- restriction of oxygen availability to the embryonic tissues imposed by the combined hulls and pericarp-testa;
- insufficient functioning of the pentose phosphate (PP) pathway in dormant seeds that is essential for the initial stages of germination (Roberts, 1973).

Dormant seed have a high activity of conventional respiration involving cytochrome oxidase that competes with the oxidase of the PP pathway. Treatments such as removal of the hulls and rupture of the pericarp-testa increase oxygen availability, which favours the PP pathway and releases dormancy. However, more recent work has cast considerable doubt on the PP pathway theory.

Leopold, Glenister and Cohn (1988) examined the loss of dormancy via after-ripening of red rice seeds as a model case to test the hypothesis that reactions regulating seed dormancy can proceed at water contents that are “probably” too low for significant metabolic activity. They found that after-ripening, i.e. release of dormancy, was most rapid at 6–14-percent moisture content (dry weight). The release of dormancy did not occur at more than 18-percent moisture and was severely inhibited at less than 5-percent moisture. The calculation of water-binding enthalpy values placed the optimal water content for after-ripening between water binding regions 1 and 2, i.e. the least to intermediate water contents. The authors speculated that there is a requirement for the completion of some chemical transformations in the dry seeds in order to produce a germination-ready state. At the 6–14-percent moisture content they determined

as optimal for release of dormancy, the necessary reactions would probably involve non-enzymic oxidations. At moisture contents below about 6 percent, the necessary reactions would be hindered by the increasing free energy required for reactions. At moisture contents above about 18 percent, increasing oxidative metabolic activity would gain dominance and suppress the non-enzymic oxidations involved in the release of dormancy. These speculations fit very well with previous observations that 8–12-percent seed moisture (wet basis) is the most favourable level for release of dormancy (Roberts, 1962; Jennings and de Jesus, 1964; Ellis, Hong and Roberts, 1983), that high moisture content seeds are more persistently dormant than those at lower (< 14 percent) moisture levels (Weir, 1959; Buenaventura, 1956), and that dormancy persisted in near fully imbibed seeds, circa 28-percent moisture content (Delouche and Nguyen, 1964; Teekachunhatean, 1985). It also fits findings on the persistence and seasonal variations in dormancy of rice seeds on or in the soil (Chapter 6).

Simpson (1990) reviewed and analysed the available and relevant information on all aspects of dormancy in grass seeds, including speculations, ideas, concepts and theories. The logical format adopted for the review illuminated the many similarities in response/reactions among species of *Poaceae* but did not produce a general theory of dormancy.

Dormancy release in nature

The operative factors involved in the release of dormancy in weedy red rice seeds under “natural” conditions, which is where dormancy is maintained or released, are considered in Chapter 6.

Chapter 5

Vigour and competitiveness of weedy rices

The vigour and competitiveness of weedy rices (including red rices) in rice fields is perhaps their most obvious characteristic. In North and South America and in Europe, the competition is primarily intraspecific and intense. The common red rices that infest rice fields have traits, properties and responses that give them a decided advantage over most cultivated varieties. In SSA, the competition is mainly interspecific but equally intense. The main weedy rices there are *Oryza barthii*, *O. longistaminata* and *O. punctata*. *O. barthii* and *O. longistaminata* are the most important and widely disseminated (Johnson *et al.*, 1999). *O. longistaminata*, a perennial with deep rhizomes that enable it to survive brush fires, shallow cultivation, and prolonged drought, is an especially fierce competitor. In Asia, where red rice originated, the competition has been largely interspecific but is becoming increasingly intraspecific (Chin *et al.*, 1999). Although some important weedy rices with and without the red pericarp belong to different species, their competitiveness is associated with many of the same traits, properties and responses possessed by the *O. sativa* red rices.

ECONOMIC LOSSES FROM WEEDY RICES

For more than 100 years, red rice has been considered the most abundant and difficult to control among rice field weeds in Louisiana (Stubbs, Dodson and Brown, 1904). In the 1970s, the annual economic loss from weedy rices in the United States of America related only to the discounted value of contaminated rice grain was estimated at US\$50 million (Eastin, 1978a). However, the total economic loss from weedy rice infestations is much greater when yield reductions caused by competition from red rice are taken into account. The newest, high-yielding rice variety in Arkansas, ‘Wells’, sustained a 35-percent yield loss when grown in a field infested with 22 red rice plants per square metre at Stuttgart (Burgos and Anders, ongoing research). Yield losses in producers’ fields can be lower or higher depending on the infestation level. Rice grain contaminated with red rice is discounted at the rice mill, so the total economic loss with a 35-percent yield reduction amounts to about 95 percent of the value of rice produced from a red rice-free field. Of the 0.6 million ha of rice in Arkansas, an estimated 60 percent are infested with red rice at some level. Based on the yield of Wells and a grain price of US\$86/tonne, the losses to producers could be as high as US\$200/ha. With 0.39 million ha infested with red rice in Arkansas, the total losses at current grain prices could be US\$78 million/year. The other rice-producing states in the United States of America, except California, have probably sustained proportional losses in recent years. The discounted mill price for red rice contaminated grain reflects the added costs of processing to reduce or eliminate the red rice, the decrease in head (whole grain) rice yield, and usually a reduction in grade, while the yield loss is the result of the considerable competitive capacity of red rice in rice fields.

COMPETITIVE TRAITS OF RED RICES COMPARED WITH CULTIVATED RICES

Compared with varieties they infest, the main weedy rices (including red rices) are generally taller, more heavily tillered, more open or spreading, have weaker culms, are more susceptible to lodging, produce more straw, germinate and emerge a day or two earlier, emerge from greater depths, and exhibit more rapid seedling growth (Sonnier, 1978; Eastin, 1978a; Do Lago, 1982; Teekachunhatean, 1985; Diarra, Smith and Talbert, 1985a; Kwon, Smith and Talbert, 1991a, 1992; Pantone and Baker, 1991a, 1991b; Wague, 1992; Carroza, 1999; Khodabaks, 1999; Fischer, 1999; Ferrero and Vidotto, 1999; Estorninos, Gealy and Talbert, 2002). These and other traits, properties and responses of weedy rices (including red rices) give them a competitive advantage over the cultivated varieties they infest.

Plant height

All 31 red rice phenotypes (21 SHR, 9 BHR and 1 BrHR) collected and characterized by Do Lago (1982) were substantially taller than Starbonnet, the tallest of the four varieties used for comparison (Table 2 – the red rice types designated with numbers larger than 80 or with a T, e.g. 86/1 and T/9, were collected by other workers after Do Lago had completed his work). The shortest SHR type was 19 cm taller than Starbonnet while the tallest was 51 cm taller. The BHR types were the tallest of the red rices with a height advantage over Starbonnet of 32–66 cm. The five SHR types collected in Mississippi after 1980 (designated with number greater than 80) were the offspring of crosses of an SHR type and one of the semi-dwarf varieties, e.g. Lemont, that had been released. The 19 red rice ecotypes (11 SHR, 6 BHR and 2 goldhull types) from four states characterized by Noldin (1995) were all significantly taller than the three cultivated varieties used for comparison. The height advantage of the red rice ecotypes over Mars, the tallest variety, ranged from 19 to 51 cm, while compared with the semi-dwarf Lemont, the height advantage ranged from 31 to 63 cm. Similar height advantages have been reported by Fischer and Ramirez (1993) in Colombia, De Souza (1989) in Brazil, Chin *et al.* (1999) in Viet Nam, and Ferrero and Vidotto (1999) in Italy. About a century ago, Dodson (1898, 1900) and Nelson (1907, 1908) described red rice as shorter than the varieties then cultivated. However, cultivated varieties have been progressively shortened to accommodate high levels of fertilizer and reduce lodging. The rice varieties of the green revolution developed by the International Rice Research Institute (IRRI) were much shorter and stiffer-strawed than the tropical varieties planted in the 1950s and 1960s. The semi-dwarf *indica* varieties, such as Lemont, introduced in the agriculturally advanced countries in the 1970s increased the height advantage of red rices considerably (Kwon, Smith and Talbert, 1991a, 1991b; Noldin, 1995; Ferrero and Vidotto, 1999). Tallness is a competitive trait in plant communities. Weeds taller than the crop are usually most competitive during the latter half of the season and have a greater effect on the yield components than growth of the crop as a result of the shading effect and lodging (Stansel *et al.*, 1965; Smith, 1968).

Tillers

Red rices produce many tillers, especially compared with the modern varieties bred for direct seeding and mechanized harvest. High densities of low-tillering plants produce high yields of uniformly maturing grain that facilitate harvest and post-harvest operations, e.g. drying. On the other hand, the high tillering capacity of red rices is a competitive advantage important for their success as weeds. All except two of the red rices characterized by Do Lago (1982) produced more tillers than Starbonnet, the most heavily tillered variety (Table 2). The two exceptions were tall, glabrous,

erect, moderately shattering, long-grain SHR types that mimicked the Bluebonnet 50 variety that Starbonnet replaced. The SHR types produced 10–100 percent more tillers than Starbonnet. The BHR types were more heavily tilled than the SHR types and produced 2–3 times as many tillers as Starbonnet. Similar results were obtained later by Noldin (1995) in studies where 2 of 19 red rice ecotypes produced fewer tillers than the Maybelle variety. Most of them produced 25–50 percent more tillers. Chin *et al.* (1999) reported that weedy rices in Viet Nam produced about 30 percent more tillers per plant in rice fields than did cultivated varieties. Sonnier (1978) described both SHR and BHR types as taller, more open, and heavily tilled compared with cultivated varieties and noted that the BHR types were the most heavily tilled with up to 50–75 tillers/plant in field infestations. Ferrero and Vidotto (1999) reported that in Italy red rices in the seedling stage are difficult to distinguish from those of the crop, but that, once tillering starts, the red rices are easily identified by their more numerous, longer and more slender stems. Plate 15 compares the tillering of two red rices with the Starbonnet variety.

Lodging

The competitive advantages of height and heavy tillering of the red rices combined with the “spreading” habit of the tillers contribute to early and severe lodging of the rice crop, a situation that further reduces competition from the shorter cultivated varieties (Quereau, 1920; Smith, Flinchum and Seaman, 1977). The taller BHR types lodge more easily than the shorter SHR types (Larinde, 1979), but both are susceptible to lodging and frequently collapse onto the cultivated rice, usually causing it to also lodge (Huey, 1978; Huey and Baldwin, 1978).

Germination and emergence

In the past, there seems to have been a general impression that red rice germinates and emerges more slowly than cultivated varieties. It probably derived from observations during germination testing and/or emergence trials of the seeds at times, e.g. within weeks after harvest, when there is a wide difference in the intensity of dormancy between red rices and cultivated varieties. As dormancy is manifested not only in the complete inhibition of germination but also by slower germination/emergence and greater specificity in the conditions required (Delouche and Nguyen, 1964), the less dormant or non-dormant seeds of the varieties germinate/emerge much faster than those of the red rices. However, such observations made during trials and experiments are not representative of the competitive situation during the planting season. For example, the red rice seeds that contaminate seed rice and are planted along with them were dried along with the seed rice and stored for months so that dormancy is released fully at the time of sowing.

Studies in Texas in the late 1970s compared the daily germinative responses of non-dormant seeds of a BHR ecotype with those of 22 rice varieties at temperatures of 15–40 °C during a seven-day period (Eastin, 1978b; Helpert and Eastin, 1978; Helpert, 1981). The lower limit for germination during the seven-day period was 15 °C, while 40 °C was detrimental. The optimal temperature for germination of the BHR type was 30–35 °C compared with 30 °C for the cultivated varieties. On average, the BHR germinated about 1 day earlier than the varieties over the range 20–35 °C. Pitty (1988) determined germination rates and percentages for non-dormant seeds of the Nato and Starbonnet varieties and the BLKH, SHA- and 79/15 red rices on a one-way thermogradient plate with a temperature range from 14 to 44 °C in a 14-day period. The three red rices germinated 1–2 days earlier and at cooler and warmer temperatures than the two varieties, which did not reach 50 and 80-percent germination within

TABLE 18

Temperature ranges for germination for cultivated varieties and red rice ecotypes at intervals during a 14-day period

Variety or ecotype		Germination period (days)				
		2	4	6	8	14
Temperature range for germination $\geq 50\%$ (°C)						
Nato	None	30-40	22-42	20-42	20-42	20-42
Starbonnet	None	26-40	22-42	20-42	20-42	20-42
79/15 (RR) *	34-40	24-42	22-42	20-42	20-42	20-42
BLKH (RR)	30-40	24-42	22-42	20-42	18-42	
SHA- (RR)	28-40	22-42	20-42	20-42	20-42	
Temperature range for germination $\geq 80\%$ (°C)						
Nato	None	30-40	26-40	26-40	22-42	
Starbonnet	None	26-40	26-40	24-40	20-42	
79/15 (RR)	34-40	28-40	24-40	22-42	22-42	
BLKH (RR)	34-40	26-42	24-42	22-42	20-42	
SHA- (RR)	32-40	24-42	24-42	22-42	22-42	

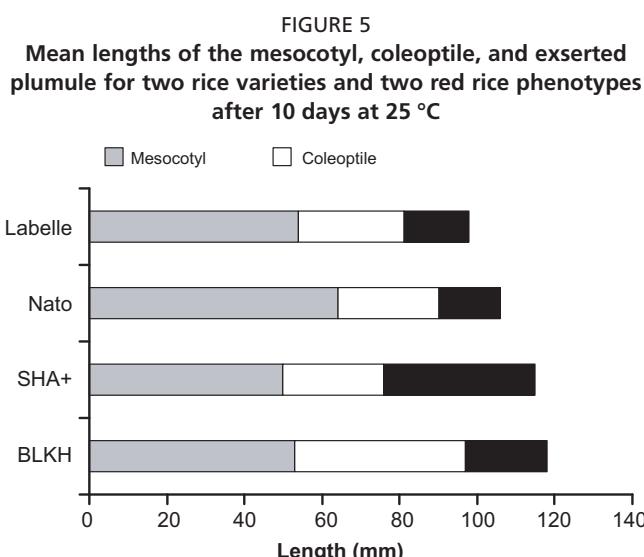
* RR = red rice.

Source: Pitty, 1988.

two days at any temperature (Table 18). The three red rices reached the 80-percent germination level in six days at temperatures 2 °C cooler and 2 °C warmer than the cultivated varieties. The optimal constant temperature for germination of the red rices was about 35 °C compared with 30-32 °C for the cultivated varieties. The three red rices germinated earlier and at much higher rate at 42 °C than the cultivated varieties, but there was little germination above 42 °C and below 18 °C for any of the entries during the test period.

Teekachunhatean (1985) compared development of the mesocotyl, coleoptile and plumule for the SHA+ and BLKH red rices and the Labelle and Nato varieties after ten days at 25 °C. Total seedling development was only marginally greater for the red rices than the varieties (Figure 5). However, the author noted that differences were much greater during the early days of the ten-day period and that, apparently, either the varieties "catch up" to the red rices or the red rices slowed development after about

five days. Wague (1992) repeated the study using two different and current varieties, Maybelle and Lemont, but the same two red rices at 30 °C for eight days rather than 25 °C for ten days. Seedling development of the red rices at eight days was about 50 percent greater than that of Maybelle and more than two times greater than that of Lemont (Figure 6) – the exceptionally short mesocotyl of the semi-dwarf Lemont variety and some of the later semi-dwarfs caused emergence problems and led to the development of the gibberellin seed treatment to increase seedling length, especially the mesocotyl. Both red rices were superior to Maybelle and Lemont in terms of root length at four and



Source: Teekachunhatean, 1985.

TABLE 19

Comparison of seedling vigour for the Maybelle and Lemont varieties and the SHA- and BLKH red rice phenotypes during an 8-day period at 25 °C in dark conditions

Variety or phenotype	Shoot length (cm)	Root length at		Seedling dry weight (mg)	Speed of germination index *
		4 days (cm)	8 days (cm)		
Maybelle	5.3c	10.0c	16.8b	2.24c	19.9c
Lemont	4.6c	8.4d	15.2c	2.05c	19.6c
SHA-	7.8b	14.0b	20.0a	3.33b	22.1b
BLKH	10.3a	15.0a	19.5a	3.68a	28.4a

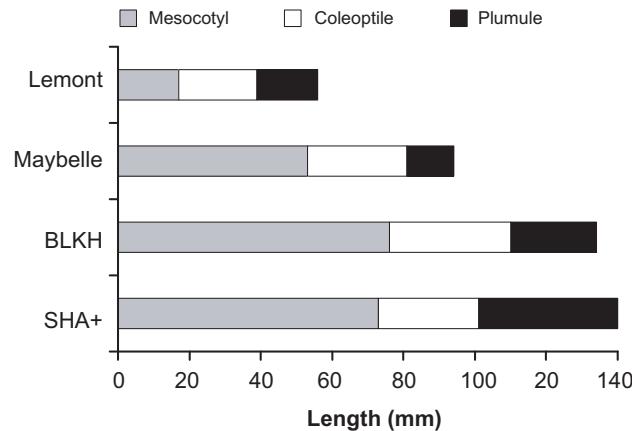
* Speed of germination index is based on the daily rate and percentage of germination (Maguire, 1962)

Source: Wague, 1992.

eight days, seedling dry weight and speed of germination. The BLKH phenotype exhibited a significantly greater rate of germination and seedling development than that of SHA+ (Table 19).

Helpert and Eastin (1978) conducted four depth-of-emergence studies in Texas in the late 1970s in order to compare the emergence of SHR and BHR ecotypes and five varieties from soil depths of 0, 1, 2, 4, 8 and 16 cm in the field and greenhouse. The emergence percentages and plant heights of the two red rices were higher than those of the cultivated varieties over all soil depths during the first half of the 24-day observation period. Emergence percentages for the red rices were still higher at 24 days but the varieties had about the same plant height. The two red rices emerged more rapidly and with higher percentages than any of the five varieties. Some seeds of the SHR type emerged from the 16-cm depth.

FIGURE 6
Mean lengths of the mesocotyl, coleoptile, and exserted plumule for two rice varieties and two red rice phenotypes after 8 days at 30 °C



Source: Wague, 1992.

EFFECTS OF RED RICE DENSITY AND PERIOD OF INTERFERENCE

Field experiments were conducted in Arkansas in order to evaluate the effects of season-long competition of 0, 5, 108 and 215 red rice plants per square metre on yield and yield components of the long-grain Lebonnet and medium-grain Mars varieties (Diarra, Talbert and Smith, 1984; Diarra, Smith and Talbert, 1985b). Red rice densities of 5 plants/m² reduced grain yield by 19–22 percent, while the highest red rice densities reduced grain yield by as much as 83 percent. Yield components negatively affected by competition with red rice at the higher densities included panicles per square metre and grains per panicle. However, the number of tillers was reduced significantly only at red rice densities of 108/m² or higher.

Teekachunhatean (1985) evaluated the effects of competition by the SHA- and BLKH phenotypes on the growth, development and yield of the Starbonnet variety. The competition level was a 1:1 ratio of each red rice type with Starbonnet with plants 15 cm apart in rows 30 cm apart. Plants were established by direct seeding and arranged in chequerboard fashion so that a red rice plant was surrounded by Starbonnet plants

TABLE 20

Effects of season-long competition between the Starbonnet variety and the SHA- and BLKH red rice types in a 1:1 ratio on the time of 50-percent anthesis, harvest maturity, tiller number, plant dry weight, and grain yield

Types in competition ¹	Days to		Plant height	Tillers	Dry weight per plant	Grain yield	
	50% anthesis	Harvest maturity ²				0.5 m ²	As % pure culture
			(cm)	(no./plant)	(g)	(g)	
Starbonnet							
Star/Star	93	123	115c	10.0d	34.6c	29.6b	–
Star/SHA-	93	123	117c	6.0e	17.0d	14.9cd	50.4
Star/BLKH	94	124	113c	5.8e	15.7d	11.7d	39.6
SHA-							
SHA-/SHA-	85	116	157b	14.8c	48.2bc	27.4bc	–
SHA-/Star	90	119	146b	18.2c	60.7b	38.0b	138.6
BLKH							
BLKH/BLKH93		123	177a	24.5b	66.6b	33.9b	–
BLKH/STAR91		121	153b	35.7a	95.2a	56.1a	170.6

¹ Star/Star, SHA-/SHA- BLKH/BLKH were pure culture. In the competitive 1:1 plantings, the data in the row are for the first type, e.g. Star/SHA- – data for Starbonnet. Means in each column not followed by the same lower case letter differ significantly at the 1-percent level of probability as determined by least significant difference.

² Grain moisture about 20 percent.

Source: Teekachunhatean, 1985.

and vice versa. The plant density per plot was about 30 plants/m². Table 20 shows the results of season-long 1:1 competition between Starbonnet and the SHA- and BLKH phenotypes, i.e.:

- no effect on time of anthesis, harvest maturity (circa 20 percent moisture) and plant height, with the exception that height of BLKH was reduced significantly by competition with Starbonnet;
- the number of tillers and dry weight per plant was reduced significantly for Starbonnet and increased for both BLKH and SHA-;
- grain yield of Starbonnet was reduced to 50 and 40 percent in competition with SHA- and BLKH, respectively, while the yields of SHA- and BLKH increased to 139 and 171 percent, respectively.

Grain yields of Starbonnet and the two red rices were comparable in pure culture. However, in competition, yield shifted to the red rices at the expense of Starbonnet, and increased significantly for BLKH.

Moreno (1990) examined the effects of season-long competition between the Maybelle and semi-dwarf Lemont varieties and the SHA- and BLKH red rices in a 1:1 ratio in both transplant and direct seeded culture. The number of tillers per plant, green weight per plant at 100 days, panicles per plant, grains per panicle and grain yield were reduced significantly for both varieties in both cultures (Table 21). The negative effects of competition with the red rices were greatest for the semi-dwarf Lemont.

The effects of season-long interference of an SHR ecotype at densities of 1–40 plants/m² on the growth, development and yield of the Newbonnet and Lemont (semi-dwarf) varieties were reported by Kwon, Smith and Talbert (1991a). Season-long interference had moderate to severe effects on the performance of the varieties depending on the density of the red rice. Straw dry weights of the Newbonnet and Lemont varieties were reduced by 100 and 130 kg/ha, respectively, for each red rice plant per square metre, while grain yields were reduced by 178 and 272 kg/ha for each red rice plant per square metre. The height of plants of the semi-dwarf Lemont was reduced by 10 red rice plants per square metre while that of the taller Newbonnet was reduced only at the highest density of 40 plants/m². The plant height of the red rice increased as the density of red

TABLE 21

Effects of season-long competition between the Maybelle and Lemont varieties and the SHA- and BLKH red rice types in transplant and direct seeded culture on biomass and some yield components of the two varieties

Types in competition	Tillers per plant at 100 days		Green weight per plant at 100 days		Panicles per plant at maturity		Grains per panicle at maturity		Relative yield in grains per plant ⁴	
	TP ¹	DS ²	TP	DS	TP	DS	TP	DS	TP	DS
	(no.)	(g)	(no.)	(no.)	(%)	(%)				
Maybelle (solo)	17a ³	18a	294a	330a	14a	15a	132a	172a	100	100
1:1 Ratio										
Maybelle/SHA-	11b	12b	178b	160b	8b	7b	81c	73c	35	20
Maybelle/BLKH	11b	10b	173b	180b	7b	8b	78c	66c	29	21
Lemont (solo)	16a	17a	276a	362a	12a	13a	111b	127b	100	100
1:1 Ratio										
Lemont/SHA-	10b	11b	161b	172b	6b	6b	45d	60c	20	21
Lemont/BLKH	9b	10b	164b	148b	6b	5b	50d	70c	23	21

Notes: Means in each column not followed by the same lower case letter differ significantly at the 1-percent level of probability.

¹ Transplant culture.

² Direct seeded culture.

³ All data are for the cultivated variety.

⁴ Yield based on grains per plant of variety in 1:1 competition relative to its yield in monoculture.

Source: Moreno, 1990.

rice increased but was greater in competition with the conventional variety Newbonnet than with the semi-dwarf Lemont. Overall, the interference of red rice was greatest with the semi-dwarf Lemont, which the authors attributed to increased shading.

In a related study, Kwon, Smith and Talbert (1991b) evaluated the influence of interference durations of an SHR ecotype on the growth, development and yield of rice of the Newbonnet and semi-dwarf Lemont varieties in order to obtain information useful in managing and timing control operations. Red rice at 20 plants/m² was grown with the two varieties for durations from 0 to 120 days after emergence. Competition of red rice for 120 days, i.e. full season competition, reduced straw dry weights by 58 and 34 percent and grain yields by 86 and 52 percent for Lemont and Newbonnet, respectively. Straw dry weights of the varieties were affected progressively and negatively as red rice interference extended beyond 40 days, while grain yields decreased progressively as the period of interference extended beyond 60 days. Other parameters of performance affected negatively by extended red rice interference included: plant height, panicles per square metre, spikelets per panicle, and filled grains per panicle. For the all parameters measured, the semi-dwarf Lemont was affected more negatively than was the conventional Newbonnet. Similarly, straw dry weight and number of tillers were greater for the red rice in competition with the short stature Lemont. Therefore, red rices are more similar to other common rice field weeds, such as hemp sesbania (*Sesbania exaltata*) and northern jointvetch (*Aeschynomene virginica*), that become very competitive in the latter half of the season than like barnyard-grass (*Echinochloa crus-galli*), the most common weed in rice, which is a vigorous early-season competitor (Smith, 1968). More recent studies by Pantone and Baker (1991b) and Pantone, Baker and Jordan (1992) found that intervarietal competition had more effect than intravarietal competition, and that competition with weedy rice reduced the number of rice panicles and florets per panicle but not the number of filled florets or their weight, i.e. the quantity of yield was reduced rather than its quality. Estorninos *et al.* (2005b) reported that rice growth in competition with weedy rice was reduced only when the interference persisted longer than 70 days, which is somewhat longer than the 40 days of interference for biomass reduction and 60 days for yield reductions reported earlier by Kwon, Smith and Talbert (1991b).

OVERALL EFFECTS OF COMPETITION

The earliest workers in rice culture in the United States of America noted that, without the rigorous and conscientious use of the then available control measures, the population or density of red rice in continuous rice culture often increased to the extent that the infested fields became unfit for rice production (Dodson, 1898; Knapp, 1899; Quereau, 1920). Most of the discussions at the pioneering 1978 symposium on red rice research and control (Eastin, 1978a) emphasized the seriousness of the problem and the need for rice producers to exploit all available measures for control of red rice. Dishman (1978) related how a 100-ha field had to be abandoned for rice production because of the severity of the red rice infestation and the steps that were taken to reduce the density of red rice sufficiently to begin rice production again. Sonnier (1978) discussed in detail the alternatives and options available to rice farmers to control red rice sufficiently in order to maintain economically viable production. Although additional weapons in the battle against red rice have been developed since 1978, those discussed and recommended at the 1978 symposium remain the core of the package of control measures.

The consequences of red rice infestations depend on the degree of infestation and the control measures taken. From most to least serious, they include:

- the eventual abandonment of the area for rice production owing to an overwhelming population of red rice;
- substantial reductions in yield and lower grain prices owing to discounts for the presence of red rice in the grain;
- increased costs of production, e.g. labour, chemicals, equipment and energy used for control;
- the inconvenience of roguing minor infestations.

Reductions in yield are a common and frequently serious consequence of red rice infestations. Infestations of 60 red rice plants per square metre reduced yield by 30–50 percent in Brazil (De Souza, 1989), while 24 plants/m² reduced yields in Colombia by 50 percent (Fischer and Ramirez, 1993). Ten or fewer weedy rice plants per square metre did not affect yield in Costa Rica, but each weedy rice plant above 10 plants/m² decreased yield by 0.09 tonnes/ha (Espitia, 1999). Garcia de la Osa and Rivero (1999) reported red rice infestations of up to 240 plants/m² in some heavily infested areas in Cuba and noted that the short-cycle varieties were most affected. Yield reductions can be as high as 40–60 percent in Mexico (Martinez, 1999), while in Suriname yield was reduced by 6 percent for every 1-percent increase in the rate of infestation (Khodabaks, 1999). Chin *et al.* (1999) reported on results of studies in Viet Nam that showed that rice yield began to decrease as the number of weedy rice tillers exceed 12 tillers/m². In Europe, red rice infestations can reduce rice yield by 50 percent in France (Mouret, 1999) and even more from heavy infestations in Italy (Ferrero and Vidotto, 1999).

THE PHYSIOLOGY AND COMPETITIVENESS OF RED RICES IN THE UNITED STATES OF AMERICA

Timely, effective and economical weed control technology for rice production is influenced by several factors including interference thresholds, biology, and growth habits of weeds in rice culture (Smith, 1988). The impact of weedy rice on rice depends on crop-weed densities, interference duration, the variety planted, soil fertility levels, and soil moisture regime. Short-stature cultivars grow more slowly than the old tall varieties. Therefore, it takes longer for the crop canopy to close. This gives more possibility for weeds, such as red rice, to overcome rice. The switch from tall- to short-stature rice varieties had the undesirable side-effect of exacerbating the weed

problem because it favours the growth and competition of *Echinochloa crus-galli*, red rice, sprangletop (*Leptochloa* spp.), and aquatic weeds (Smith, Flinchum and Seaman, 1977; McGregor, Smith and Talbert, 1988). The competitive advantage is tipped further in favour of weeds where fertilizer is applied early in the season, as is necessary for the rice crop.

C_4 plants are expected to be more competitive than C_3 plants because the latter are less efficient in carbon assimilation than the former (Orsenigo, Patrignani and Rascio, 1997), especially in warm and water-deficient climate zones. For example, grain sorghum (*Sorghum bicolor*) is a C_4 crop species that is very productive in Kansas and Texas, where summer temperatures are high and rainfall is limited. Many of the problem weeds in rice are C_4 , except for red rice, which is a C_3 plant like cultivated rice. Smith (1988) reported on weed thresholds in the south of the United States of America. Of the ten weedy species studied, season-long competition with red rice caused the highest yield reduction in rice (about 80 percent). The shorter the duration of red rice competition, the less effect it had on rice yield. *Echinochloa crus-galli*, the most prevalent weed in rice production, was only second to red rice in terms of season-long effect on rice yield, with a 70-percent reduction. Red rice was also a more aggressive and damaging competitor in rice fields than other grass weeds, such as bearded sprangletop (*Leptochloa fascicularis*), and broadleaf signalgrass (*Brachiaria platyphylla*). Studies in Arkansas in the early 1980s using drill-seeded Newbonnet rice demonstrated that one red rice plant per square metre reduced rice yield by 219 kg/ha (Smith, 1988). There appears to be a narrow window from planting up to the 2- to 3-leaf stage when red rice has no impact on rice growth and is also susceptible to chemical control measures. Beyond this point, it becomes increasingly aggressive as it grows taller and larger than rice. Acceptable levels of red rice control were attainable only with great difficulty, expense, and/or long-term rotations until the commercialization of recent herbicide-resistant Clearfield rice technology.

Regarding economic thresholds for control, Smith (1988) advocated a low tolerance for red rice in rice production fields, as densities of 1–3 plants/m² were considered the trigger point for red rice control measures, a relatively stringent criteria that has not changed. In contrast, up to 10 plants/m² is considered the economic threshold for *Echinochloa crus-galli*, and threefold or more for other species.

Competition mechanisms

Competitiveness is the ability to deplete rapidly consumable resources, such as water and nutrients, or to grow better than associated species when these resources are limiting (Radosevich, Holt and Ghersa, 1997). There needs to be an explanation as to why a C_3 plant, red rice, is more competitive than another C_3 plant, cultivated rice. There are several possible causes for the underlying differences between cultivated and weedy red rice in terms of genetic differences and the resulting physiological responses to the environment. However, only recently have preliminary experiments been conducted to elucidate possible competitive mechanisms, some highlights of which are discussed below.

Many of the morphological traits that contribute to the competitiveness of red rices in rice fields have been identified and discussed above. Red rices are generally taller, produce more tillers, and have a larger leaf area than rice (Kwon, Smith and Talbert, 1992; Noldin, Chandler and McCauley, 1999; Estorninos, Gealy and Talbert, 2002). Height, aboveground and belowground biomass production, and leaf area are among the strongest indicators of the competitive ability of a plant (Gaudet and Keddy, 1988). Red rices possess these competitive traits and are much more aggressive competitors than cultivated rices (Pantone and Baker, 1991b; Estorninos, Gealy and Talbert, 2002).

TABLE 22
Comparative agronomic and physiological traits of rice and weedy rice grown in non-competitive conditions at the Rice Research and Extension Center, Stuttgart, Arkansas, between May and August in 2000 and 2001

Rice cultivar or red rice type	Shoot biomass ¹		Tiller number	Panicles per plant	Grains per panicle	(no.)	Total chlorophyll ³ (mg/g f wt)	Photosynthesis reduction ³ (%)	$\delta^{13}\text{C}$ (‰)
	100 N	200 N							
Bengal	175	210	54	51	70	3 794	1.67	42	-26.96
Wells ²	270	290	64	32	73	2 399	2.02	46	-28.04
Katy red rice	230	260	51	45	101	4 136	1.29	27	-27.98
Strawhull red rice	380	400	76	86	159	15 133	1.40	32	-28.09
LSD _{0.05}			12	8	28	1 201	0.35	11	
N rate = 44									

Note: Factors involved in these experiments are: (i) plant type (as indicated in the table); (ii) N rate (0, 100 and 200 kg/ha); and (iii) shade (0 and 50%). Shade treatment was imposed 10 days after initiation of flowering of each plant type and imposed for 7 days. This duration of shade did not affect tillering, shoot biomass, and grain production.

¹ N rates are in kilograms per hectare.

² Yield parameters for Wells were available only in 2001. It did not mature before the onset of cold weather in 2000.

³ Chlorophyll and photosynthesis were measured from flag leaves, two days after imposing the shade treatment.

⁴ Analysed using the youngest leaf of each plant sampled, at 100 kg N/ha, 40 days after planting in 2000 and at flag leaf exertion in 2001, which was before the shade treatment. The values obtained are representative of C₃ plants in contrast to that of *Echinochloa crus-galli* (-12.13), which is a typical C₄ plant.

Source: Data extracted from Stiers (2002).

The advantages of light interception and occupying space

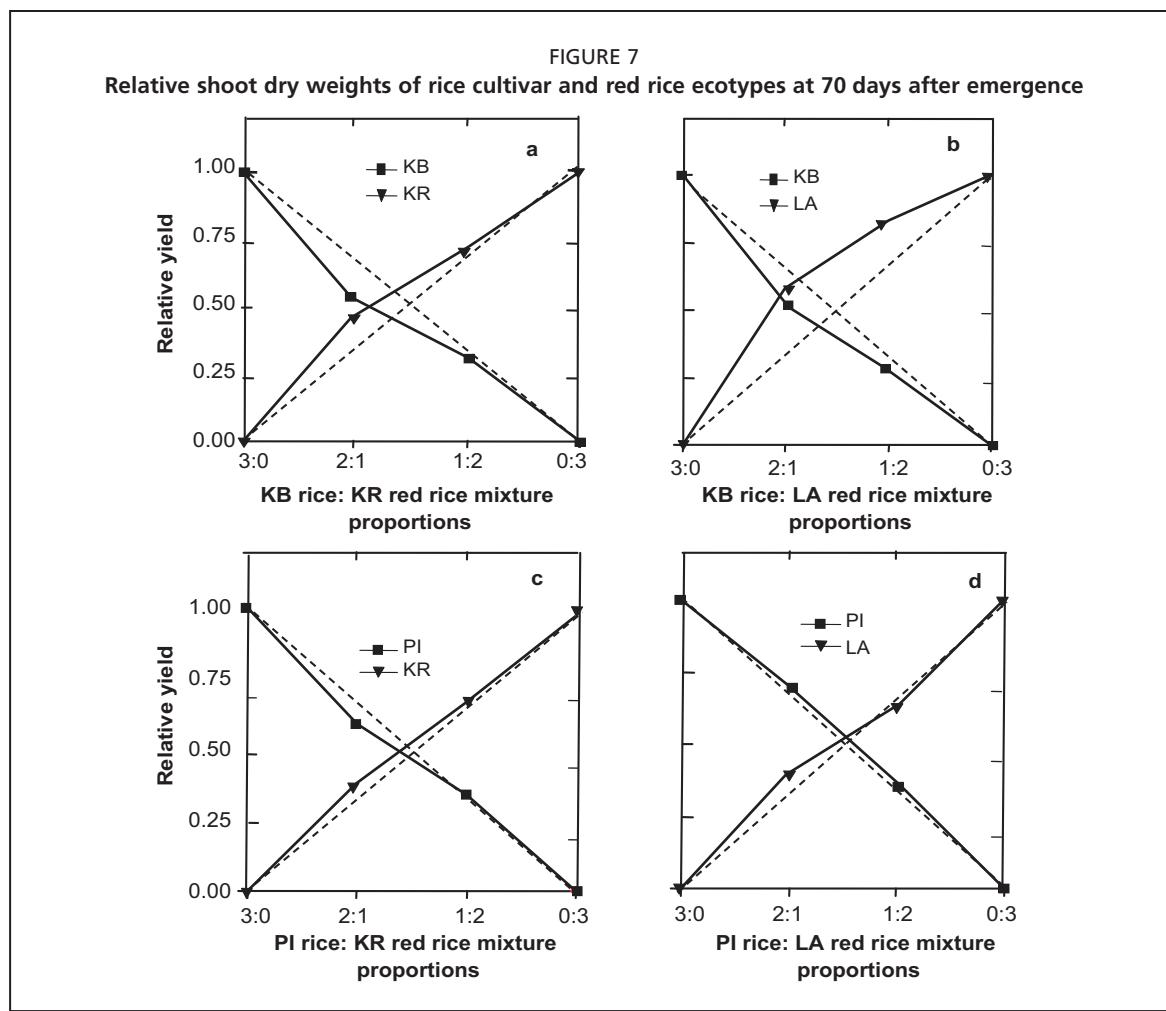
Tiller production in *Poaceae* (grasses) correlates strongly with biomass production and resource acquisition. Therefore, red rice, which can produce twice as many tillers as rice can, has the competitive advantage. High-tillering red rice occupies more space, crowds out other plants, and has a higher leaf area for greater light interception. In the absence of competition, SHR rice produced significantly more tillers than cultivated rice under similar conditions (Table 22). When grown in competition, red rice (LA3) also produced more tillers and shoot biomass than the variety Kaybonnet (Estorninos *et al.*, 2005b). However, the competitiveness of red rice is influenced by the red rice biotype and the variety it infests. Potential tiller production (and plant height) varies greatly among red rice types (Chapter 3 and earlier in this chapter). In studies in Arkansas (Shivrain, 2004), the most common tiller number per plant for BHR and BrHR rice in the absence of competition was about 120/plant with a range of 70–140/plant. SHR rice, the dominant type of weedy rice, had a lower potential tiller production at 70–120/plant, but this is still much more than the tillering capacity of the rice varieties developed for mechanized rice production.

Another means of plants gaining a competitive edge over other plants for light interception is tallness. The height advantage of red rice over cultivated rice has already been discussed. The height of red rice ecotypes affects the varieties it infests and, in turn, is affected by the variety. The tall red rice (LA3) planted over a range of densities in competition with Kaybonnet planted at the usual rate (100 kg/ha) produced dramatically more tillers, panicles, biomass, and seed yield than did a short red rice type, KatyRR, derived from a cross with the Katy variety (Estorninos *et al.*, 2005b). Similarly, yield, panicle density and aboveground biomass of Kaybonnet rice were substantially lower when grown in competition with the tall LA3 ecotype than with the short KatyRR.

Height advantage and tillering capacity have compensatory effects for competition. A red rice biotype might not be significantly taller than the rice variety but still compete aggressively by producing more tillers. In pot studies (Figure 7), semi-dwarf varieties with high-tillering capacity, such as PI 312777, 82 cm, 12 tillers/plant, were as competitively aggressive as red rice in contrast to tall but low-tillering varieties such as Kaybonnet, 100 cm, 5 tillers/plant (Estorninos, Gealy and Talbert, 2002). Similar results were obtained in field studies where high-tillering *indica* cultivars PI 312777 and Guichao at commercial planting rates (100 kg/ha) reduced red rice tiller numbers much more than did Kaybonnet (Estorninos *et al.*, 2005a).

Because the agronomic characteristics of a rice variety influence its capability to withstand competition (Johnson *et al.*, 1998), competitive traits should be considered in breeding for high yield and good grain quality. Tall rice varieties, which have not undergone intensive selection for specific agronomic traits, or are still genetically closer to the wild relatives, are more competitive than semi-dwarf ones in mixed populations (Jennings and Aquino, 1968; Jennings and de Jesus, 1968). For example, Newbonnet, a tall variety, suffered less yield loss from red rice competition compared with Lemont, a semi-dwarf variety: 10 red rice plants per square metre caused a 27-percent yield reduction in Newbonnet, but a substantially greater yield loss of 45 percent in Lemont (Kwon, Smith and Talbert, 1991a).

The newer rice varieties including CL161, Cocodrie, LaGrue, and XL8 (hybrid rice) are generally less affected by red rice competition at densities of up to 12 plants/m² compared with the older, semi-dwarf variety Lemont (Ottis *et al.*, 2005). At the very low red rice density of fewer than 1 plant/m², Lemont generally produced the lowest yield (about 5–7.5 tonnes/ha) while the hybrid XL8 produced the highest yield (9–11.8 tonnes/ha) across different locations. The newer, non-hybrid cultivars either had



Note: As influenced by 3:0, 2:1, 1:2, and 0:3 rice-red rice mixture proportions: (a) Kaybonnet rice (■KB) and KatyRR red rice (▼KR); (b) Kaybonnet rice (▼KB) and LA3 red rice (▼LA); (c) PI 312777 rice (■PI) and KatyRR red rice (▼KR); and PI 312777 rice (■PI) and LA3 red rice (▼LA). The dashed lines in each frame indicate the theoretically expected response for two equally competitive species, which intersect at the point of equivalency.

Source: Estorninos, Gealy and Talbert, 2002.

the same or a higher yield than Lemont, but were less productive than the hybrid. This indicates that selection for higher yields did not eliminate the competitive ability of the newer cultivars. The hybrid rice has larger plants with more tillers than the modern, conventional rice varieties, and it is thought to be more competitive than them. This was most apparent where red rice density was high (12 plants/m²).

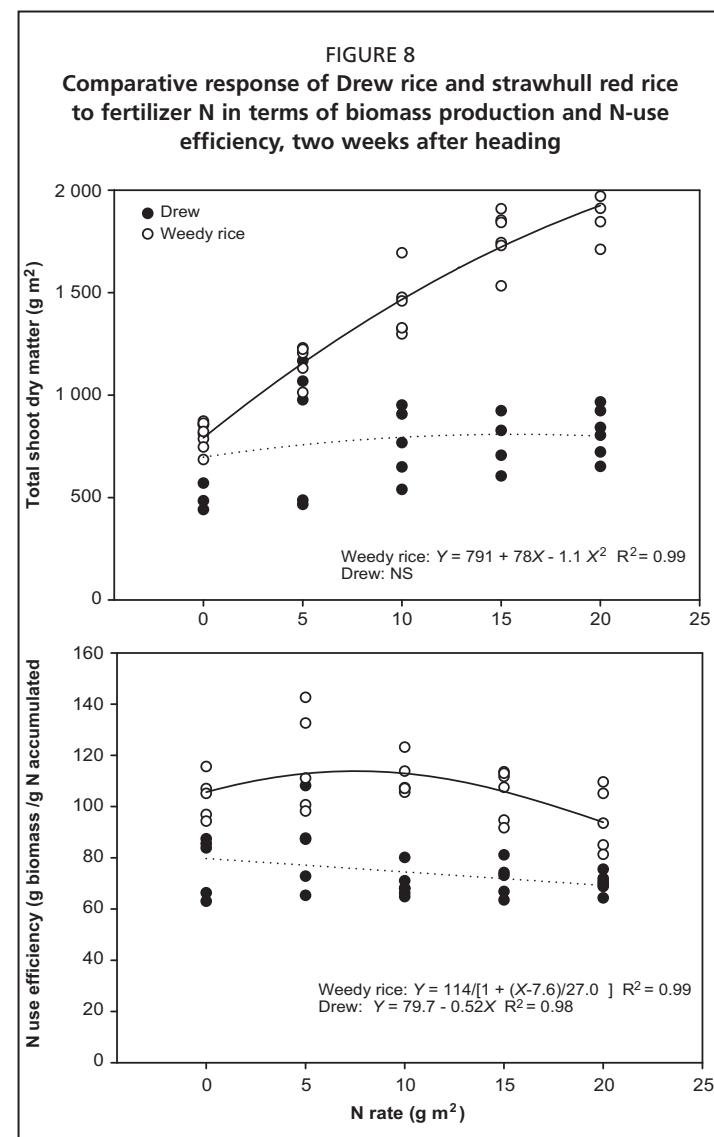
Nitrogen uptake and nitrogen-use efficiency

Red rice grows faster and matures earlier than many modern rice varieties and even older varieties such as Newbonnet and Lemont (Kwon, Smith and Talbert, 1992). This difference in biomass production between the weed and the crop is magnified in the field. Even in the absence of competition, rice and red rice respond differently to fertilizer nitrogen (N). At N doses optimal for the varieties Bengal and Wells (100 kg N/ha), SHR rice produced 1.4–2.2 times more biomass than the varieties (Table 23). At a high fertilizer N dose (200 kg/ha), the rates of leaf emergence of Bengal (medium grain) and Wells (long grain) declined relative to those under the optimal N rate. Conversely, the rate of leaf emergence of the SHR rice grown with 200 kg N/ha increased significantly relative to those with the lower N rate (Stiers, 2002). This indicates that excessive N fertilization delays the maturity of rice but not that of red rice.

Differences in red rice biology influenced its interference with rice. Burgos *et al.* (2006a) found that in a mixed population of three plants of the Drew variety to one SHR rice plant, the latter accumulated more N in its shoot tissues, produced more shoot biomass per unit N absorbed, and responded to higher N levels than the variety (Figure 8). Without N fertilizer, the red rice produced 791 g of shoot biomass per square metre compared with 686 g/m² for Drew two weeks after heading at Stuttgart, Arkansas. Drew did not respond significantly to added N up to a rate of 20 g/m² whereas red rice continued to produce significantly more shoot biomass in response to added N and did not reach maximum biomass production within the fertilization dose range used. The response of red rice to fertilizer N became much greater relative to the Drew variety two weeks after heading than at panicle initiation. This supports the general observation and contention that red rice becomes more vigorous and more competitive as the growing season progresses. Two weeks after heading, red rice also showed a steady rate of N uptake as more N was applied up to 20 g/m². In contrast, Drew rice showed a declining rate of N accumulation in shoot tissue as more N was applied.

These results indicated that red rice was able to remove more N from the soil than Drew rice. On average, red rice accumulated 63 percent of applied N in its shoot tissue two weeks after heading, apparently as a result of the large amount of biomass that it produced both aboveground and belowground. SHR rice produced at least 1.5 times the root biomass of the medium-grain Bengal and long-grain Wells varieties under non-competitive conditions (Table 22).

The rate of shoot biomass production for every unit of total N accumulated (N-use efficiency) was higher in red rice than in Drew rice when fertilizer N was added, and this became more apparent at two weeks after heading (Burgos *et al.*, 2006a). At an earlier growth stage (panicle initiation), Drew and red rice produced equivalent amounts of shoot biomass per gram of N accumulated when no fertilizer N was added, 69 and 72 g/g, respectively. While N-use efficiency for both Drew and red rice declined linearly with increasing N, red rice produced significantly more shoot biomass per unit of total N accumulated than Drew averaged over N rates. Two weeks after heading, N-use efficiency for Drew declined linearly with N dose while that of red rice reached



Note: Rice and red rice were grown under competitive conditions (alternate rows, 19 cm apart) with red rice at one-third the population of Drew rice, Stuttgart, Arkansas, USA.
Source: Adapted from Burgos *et al.* (2006a).

TABLE 23

Comparative growth between rice and red rice under non-competitive condition, with optimal soil fertility level, in pot experiments conducted outdoors, May–September 2001, at Main Agricultural Research and Extension Center, University of Arkansas, Fayetteville, USA

Harvest time ¹ DAP	Rice or red rice type ²	Root biomass	Shoot biomass (g/plant)	Total biomass	Growth rate (g/day)
14	Bengal	0.02	0.02	0.04	—
	Wells	0.02	0.02	0.04	—
	Strawhull red rice	0.03	0.02	0.05	—
21	Bengal	0.24	0.11	0.35	0.04
	Wells	0.16	0.08	0.24	0.03
	Strawhull red rice	0.21	0.13	0.34	0.29
28	Bengal	0.55	0.19	0.74	0.39
	Wells	0.21	0.27	0.48	0.24
	Strawhull red rice	0.36	0.31	0.67	0.33
90	Bengal	231.80	86.19	317.99	5.12
	Wells	211.08	79.09	290.17	4.67
	Strawhull red rice	390.78	137.81	528.59	8.51
130	Bengal	191.75	73.88	265.63	-1.31
	Wells	190.62	71.38	262.00	-0.70
	Strawhull red rice	237.50	138.88	376.38	-3.81
LSD _{0.05}		72.70	12.81	22.70	0.93

Note: Values are average of four replications.

¹ DAP = days after planting.

² Bengal = medium-grain rice; Wells = long-grain rice; strawhull red rice = biotype from Stuttgart, Arkansas.

Source: Adapted from Stiers (2002).

a peak at an N rate of less than 10 g/m². The maximum N-use efficiency for red rice was 114 g of shoot biomass per gram of total N accumulated at the 7.4 g N/m² rate, as compared with only 75.8 g of biomass per gram of N accumulated by Drew at the same N rate. Thus, regardless of the N rate, the N-use efficiency was higher for the red rice than for the variety Drew.

Red rice and a possible intermediate C₃-C₄ carbon fixation pathway

The very recent studies discussed above suggest that one of the important mechanisms for the competitiveness of red rice in rice fields is its capacity to produce more root and shoot biomass and accumulate more N than the cultivated varieties it infests. As the process of N uptake and assimilation is related closely with photosynthesis, it could be that red rice has higher photosynthetic efficiency than rice. It has been established that some wild rice types, e.g. *Oryza rufipogon* and *O. australiensis*, have evolved an intermediate carbon fixation pathway (Yeo, Yeo and Flowers, 1994) that is better than C₃ but not quite as efficient as C₄. These improvements in system efficiency, as discussed by Ku *et al.* (1991), include:

- stronger affinity for CO₂ than for O₂ in the ribulose-1,5-bisphosphate carboxylase-oxygenase (variety Rubisco) binding site;
- reduced photorespiration rate compared with C₃;
- reduced CO₂ compensation point compared with C₃;
- a tendency towards Krantz anatomy.

As noted above, the presence of these characteristics of an intermediate carbon fixation system have been reported for *O. rufipogon* and *O. australiensis*. Therefore, a preliminary study was conducted to determine the carbon fixation pathway of red rice using discrimination ratios of C¹³ to C¹². Rubisco preferentially binds the lighter carbon isotope. Therefore, C₃ plants have lower carbon discrimination ratios than C₄ plants. As these values are expressed relative to a reference with higher ¹³C/¹²C than the sample, the final isotope discrimination values (δ¹³C) are negative. C₃ plants then

would have more negative values than C₄ plants. The field experiments conducted at the Rice Research and Extension Center, Stuttgart, Arkansas (Stiers, 2002), showed that the medium-grain Bengal and long-grain Wells varieties had $\delta^{13}\text{C}$ values of -26.96 and -28.05, respectively, while *Echinochloa crus-galli*, a C₄ plant, had $\delta^{13}\text{C} = -12.13$ (Table 22). These values are typical. The red rice biotypes Katy-RR and Stuttgart SHR rice had $\delta^{13}\text{C}$ values of -27.98 and -28.09, respectively, which were similar to those of the rice varieties. These recent, preliminary studies indicate that a modified or intermediate, more efficient pathway than the normal C₃ system is probably not involved in the competitiveness of red rices.

Shade adaptation

Many weedy species of *Oryza* (*O. australiensis*, *O. brachyantha*, *O. nivara*, *O. longistaminata*, *O. barthii*, and *O. rhizomatis*) show the same photosynthesis rates as cultivated rice (Yeo, Yeo and Flowers, 1994). Preliminary experiments conducted in Arkansas also showed that red rice (*O. sativa*) has the same photosynthesis rate as cultivated rice (Stiers, 2002). However, it has been observed that in growers' fields even sparsely distributed red rice plants seem to always manage to grow above the rice canopy, and short-stature red rice plants are able to grow normally in the usual dense stand of cultivated rice. However, where the situation is reversed in terms of density, cultivated rice cannot overcome the shading effect of weedy rice. Therefore, it has been theorized that weedy rice has better tolerance to shading than cultivated rice. Experiments conducted by Stiers (2002) at Stuttgart, Arkansas, in 2000 and 2001 showed that the medium-grain Bengal and long-grain Wells varieties sustained 42 and 46 percent reduction in photosynthesis rate, respectively, 2 days after being subjected to 50-percent shade compared with only a 38-percent reduction for the Stuttgart SHR rice (Table 22). The shade treatments were applied 10 days after 50-percent anthesis. The significantly lesser effect of shading on the photosynthesis rate of red rice suggests that it is more tolerant of reduced light than cultivated rice and, thus, might be able to grow well in normal rice populations even when it emerges later than the crop, or when it is set back temporarily by herbicide application. A possible mechanism of shade adaptation could be an altered chlorophyll a/b ratio in response to shade. This was observed in Stuttgart SHR rice, which showed a ratio of 4.69 chlorophyll a:b without shade and 4.19 after 2 days of exposure to 50-percent shade. The chlorophyll a:b ratios of rice cultivars were not altered by shading. The reduced chlorophyll ratio reflects an increase in the proportion of chlorophyll b relative to chlorophyll a. An increase in chlorophyll b per unit area allows efficient harvesting of light under reduced light conditions. This type of response has also been observed in cotton, where the chlorophyll a/b ratio decreased when plants were shaded for 2–8 days (Zhao and Oosterhuis, 1998).

Chapter 6

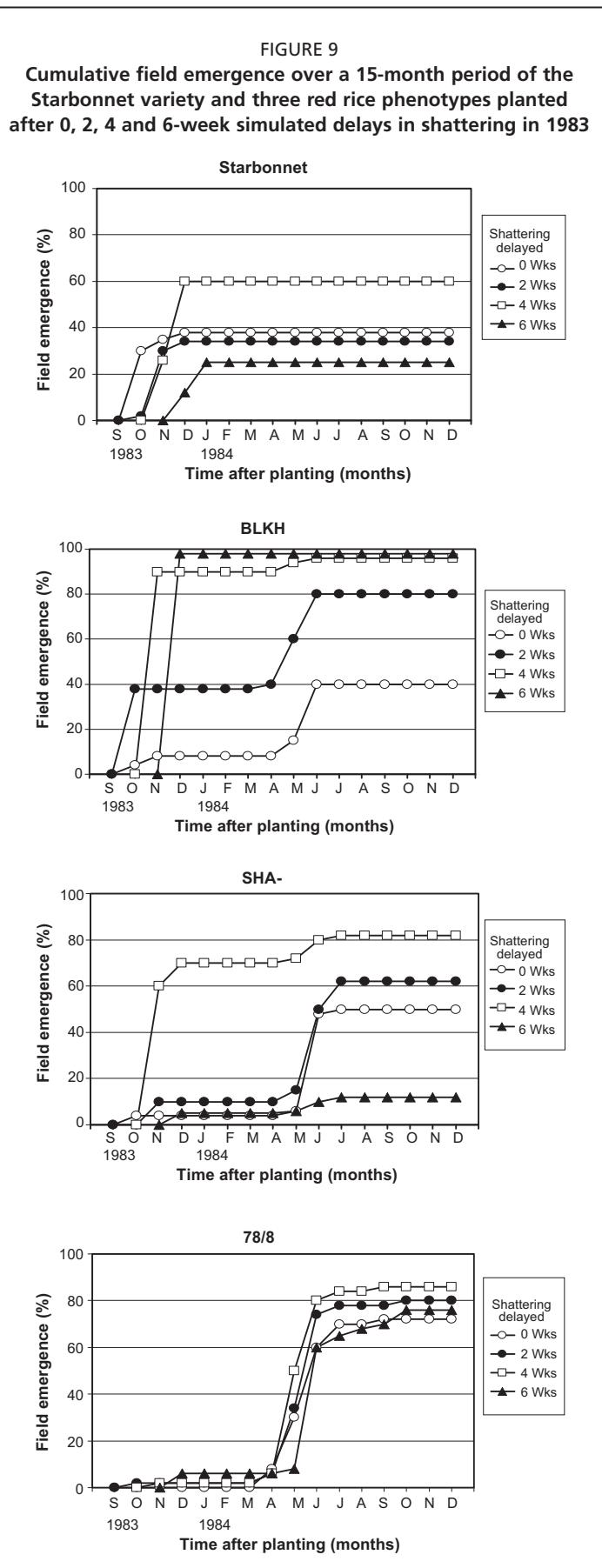
Ecological relationships

Much information is available on the diversity, characteristics/traits, and competitive capabilities of weedy rices (including red rices). However, much less is known about the ways these characteristics interact with one another and with environmental factors to adapt these rices to the ecology of various rice culture systems. Ecology is concerned with how living organisms adapt to and live in various environments, i.e. make themselves “at home” (Heydecker, 1973), and weedy rices (including red rices) have made themselves “at home” in direct-seeded rice culture in climate zones ranging from the tropics to temperate zones (Labrada, 1999). Several of the participants in the 1978 Red Rice: Research and Control symposium (Eastin, 1978a) pointed out that more research on the characteristics and ecological relationships of red rices was needed in order to find “weak links” in their life cycle that might be useful in devising effective and efficient control strategies (Sonnier, 1978; Helpert and Eastin, 1978; Eastin, 1978b). Eleven of the 21 conclusions and recommendations of the Global Workshop on Red Rice Control (FAO, 1999) dealt with the need for more information and research on various ecological aspects of infestations of weedy rices (including red rices) and on practical, integrated control measures.

Interesting and valuable research information on the ecological relationships of weedy rices (including red rices) has been developed since the late 1970s for direct-seeded, mechanized rice culture systems in temperate or near-temperate climate zones in North and South America and in Europe. A significant portion of this information has been developed by graduate students from different rice-growing countries whose studies have not been published. Some of the results of their studies have been reviewed and presented above. This chapter discusses additional results from their work and from other resources in order to illuminate the interactions between some of the traits of red rices with environmental factors that permit them to invade, spread and persist in the direct-seeded, irrigated rice production systems in temperate zones.

SEED SHATTERING AND DORMANCY

The roles of early, easy and severe seed shattering (or shedding) and seed dormancy of varying intensity in the establishment, maintenance and survival of communities of “native”, i.e. unimproved, plants have been reviewed and discussed in Chapter 4. In the case of red rice, the seed-shattering trait ensures that a sufficient portion of the seeds produced falls to the soil to produce the next cycle of plants rather than being taken away as contaminants in the harvested grain (Constantin, 1960). The role of seed dormancy in the survival of red rice during periods of freezing temperature in the winter season has long been recognized (Dodson, 1898). In considering these two critical and invariable traits of red rice, questions arose regarding their relationship (Do Lago, 1982), specifically, as to whether and how the two traits interact to enhance the survivability and persistence of red rices. Teekachunhatean (1985) designed some studies to answer this question taking into account earlier work that demonstrated the great effect of drying and warm temperatures on the release of seed dormancy in cultivated rice (Weir, 1959; Umali, Parker and Dumla, 1960; Roberts, 1962; Jennings and de Jesus, 1964; Delouche and Nguyen, 1964) and the more recent work showing that red rice seeds responded similarly (Larinde, 1979; Do Lago, 1982).



Source: After Teekachunhatean (1985).

Teekachunhatean simulated delays in shattering, i.e. varying resistance to shattering, of BLKH, the common BHR, SHA-, the common SHR, and the very early shattering and deeply dormant 78/8 BrHR phenotype by "catching" the first flush of shattered seeds in September and maintaining them in the air at panicle height on woven plastic screens for periods of 0, 2, 4 and 6 weeks. "Shattered" seeds of the non-shattering Starbonnet variety used for comparison were obtained by hand-stripping seeds at about 28 days past 50-percent anthesis from the middle of panicles. At the end of each period, the seeds were retrieved, planted about 0.5 cm deep in fumigated soil in a special area of the experimental plot, and watered thoroughly. Thereafter, watering was entirely by natural rainfall. The plantings were examined and emergence recorded at weekly intervals for about 15 months. Figure 9 presents selected results from the 1983 studies. Emergence of the lightly dormant Starbonnet seeds for all shattering-delay periods was relatively low and occurred entirely during the first three months after planting. Dormancy of BLKH seeds was released completely by 4-week and 6-week shattering delays, i.e. aerial drying, with the result that essentially all of seeds emerged within a couple of months. Seeds planted at the time of shattering (0 weeks) and after just a 2-week delay were dormant, so that 30–40 percent of them survived the winter as seeds and emerged in April and May of the following year, when rice is usually planted. Responses of the SHA- phenotype were similar with the exception that dormancy of the seeds from the six-week shattering delay was released completely so that most of the seeds germinated and were killed by an early freeze before or during emergence. Dormancy of seeds of

the deeply dormant 78/8 phenotype was maintained sufficiently through the six-week shattering delay so that the full flush of emergence did not occur until April, May and even June of the following year.

Garcia-Quiroga (1987) extended the shattering-delay studies to include placement of the seeds after the periods of simulated shattering delay on both rainfed and “marshy” or wet soil, “as encountered in rice fields during the fall and winter seasons.” While the results were somewhat inconsistent over the two years of the studies, he concluded that dormancy in shattered seeds was prolonged greatly compared with those maintained in the air, with the result that “more of the seeds, therefore, over-wintered in the dormant state and germinated the following spring when conditions were favourable for completion of the life cycle of rice.” The beneficial effects of early shattering were more pronounced under “marshy” than rainfed conditions.

The results from the studies by Teekachunhatean and Garcia-Quiroga suggest that seed shattering and dormancy interact to increase the probability that seeds of red rice survive the winter season as seeds to germinate and emerge when conditions become favourable for rice in the following spring season. Seed shattering in the common red rice ecotypes begins soon after the seeds attain physiological maturity at moisture contents from 25–28 percent (Chapter 4), which is also the time of maximum intensity of dormancy. As dormancy is released most rapidly at 8–14-percent moisture content (Roberts, 1962; Ellis, Hong and Roberts, 1983; Leopold, Glenister and Cohn, 1988) and very slowly or not at all at moisture contents of more than 18 percent, shattering places the seeds on the soil beneath the plants where maintenance of a moisture content of more than 18 percent is more probable than if the seeds remain on the plant drying to lower moisture contents in warm air temperatures. Conversely, if red rices were as non-shattering as most varieties, the seeds not gathered in the harvest would remain on the plant and lose dormancy to the extent that most of them would germinate, emerge and be killed by freezing early in the winter. These findings and conclusions have important implications relating to the fate of segregates spawned in the hybrid swarms resulting from cultivated and red rice crosses.

VARIATION IN MATURITY

The days to 50-percent anthesis and/or the heat units required for flowering varied widely among the red rice types collected in Mississippi, Texas and Arkansas. In Mississippi, the time of 50-percent anthesis ranged from 86 to 109 days for 26 SHR rices, from 93 to 112 days for 9 BHR rices and 1 BrHR rice, and from 90 to 105 days for four widely grown varieties (Table 2). All but two of the SHR types collected from Starbonnet fields in 1978–1980 were 1–16 days earlier than Starbonnet, the two exceptions were 3–4 days later, while all but one of the BHR types had essentially the same maturity as Starbonnet or were a few days later. As none of the red rices was more than 4 days later than Starbonnet and shattering began early in most of them, many of the red rice seeds, perhaps more than 50 percent, would be on the soil surface before the crop was harvested, with additional seeds shattered at the time of harvest. On the other hand, if the red rices had infested fields of the new earlier-maturing Lemont variety, 90 days to 50-percent anthesis, rather than fields of Starbonnet, 105 days to 50-percent anthesis, seeds of the latest red rice types would not have been sufficiently developed to shatter and, thus, would have been gathered in the harvested grain and/or separated with the light debris and dropped onto the soil. The results from the Arkansas studies were similar. While the onset of flowering varied by weeks for some of the SHR rice accessions depending on latitude of origin (Shivrain, 2004), the majority of SHR rices flowered earlier than the cultivated rices. Latitude of origin had a strong influence on time of flowering for the SHR rice accessions but not for the BHR and BrHR types.

As pointed out in Chapter 3, the considerable variability in flowering times of red rices has significant implications for gene flow between cultivated and red rice as well as for the fitness of segregates from red and cultivated rice crosses.

The considerable variation in maturity, height and plant form of red rice types provides a powerful buffer against substantial changes in the maturity and stature of the varieties cultivated. Natural and cultural selection results in shifts in red rice populations to types that can best survive and compete with the new varieties and the suppression or elimination of types that are not competitive.

PROTRACTED EMERGENCE

Dodson (1898) reported that his field observations were in accord with the then prevalent view that red rices germinate and emerge early in the spring and, thus, cultivation just before sowing to destroy red rice seedlings was “productive of some good.” However, he also noted that many red rice seeds remained in the ground, i.e. the seed bank, to emerge after the soil is disturbed during sowing, later in the spring as the “white rice is growing” before the flood, and even in late summer. More recent work and observations on the emergence of shattered red rice seeds during the autumn, winter and following spring seasons confirm Dodson’s observations. Sonnier (1963, 1965, 1978) described the differences in winter and spring emergence between cultivated and red rice seeds shattered from the previous crop at Crowley, Louisiana. Rice seedlings that emerge in the autumn and during warm periods in February and March are nearly all of cultivated varieties. However, the seedlings that appear later in April after the soil warms are nearly all of red rices because the earlier emerging cultivated rice seedlings have succumbed to frost and the few remaining non-germinated seeds have decayed. Do Lago (1982) planted freshly harvested and dormant seeds of three cultivated varieties and four red rice phenotypes 2.5 cm in soil on 28 September in northeast Mississippi about 200 miles north of the Crowley location. Essentially, all of the seeds of the cultivated varieties except Nato had germinated, emerged and succumbed to frost by early winter (Table 24). About half of the seeds of Nato, a deeply dormant variety, had emerged by early winter, but an additional 28 percent emerged between mid-winter and 13 April, and 3 percent emerged even later. Emergence of three of the four red rices was ≤ 16 percent by 13 April, after which emergence increased incrementally through to the end of May. The SHA- phenotype had 50-percent emergence by mid-April and emergence had increased to 80 percent by the end of May. The last killing frost in 1982 occurred in late March, so that all seedlings emerged before then were killed. The relatively low cumulative emergence percentages of the BLKH, SHA+ and 78/8 red rices were probably the result of termination of the experiment at the end of May. In other studies, germination and emergence of red rice seeds in non-flooded areas continued throughout the summer.

TABLE 24
Cumulative emergence percentages over an 8-month period of three cultivated varieties and four red rice types planted on 28 September 1981

Variety or ecotype	Cumulative emergence at indicated date					
	11/12/81	23/3/82	13/4/82	28/4/82	13/5/82	28/5/82
	(%)					
Labelle	87	92	93	93	93	93
Starbonnet	92	96	96	96	96	96
Nato	47	66	75	78	78	78
BLKH	11	11	16	40	56	60
SHA-	37	49	50	65	75	80
SHA+	0	0	8	25	25	48
78/8	0	0	0	26	36	44

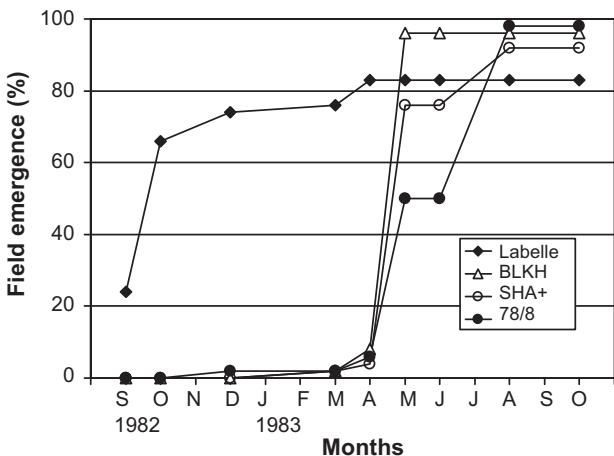
Source: Do Lago, 1982.

Teekachunhatean (1985) compared germination and emergence of three red rice types and the Labelle variety in two additional studies. He planted freshly harvested and dormant seeds of each type 2.5 cm deep on 15 September 1982 and seeds of the same batches (stored at -5 °C to maintain dormancy) the following June. Emergence was determined every 2 weeks over a 13-month period after planting. Figures 10 and 11 show the results in terms of cumulative emergence percentages. Most of the emergence of the September-planted seeds of Labelle emerged by December, those of BLKH emerged in April–May, while many of those of the SHA+ and 78/8 phenotypes also emerged in April–May but emergence continued into August. Emergence of the June-planted seeds was completed by August for Labelle and the BLKH ecotype, by September for the SHA+ ecotype, but not until April of the following year for 78/8.

The later and more protracted emergence for red rices compared with cultivated varieties reflects differences in the intensity of dormancy and the rates of its release. This statement is not contradictory to the conclusions in Chapter 5 that red rices are superior to most cultivated varieties in speed of germination and seedling growth. The present statement refers to red rice seeds shattered and/or planted about harvest time when dormancy is most intense, while the previous conclusions relate to red rice seed contaminants in planting seeds that have completely lost their dormancy during drying and storage.

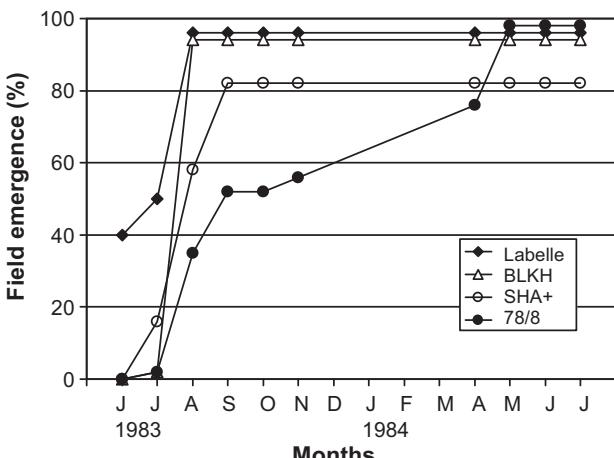
Environmental factors, especially temperature, are probably also involved in these differential responses. Temperature has a considerable effect on the rate at which dormancy is released and on its induction as well as a direct effect on the rate of germination and seedling growth (Chapter 5). Moreover, dormancy is manifested in a greater specificity of the conditions required for germination, e.g. temperature, as well as in the complete inhibition of germination (Vegis, 1964). Therefore, germination of

FIGURE 10
Cumulative emergence over a 13-month period of seeds of the Labelle variety and three red rice phenotypes planted on 15 September 1982



Source: Adapted from Teekachunhatean (1985).

FIGURE 11
Cumulative emergence over a 13-month period of seeds of the Labelle variety and three red rice phenotypes planted on 9 June 1983



Source: Adapted from Teekachunhatean (1985).

TABLE 25

Effects of planting depth for two different dates on emergence and seedling height of the Starbonnet variety and the SHA-, SHA+ and BLKH red rices 20 and 30 days after planting

Variety or ecotype	1st planting date: 17 September 1983							
	Planting depth in a Catalpa silty clay soil							
	5 cm ¹	Plant height (cm)	10 cm	Plant height (cm)	15 cm	Plant height (cm)	20 cm	Plant height (cm)
	Emergence (%)		Emergence (%)	Plant height (cm)	Emergence (%)	Plant height (cm)	Emergence (%)	Plant height (cm)
Starbonnet	97	20.2	63	12.7	0	0	0	0
SHA-	98	20.2	65	9.8	0	0	0	0
BLKH	97	21.6	93	18.5	0	0	0	0
2nd planting date: 19 October 1983 ³								
Planting depth in a Catalpa silty clay soil								
	7.5 cm ²		10 cm		12.5 cm		15 cm	
Starbonnet	73	10.1	32	7.7	4	2.0	0	0
SHA-	78	10.0	30	7.5	3	1.0	0	0
SHA+	86	10.0	63	10.0	5	4.2	0	0
BLKH	88	11.6	70	10.0	27	6.8	0	0

¹ Data are measurements at 20 days after planting.

² Data are measurements at 30 days after planting.

³ Air temperatures during the 2nd planting were about 6 °C cooler than for the 1st planting.

Source: Teekachunhatean, 1985.

red rice seeds with differing levels of residual dormancy did not occur until individual seeds were subjected to rather specific warm-temperature regimes.

There are some important implications of the late and extended period of emergence of red rices for the management and control of infestations. As noted by Dodson (1898) and Sonnier (1978), destroying red rice seedlings by cultivation (or chemicals) before sowing is a good but not always a wholly sufficient control measure. Red rice seeds germinate and emerge at the time rice is planted, while the seedlings are being established before the flood and anytime the flood is lifted for operations including harvest. Maintaining the flood as is done in water seeding is important to prevent or reduce the emergence and development of red rice plants. Similarly, the use of fallowing to renovate red rice infested fields must be accompanied by multiple cultivations over a two-year period (or longer) in order to deplete the population of seeds buried in the soil and reduce the red rice infestation to a manageable level.

In their search for a “weak link” in the life cycle of red rices, Helpert and Eastin (1978) conducted field studies to determine the soil depth from which two types of red rice, a BHR and an SHR, and four current rice varieties (Dawn, Nato, Early Colusa, and Starbonnet) would emerge. Seeds with high germination (> 90 percent) were buried 0, 1, 2, 4, 8 and 16 cm deep in tubes made of polyvinyl chloride (PVC) in a fine sandy loam soil near Beaumont, Texas, in March 1977. The first seedling emerged after ten days. Seedling emergence and plant height were recorded at 3, 10, 17 and 24 days after the date of the first emergence. For all soil depths, the SHR and BHR types had higher emergence percentages from the 3rd day after first emergence through to the 24th day and produced taller plants during the early part of the 24-day period. Germination and emergence for all entries were higher from depths of 4 cm or less than from depths of more than 4 cm, but the red rices emerged a day sooner than the varieties at the 4-cm depth and had higher emergence percentages and more growth at the 8-cm depth. Some seeds of the SHR emerged from the 16-cm depth. Somewhat similar results were obtained by Teekachunhatean (1985) is a comparative study of the emergence and seedling growth of the Starbonnet variety and the SHA-,

SHA+ and BLKH red rice types in soil depths of from 5 to 20 cm in September and October 1983. In the September planting, the emergence and seedling growth of the Starbonnet, SHA- and BLKH were comparable from 5 cm, but the BLKH displayed a superior performance from the 10-cm depth (Table 25). There was no emergence from 15 cm. The SHA+ and BLKH ecotypes emerged marginally better than Starbonnet and SHA- from the 7.5-cm depth in the October planting and much better from the 10-cm depth. The BLKH emerged more than 25 percent from 12.5 cm while the other entries emerged less than 5 percent.

ENVIRONMENTAL INTERACTIONS ON AND IN THE SOIL

The red rice soil seed bank

The term seed bank is used for viable and dormant seeds that are in and on the soil. The term is appropriate because seeds stored in the soil represent deposits of the genes and genetic variation of species that can be withdrawn as needed to maintain them (Murdoch and Ellis, 1992; Stiles, 1992; Vidotto and Ferrero, 2005). Dormancy is the key criterion for successful seed banking because non-dormant seeds in the soil either germinate or decay whenever adequate moisture is available and the temperature is favourable. Crawley (1990) emphasized the powerful buffer provided by seed dormancy against environmental and other adversities encountered by plant species that prevent or reduce seed production – seeds from the seed bank make up the deficit. The existence of a bank of red rice seeds in the soil is the reason why complete control of red rice in one or even two years in even a moderately infested field does not prevent a substantial infestation in the third year (Sonnier, 1978; FAO, 2003).

The red rice seed bank is depleted rather slowly but can be augmented rapidly by escapes from inadequate control measures or planting contaminated seeds. A calculation originally made by Dr R.J. Smith, Jr., is frequently cited to emphasize how planting red rice contaminated seeds can result in a red rice population explosion in just two years with a huge deposit in the red rice seed bank (Huey and Baldwin, 1978):

- Year 1: one red rice seed contaminant develops into a plant with 10 fertile tillers that produce 1 500 seeds.
- Year 2: the 1 500 seeds germinate, develop into plants that each produce 10 tillers and 1 500 seeds for a total of 2.25 million seeds.

While this calculation is exaggerated (as it is based on perfect seed responses) in order to make the point that rice farmers should not plant rice seeds contaminated with red rice, it illustrates how a clean rice field or one with a low red rice infestation under control can rapidly become heavily infested or out of control if management becomes careless.

The red rice seeds shattered to the ground before or at the time of harvest remain on the soil surface among the debris until disturbances of the soil by the passage of animals and equipment and cultural operations preparatory to sowing the next crop cause them to become incorporated in the soil to varying depths. In rice-growing areas that have a temperate winter, i.e. killing frosts, the seeds that remain on the soil can be depleted by germination and freezing during the autumn and winter seasons and by predation by birds, mice, and especially by migrating waterfowl where the field is maintained in a “wet” condition after harvest (Fontenot, 1973; Sonnier, 1978; Huey and Baldwin, 1978; Do Lago, 1982; Teekachunhatean, 1985). However, as depletion is never complete, at least some of the viable and dormant red rice seeds are buried in the soil to varying depths during the cultivations that precede sowing and, thus, deposited in the red rice seed bank. The fate of shattered red rice seeds in humid subtropical and tropical areas is not appreciably different. Red rice seeds that germinate in the interval between rice crops are destroyed by cultivation preparatory to planting, which incorporates the remaining viable dormant and non-dormant seeds in the soil.

The population of red rice seeds in the seed bank varies with cultural practices used after harvest and in preparation for sowing the next crop including control measures such as the stale seed bed and other factors included in the model of red rice population dynamics proposed by Vidotto and Ferrero (2005). There are relatively few data on the range in the numbers of seeds per unit area and their distribution by depth because most studies on red rice infestations focus on the number of plants per unit area rather than the number of seeds in the soil. Sonnier (1978) stated that 250 red rice seeds per square foot (circa 2 500/m²) was not an uncommon number in heavily infested areas. In laborious studies, Ferrero and Vidotto (1999) determined the number and distribution of red rice seeds in the seed bank of an experimental plot: 2 504/m² to 10-cm depth with 29 percent at 0–1 cm deep, 69 percent at 1–5 cm and 2 percent at 5–10 cm. Shallow ploughing reduced the total number of seeds per square metre considerably but increased sharply the percentage of seeds in the 5–10-cm depth. There is now more widespread recognition that ploughing after harvest buries red rice seeds rather deeply in the soil, where they survive for many years. This has led to the increasing practices of no-tillage and stale seed bed until preparation for planting the next crop, and then only minimum tillage and/or shallow cultivation in order to induce germination in red rice seeds on the soil or only lightly covered so that they can be destroyed chemically or mechanically before sowing (Sonnier, 1978; Fischer, 1999). The weedy rice plants (including red rice plants) that escape these and other control measures provide the “rain” of shattered seeds that constitute the main input regulating seed bank dynamics and deposits into the seed bank (Vidotto and Ferrero, 2005).

Longevity of red rice seeds in soil

Quereau (1920) observed that shattered red rice seeds were more or less mixed with the soil by the work animals and implements used for harvesting. He then stated that there were a number of instances “on record” where red rice seeds germinated after being in the “ground” for 12 years, and that, on his station, it was possible to obtain a good stand of red rice by simply ploughing a few inches deeper than the depth tilled for the previous 7 years. While Quereau’s observations were in accord with the general views of the times, the classic studies on longevity of buried red rice seeds were not undertaken until the 1930s (Goss and Brown, 1939). Seeds of five red rice ecotypes and two cultivated varieties were buried 12.5 cm deep in soil at locations near Beaumont (Texas), Stuttgart (Arkansas) and Biggs (California) under rainfed and irrigated conditions. Batches of seeds were removed from the soil annually for five years (and winters) and tested for germination. The results were:

- Seeds of the two cultivated varieties (Caloro and Supreme Blue Rose) lost their viability during the first winter at all locations under both rainfed and irrigated conditions.
- The “California” red rice behaved similarly to the cultivated varieties except that it was slightly more persistent at the Stuttgart location; a small percentage (< 16 percent) of the “Italian” red rice from the Biggs rainfed location germinated after 3 years.
- The three “southern” red rices, 2 SHRs and 1 BHR, maintained good viability for 3 years, about 50 percent viability for 4 years, 12–25 percent for 5 years, and 2–20 percent after 7 years. The southern BHR was longest-lived, and longevity of all three southern red rices was favoured by the irrigated condition and the southern locations.

A year later, Goss and Brown (1940) reported on the ten-year retrieval of seeds of four of the red rices at the Stuttgart location. The southern BHR and one of the southern SHR rices germinated 28 and 21 percent, respectively.

Response/reactions of deeply buried red rice seeds

The survival of deeply buried seeds of the red rices for long periods in soil is recognized as a critical trait in their success as rice field weeds and attributed to deep and persistent dormancy. However, until the 1980s, little was known about the physiological responses and reactions of the deeply buried seeds during changes in the environment associated with the seasons and cropping cycles. On 1 November 1981, Do Lago (1982) buried dormant seeds of the Nato variety and the BLKH, SHA- and 78/8 red rices 15 cm deep in rainfed (occasionally flooded) and perennially flooded soil environments for a 30-month study of buried seed response/reactions. Enough seeds were buried for retrieval every three months for tests. Seeds of the same variety and red rices were stored in the “air” but under cover above the buried seeds as a sort of control. Table 26 presents the results of the first six months of the study. After six months of deep burial in soil, none of the seeds of the rice variety and the three red rice types was dormant. Do Lago considered these results surprising as they raised the question as to whether dormancy was as critical for survival of red rice seeds in the seed bank as generally believed.

Continuing this buried-seed study, Teekachunhatean (1985) retrieved buried seed samples every 3 months for the first year and then every 6 months for the remainder of the 30-month period. Dormancy in seeds deeply buried in November was released during the winter, mostly by February for Nato and the SHA- red rice, so that 90 percent or more of the seeds of the red rice germinated and emerged in May when moved to a shallower depth of 3 cm (Figure 12). Germination of seeds of Nato was less than 40 percent in May in the rainfed soil but more than 90 percent in the flooded soil. Germination of the deeply buried seeds of the red rices began to decrease and dormancy to increase by August, so that in November nearly all of the seeds in the rainfed soil were dormant. In contrast, seeds of the deeply dormant Nato were mostly all dead and decayed by August. During the remaining 18 months of the study, the deeply buried seeds of the red rices that were still viable in the rainfed soil were essentially all germinable by May and all dormant by November. Viability of the seeds decreased in both field conditions, but more rapidly in the flooded soil, so that less than 10 percent of the seeds were viable at 30 months. The periodicity in germinability and dormancy of the buried red rice seeds corresponded to seasonal climate changes in such a manner as to favour survival and reproduction. The seeds were in a dormant condition with the advent of freezing temperatures during the late autumn and winter, and most of them remained dormant until dormancy was fully released as the danger of freezing temperatures receded the following spring and conditions became favourable for germination, growth and reproduction.

TABLE 26
Germination and dormancy of seeds after air storage in the field and buried 15 cm deep in soil under rainfed and flooded conditions

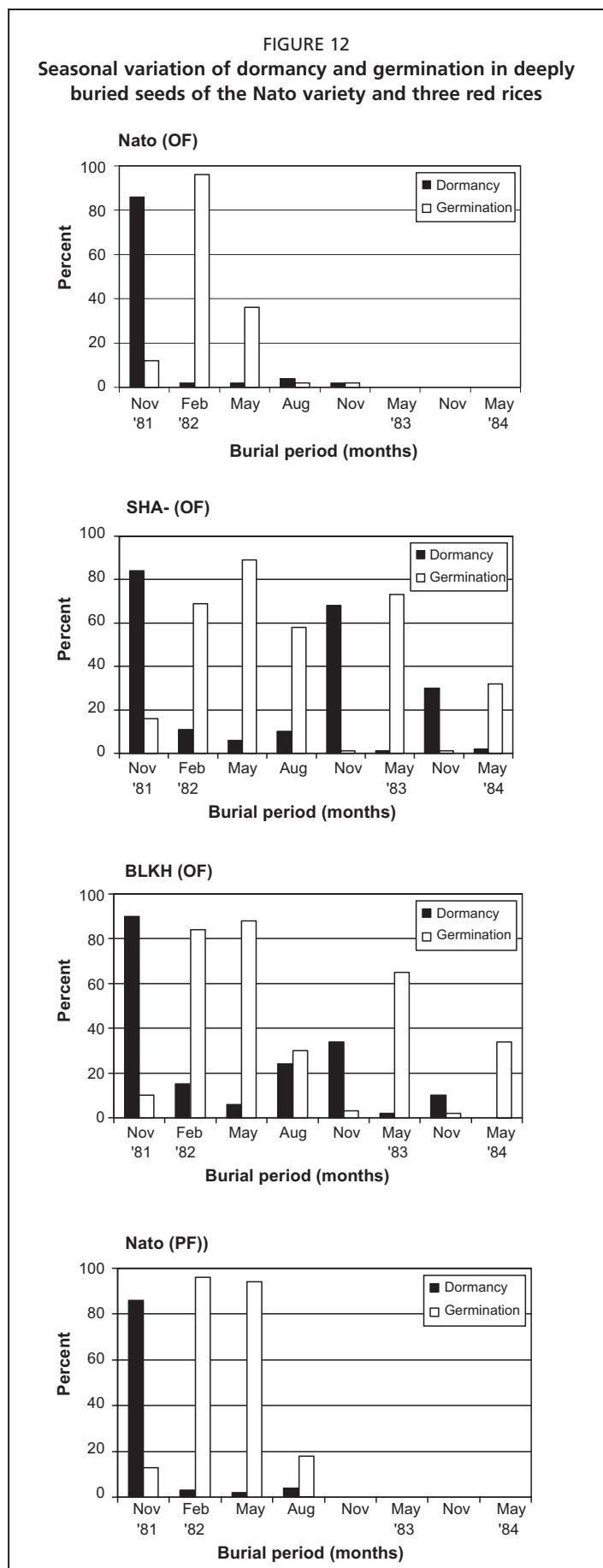
Variety/ ecotype	Initial ¹	Field condition																					
		Air storage				Soil/rainfed				Soil/flooded													
		G		D		G		D		G		D											
Variety																							
		(%)																					
Nato	11	88	88	9	97	1	96	0	35 ²	0	95	3	95	0									
Red Rice																							
BLKH	8	90	98	1	88	6	73	15	85	7	68	30	98	0									
SHA-	9	90	90	7	91	4	62	31	87	10	40	58	90	9									
78/8	0	100	16	84	63	29	46	52	97	0	23	75	98	0									

Note: The 3 and 6-month data were the first two data points of a study that continued for 30 months.

¹ Seeds buried = 1 November 1981; 3 months = 1 February 1982; 6 months = 1 May 1982.

² Sixty-one percent of seeds germinated but did not emerge.

Source: Do Lago, 1982.

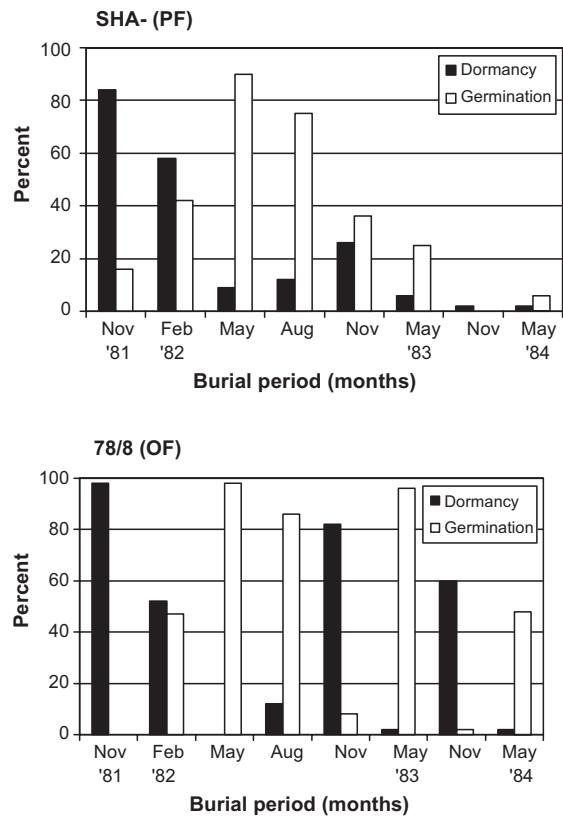


The re-imposition or induction of dormancy in late summer and autumn prevented germination in the following winter, when seedlings would be killed by freezing temperatures. The seeds of Nato, one of the most deeply dormant varieties, did not exhibit a distinct periodicity in germination and dormancy. Dormancy was released in the first winter season so that all viable seeds were germinable even in February, but most of the seeds not retrieved in May died and decayed by late-summer. In a related study, dormant and non-dormant seeds of Nato and the BLKH and SHA+ red rices were submerged 20 cm deep in water under ambient conditions in October 1983 and sampled for testing every 3 months for 1 year. The non-dormant seeds of Nato and the two red rices died during the first three-month period, October–January (Table 27). Dormancy was released completely in the Nato seeds during the first 3 months and all the seeds were dead by the sampling at 9 months in July. Dormancy was also released in 71 and 45 percent of the seeds of BLKH and SHA+, respectively, in the October–April period (first 6 months), then completely by July (9 months), after which most of the seeds reverted to the dormant condition again by October, the end of the 12-month period. Again, dormant seeds of the Nato variety either became germinable or died by April as they did when buried in soil. Petrini *et al.* (1993a, 1993b) also found that the viability of dormant red rice seeds was not much affected by flooding or saturated soil, while non-dormant seeds decreased in viability but not as much when buried deeply in the soil. The latter response was probably caused by induced dormancy. The seasonal patterns in the release and induction of seed dormancy demonstrated in the buried seed studies for red

rice were confirmed by Garcia-Quiroga (1987) in later studies in Mississippi, the United States of America, with some of the same red rice phenotypes, and in Brazil by Barros (1994) and Peske *et al.* (1997). These seasonal rhythms in readiness to germinate were neither unique nor surprising. Vegis (1964) proposed a general model for germination behaviour associated with the seasonal release and induction of dormancy that focused on the narrowing of the temperature range for germination as dormancy is induced and its widening as dormancy is released.

Baskin and Baskin undertook studies on the germination ecology of annual species including many weeds in the early 1970s, and in 1985 they published a review of their and other related works of others (Baskin and Baskin, 1985). Karssen (1982) and Karssen, Derkx and Post (1988) have argued that seasonal patterns of dormancy release and induction are of high survival value to plant species and that, in annual species, dormancy is released during the season that precedes the time conditions become favourable for

FIGURE 12
Seasonal variation of dormancy and germination in deeply buried seeds of the Nato variety and three red rices
(continued)



Note: OF = occasional flooding; PF = perennial flooding.
Source: After Teekachunhatean (1985).

TABLE 27
Germination and dormancy percentages of dormant and non-dormant seeds after periods of submergence 20 cm deep in water under ambient conditions

Variety/ ecotype	Response (%)	Period of submergence (20 cm) in water				
		0 months (Oct. 83)	3 months (Jan. 84)	6 months (Apr. 84)	9 months (Jul. 84)	12 months (Oct. 84)
Non-dormant seeds						
Nato	Dormancy	0	0	0	0	0
	Germination	100	0	0	0	0
BLKH	Dormancy	0	0	0	0	0
	Germination	100	0	0	0	0
SHA+	Dormancy	0	0	0	0	0
	Germination	100	0	0	0	0
Dormant seeds						
Nato	Dormancy	78	0	0	0	0
	Germination	21	30	18	0	0
BLKH	Dormancy	96	17	16	1	66
	Germination	4	71	68	84	12
SHA+	Dormancy	96	60	39	0	86
	Germination	2	32	45	92	2

Source: Teekachunhatean, 1985.

germination, growth and reproduction, and induced in the season that precedes the onset of conditions that are detrimental thereto. For summer annuals, such as the red rices, dormancy is released during the late autumn, winter, and early spring and induced in the late summer and early autumn. For winter annuals, dormancy is released as temperature declines in late summer and early autumn and induced in mid-summer to late summer when temperatures rise. The results of the studies on the behaviour of buried seeds of the red rices are in full agreement with the several models of seasonal changes in germination behaviour.

Teekachunhatean (1985) undertook several additional studies in order to identify the environmental signals and conditions controlling the transition from germinability to dormancy and vice versa in seeds of the red rices. The temperature signals for the release of dormancy were investigated by imbibing dormant seeds (less than 5 percent germination) of the SHA+ red rice for 48 hours on moist germination towels at 15 °C after which batches of appropriate number were sealed in polyethylene envelopes and placed in dark incubators at 5, 10, 20 and 30 °C for 25-day periods. At the end of the first 25-day period, the seeds were transferred to a different temperature for a second 25-day period, and then transferred again for a third 25-day period, so that they were exposed to the four temperatures in different sequences. Seeds were removed at the end of each 25-day period for determination of germination and dormancy. The effects of alternating exposure of the imbibed seeds to the different temperatures were generally as expected but also surprising and revealing (Table 28). Dormancy was released sooner

TABLE 28
Effects of periods of constant and alternating temperatures on germination and dormancy of seeds of the SHA+ red rice ecotype

Period 1(25 d)			Test period and exposure duration					
Temp. (°C)	Germ. (%)	Dorm. (%)	Periods 1 & 2 (25 d + 25 d)			Periods 1, 2 & 3(25 d + 25 d + 25 d)		
			Temp. (°C)	Germ. (%)	Dorm. (%)	Temp. (°C)	Germ. (%)	Dorm. (%)
5	9	86	5-5	12	79	5-5-5	22	70
			5-10	70	24	5-10-10	68	24
			5-20	68	22	5-10-5	36	59
			5-30	70	22	5-20-20	62	31
						5-20-5	73	19
						5-30-30	84	5
						5-30-5	66	23
			10-5	63	37	10-5-5	31	62
			10-10	59	37	10-5-10	70	22
			10-20	71	24	10-10-10	93	0
10	42	54	10-30	72	23	10-20-20	70	23
						10-20-10	94	1
						10-30-30	91	3
						10-30-10	76	11
			20-5	6	93	20-5-5	4	89
			20-10	93	3	20-5-20	85	10
			20-20	6	92	20-10-10	88	6
			20-30	4	92	20-10-20	73	23
						20-20-20	37	60
						20-30-30	15	79
20	4	91				20-30-20	13	77
			30-5	6	92	30-5-5	12	80
			30-10	43	48	30-5-30	92	1
			30-20	37	58	30-10-10	80	16
			30-30	4	94	30-10-30	70	11
						30-20-20	15	52
						30-20-30	20	38
						30-30-30	2	94

Note: Germ. = germination; Dorm. = dormancy.

Source: Teekachunhatean, 1985.

and to a greater degree by exposure to alternating temperature sequences in which 10 °C was the initial temperature, and slowest and to the least extent by exposure to temperature sequences in which the first temperature was 30 °C. These results were as expected as in the buried seeds study dormancy was released as the soil temperature decreased in winter and induced as soil temperatures became warm in late summer. The surprising results were: 5 °C was not nearly as effective as 10 °C in releasing dormancy; and temperature sequences with a low temperature followed by a warm temperature, interspersed between two warm temperatures, or preceded by a warm temperature, e.g. 5–30–30, 10–30–30, 30–5–30, 20–5–20, 20–10, 20–10–10, were more effective in releasing dormancy than 10 °C for 50 days, e.g. 10–10. These revealing results appear to indicate that, for full release of dormancy, temperatures lower than 10 °C have to be combined with warm temperatures, while those higher than 10 °C have to be combined with cooler temperatures. These responses are most likely adaptations to reduce the probability of dormancy release too early in the winter and during periods of warm temperatures in late spring before the last killing frost.

Teekachunhatean's investigation of the temperature and other environmental factors involved in the re-imposition or induction of dormancy in buried seeds took into account observations during the studies on the survival benefits of early seed shattering (Chapter 4) that the high moisture contents (circa 20 percent) of shattered seeds were critical for maintenance of dormancy. He conditioned non-dormant seeds (germination \geq 98 percent) of the SHA+ red rice to seed moisture contents of 18.5, 22.5 and 26.5 percent at 15 °C, sealed batches of appropriate number in polyethylene envelopes and stored them at 10, 20 and 30 °C for periods up to 5 months. Dormancy was induced in the initially non-dormant seeds with 18.5 percent and 22.5 percent moisture by 2–3 and 3–4 months exposure to 30 °C, respectively, but not in 26.5-percent moisture seeds (Table 29). At 10 °C, dormancy was induced in about 10 percent of the 18.5- and 22.5-percent moisture content seeds in 4–5 months while up to 25 percent of the 26.5-percent moisture seeds became dormant in 2 months. Seeds at 18.5- and 22.5-

TABLE 29
Effects of storage temperature and seed moisture content on the induction of dormancy in seeds of the SHA+ red rice phenotype

Storage time (months.)	Storage temperature					
	10 °C		30 °C		40 °C	
	Germination	Dormancy	Germination	Dormancy	Germination	Dormancy
18.5% seed moisture content						
0	99	0	98	0	98	0
1	98	0	94	0	93	2
2	99	0	12	78	86	0
3	95	0	4	89	70	0
4	85	11	0	88	6	0
5	65	9	0	90	0	0
22.5% seed moisture content						
0	98	0	99	0	97	0
1	99	0	97	0	95	0
2	96	0	73	15	93	0
3	96	0	50	47	78	0
4	61	13	8	90	0	0
5	67	7	5	48	0	0
26.4% seed moisture content						
0	98	0	97	0	96	0
1	81	14	97	1	95	0
2	64	25	95	1	85	1
3	91	4	90	2	8	0
4	93	0	86	3	0	0
5	81	0	33	0	0	0

Source: Teekachunhatean, 1985.

TABLE 30

Effect of temperature regime in releasing induced dormancy in seeds of the SHA+ red rice phenotype

	Constant or alternating temperature									
	(°C)									
Germination	10	20	30	40	10–20	10–30	10–40	20–30	20–40	
Percent	91	12	0	3	24	3	36	0	24	

Source: Teekachunhatean, 1985.

percent moisture content stored at 30 °C transited from the germinable to dormant state beginning at 2 months with the transition completed in 3–4 months. The highest moisture content seeds, 26.4 percent, at 30 °C did not transit to the dormant state. None of the seeds at 40 °C developed dormancy and they began to decline in viability in 2–3 months so that they were all dead by 5 months. Seeds in which dormancy was induced (90 percent) were placed on moist media to complete imbibition and incubated at various temperatures for 30 days to determine the temperature regime for release of the induced dormancy (Table 30).

A temperature of 10 °C for 30 days reversed completely the induced dormancy to germinability. None of the other constant and alternating temperatures was as effective, but the near total ineffectiveness of alternating temperatures with 30 °C to reverse induced dormancy and the partial effectiveness of the 10–20, 10–40 and 20–40 °C alternating temperatures warrant further study. For example, Garcia-Quiroga (1987) repeated the dormancy induction study using only 18-percent moisture seeds and determined that dormancy was also induced in 2–3 months at 20 °C. Therefore, these results indicate that dormancy can be induced in non-dormant seeds of red rices from 18 to about 22 percent moisture by exposure to warm temperatures, 20–30 °C, for several months. However, they can only be considered as suggestive of what takes place in the microenvironment of deeply buried seeds and the seeds themselves. Additional studies are needed in order to gain a more complete and clearer understanding of the changes in germination behaviour of deeply buried red rice seeds. Field studies should include: continuous recording of soil temperature at the level of the buried seeds; monthly rather than quarterly retrievals of seeds for testing; and determination of seed moisture content as well as germination and dormancy. Laboratory studies on the induction of dormancy should include additional temperatures, such as 5, 15, 35 and even 40 °C, and a wider range in seed moisture content, e.g. from 16 percent to full imbibition, circa 28–30 percent, in 2-percent increments.

ECOLOGICAL MODEL OF RED RICE GERMINATION

There is much information on the germination behaviour of red rice but it is still far from sufficient for the construction of a rigorous, comprehensive model of red rice germination and longevity in soil. As discussed above, some critically focused research is needed in order to obtain the additional information required for the construction of a good model of the germination behaviour of *Oryza sativa* red rice in temperate-zone irrigated rice cultures. Additional research would be required to extend the model into the humid tropics and subtropics, where temperatures below 20 °C do not occur or are exceedingly rare, and into warm zones with distinct wet and dry seasons (as in the dry season, germination of shattered seeds would most likely be prevented by their desiccation rather than dormancy). Even more work would be required in order to determine whether other species of weedy rices, e.g. *O. latifolia*, *O. barthii*, *O. glaberrima*, *O. longistaminata* and *O. rufipogon*, could be fitted into the same model as the *O. sativa* types or would have to be modelled separately. While much more information is needed even for the development of a good model of the germination

behaviour of red rices of the *O. sativa* group in temperate zones, some of the most probable constructs for a model have been identified, characterized and documented. They are:

- Lack of uniformity in germination and emergence of red rice seeds on or in the soil provides multiple opportunities for some of the seedlings to escape destruction from environmental adversities and from mechanical and chemical control measures and to grow, develop and mature seed, i.e. reproduce. The generally superior vigour, physiological efficiency, and plant stature and type of red rices as compared with cultivated varieties ensures that a good portion of the seedlings that do escape destruction are highly competitive and produce a relative abundance of seeds.
- Heavy tillering over a long period and the wide angle of the tillers of red rices contributes to their vigour and competitiveness. Moreover, it also expands the time frame of heading, seed maturation and shattering which, as in the case of the relative non-uniformity of germination and emergence, provides multiple opportunities for favourable positioning of shattered seeds in time and space for survival until the next season.
- The early and easy seed shattering of the red rices, one of the two traits most critical to their success as weeds, has several important functions. It increases considerably the seed dispersal zone compare with what it would be if they were as resistant to shattering as cultivated varieties. It ensures that at least some of the seeds are positioned on or in the soil to continue the infestation rather than gathered in the harvested grain. It results in seed dispersal at relatively high moisture contents that favour the maintenance of dormancy over the cool or cold seasons. Resistance to shattering would result in the offtake of the seeds in harvest or a substantial decrease in dormancy as the seeds dried during “storage on the plant”.
- The intensity and persistence of dormancy ensures that the ecotypes survive the winter season as seeds, the most resistant phase of the plant cycle. Release of “most” of the dormancy, i.e. reduction in its intensity, by prolonged exposure to cool/cold temperatures, circa 10 °C, results in germination and emergence over an extended period when environmental conditions become favourable in the spring season. An induced or secondary dormancy that develops in deeply buried or submerged seeds as the soil and water temperature becomes warm in late summer, circa 30–35 °C, prevents germination of seeds turned up to a favourable depth or when the flood is lifted during warm periods in the autumn and winter. The annual cycling of germinability and dormancy with the seasons is the most probable reason for the longevity of buried red rice seeds.

FURTHER DISCUSSION ON HYBRID SWARMS FROM CULTIVATED RICE / RED RICE CROSSES

Chapter 3 reported the observation that hybrid swarms from red rices and cultivated rice crosses segregating for many traits and characteristics could generate hundreds of phenotypically distinctive, troublesome weedy rices, some with red and some with white pericarps but that they had not done so. This raises several questions:

- What happens to the hybrid swarms?
- Do the hybrid swarms die off or blend back into the red rice populations from whence they originated?
- Why have the SHR and BHR complexes maintained their dominant positions in the United States of America against the seemingly constant pressures from the hybrid swarms?

Jodon (1959) observed that, as red rice cross-pollinates “readily with ordinary rice”, hybridization would be expected to give rise to innumerable types of red rices

but it had not done so. He then noted that there were only a few types of red rices, as there are now, and that they resembled one another much more than they resembled cultivated varieties.

The SHR are still the dominant red rices and resemble one another more than they do the cultivated varieties, especially as they enter the reproductive stage. However, there is an obvious resemblance of some ecotypes to the varieties in terms of plant height, panicle and leaf colour, and maturity. The BHRs also continue as a distinctive group, more distinctive than the SHR, and resemble one another much more than they resemble the cultivated varieties or the SHR. Gealy and Estorninos (2004a) reported that BHR and variety hybrids are distinguished easily from those of SHR and varieties because of the large genetic separation between these two main red rice groups.

The ecological significance, interactions and relationships of the critical traits of red rices discussed in this chapter provide a basis for informal speculation about the fate of red rice \times cultivated rice hybrid swarms. Estorninos, Gealy and Burgos (2004) determined the reciprocal crossing rates of two varieties, Starbonnet and Kaybonnet, with BHR and SHR paired so that flowering was nearly synchronous. The rate of crossing between Kaybonnet and the BHR was 0.10 percent with the BHR as the pollen donor, but there was no detectable crossing with Kaybonnet as the pollen donor. Crossing between Starbonnet and the SHR was 0.23 percent with the SHR as the pollen donor and 0.14 percent with Starbonnet as the pollen donor. They tentatively attributed these differences among reciprocal crossing rates to the stature of the plants – the taller red rice plants are better able to function as the pollen donor than the shorter varieties. Regardless of the reason, red rice and cultivated rice crosses with the cultivated variety as the female parent have immediate serious deficiencies. First, the non-shattering trait of the cultivated maternal parent would place most of the hybrid seeds in the harvested grain for consumption rather than on the soil for propagation. Constantin (1960) reported that all of the more than 1 000 panicles of weedy rices he collected in southwest Louisiana had red pericarps and evidence of heavy shattering, and noted that the cultivated rices would most probably be the pollen donor in hybrid populations. Second, any hybrid seeds of crosses with the variety as the maternal parent that somehow escaped from the harvest would probably lose viability or be killed by freezing, as is the fate of most shattered seeds of cultivated varieties. There is evidence that dormancy in rice and other species of *Poaceae* is conditioned by properties of the pericarp and testa complex and the hulls, most of which are maternal tissues (Jana, Acharya and Naylor, 1979; Jana, Upadhyaya and Acharya, 1988). On the other hand, hybrid seeds with the variety as the pollen donor could be shattered to the soil, survive the winter, emerge in the spring, infest the crop, and produce seeds that in the next generation would produce a hybrid swarm.

Lateness and sterility are quite common traits in segregating populations from red and cultivated rice crosses (Jodon, 1959; Do Lago, 1982; Burgos *et al.*, 2006b; Gealy, 2005). The very late and sterile plants in the hybrid swarm would be eliminated. Dormancy is an inherent trait, so seeds that end up with dormancy intensity about that of cultivated varieties would not be very successful in surviving adverse periods and most would be eliminated. Similarly, most segregates inheriting the non-shattering trait would be eliminated. Some segregates would not possess the traits to compete with already established, successful red rices or even cultivated varieties, and most of these would be eliminated. There may be many other reasons why new successful and distinctive ecotypes of red rices apparently emerge only very infrequently from the hybrid swarms. However, for the present, such reasons remain essentially unknown.

Several additional questions arose many times during the red rice studies at Mississippi State University in the 1980s. One set of questions related to the Nato



Plate 16

Top two rows: A sample of the diversity of RR in plant stature, foliage and panicle characteristics compared with cultivated varieties. A, left to right: Nato, Lamont, a semi-dwarf SHR, Starbonnet, a Starbonnet-like RR, and the SHA- SHR. B, left to right: Nato, Newbonnet, Starbonnet, Lamont, a semi-dwarf purple-leaf RR, and the SHA- and BLKH RR. C, left to right: Nato, Starbonnet, SHA-, Lamont, a purple-leaf semi-dwarf RR, a purple-leaf RR, and a semi-dwarf green-leaf RR. D, left to right: SHA-, BLKH, BrHR, SHA+, a long-grain smooth-leaf RR, and a white-pericarp SH type. Bottom row: plots used for conducting the RR investigations at Mississippi State University in the period 1978–1992.

variety used as a reference or control in many of the experiments because it exhibited an intense, persistent dormancy, more intense than in most of the common red rice types in many of the experiments. The questions focused on why Nato was not an obnoxious volunteer in certified rice seed fields. As it was very non-shattering, its capacity for spread and persistence would be limited, but any seeds that did fall to the soil surface should survive the winter and persist in the soil seed bank. However, most of them do not. Another issue concerned why dormancy in Nato seems to be very persistent in air storage, more persistent than most of the common red rices but not in or on the soil. Further questions related to the seeming absence of any successful blackhull or strawhull ecotypes with a white pericarp. They emerge from the hybrid swarms, as is evident in Plates 4, 12, 13, 14 and 16. A successful weedy white-pericarp blackhull or strawhull type would raise some legal problems because red rice is defined in many seed laws as a rice seed with a red-pigmented caryopsis.

Chapter 7

Strategies for controlling weedy rices

Considering the complexities and multidimensioned aspects of the diversity, phenology and ecology of weedy rices (including red rices), it is to be expected that the control measures are also complex, difficult, multidimensioned and require exceptional discipline in crop management, patience and, perhaps most importantly, perseverance. Strategies for control are well established but the ways and procedures used for their implementation, i.e. the tactics, vary from place to place and require frequent revision. They need to be revised in order to:

- take into account the appearance of new and/or different weedy rice ecotypes;
- adapt to changes in cultivated varieties, cropping systems, cultural practices, water availability, and marketing standards for rice grain;
- take advantage of new and/or different crop rotations, advances in herbicide chemistry and usage, and biotechnology.

Many of the specific tactics employed for controlling weedy rices are continuously changing and evolving, time related, and dependent on the scale of farming and resource availability. Therefore, the primary focus of this chapter is on the broad strategies for control and the more widely adapted and used tactics, with some attention to the newer and somewhat controversial biotechnological approaches.

The main strategies for controlling weedy rices (including red rices) can be grouped into several broad categories:

- prevention of infestations or re-infestations;
- depletion of the soil seed bank by post-harvest, preplanting cultural practices;
- suppression of germination and/or emergence by sowing practices and water management;
- destruction of weedy rice plants in the rice crop;
- alteration of the rice field environment by crop rotation and/or fallowing;
- biotechnological methods.

While chemical herbicides are not mentioned specifically, they are an important element in all of the strategies except prevention.

RECOGNITION OF WEEDY RICES

The first requisite in any of the strategies for controlling weedy rices (including red rices) is recognition of local and/or introduced ecotypes. This is not easy to accomplish because many of them belong to the same species as the major cultivated rice, e.g. *Oryza sativa*, and share many of the characteristics of the cultivated rice – Vaughan *et al.* (2001) provide a different interpretation. It is especially difficult to distinguish between seedlings and juvenile plants of the rice weeds and the rice variety. Valverde (2005) argues that feral strains of rice with weedy traits can evolve from cultivated rices or other species of *Oryza*, e.g. *O. latifolia*, that are difficult to detect because they “mimic” cultivated types, and that hybrids may go undetected until a new aggressive ecotype becomes established. While most weedy rices, especially the red rice types, have hispid or pubescent leaves in contrast to the glabrous cultivated varieties, this

distinction requires quite close inspection, which is difficult at the seedling and juvenile plant stage. The weedy rices (including red rices) become much more recognizable as they develop, and especially as they enter the reproductive stage. This is because their “wild” characteristics and appearance often contrast vividly with the “selected”, more uniform appearance that characterizes cultivated varieties.

In the rice area of the southern states of the United States of America, red rice plants are usually taller, lighter green in colour and have pubescent somewhat drooping leaves, a greater number of wider-angled (open) tillers, and more open and lax panicles than cultivated varieties (Quereau, 1920; Constantin, 1960; Do Lago, 1982; Noldin, 1995, Stiers, 2002; Shivrain, 2004). The SHRs are usually shorter than the BHRs and have a more open architecture, more drooping leaves, more drooping and fully exerted panicles, fewer tillers and produce mainly awnless spikelets, whereas the BHRs are almost invariably medium- to long-awned (Cragmiles, 1978; Huey and Baldwin, 1978; Sonnier, 1978; Do Lago, 1982; Noldin, 1995). Differentiation of both types of red rices from the cultivated variety is rather easy at maturity. This is because the open panicles of the red rices exhibit very conspicuous evidence of seed shattering or shedding, which contrasts sharply with the compact, non-shattering panicles of modern varieties. The statement by Sonnier (1978) that despite the “variations and hybrid forms which occur in red rice, all of them fall into two main groups or types,” based on hull colour (strawhull or blackhull) is not entirely correct. The dominant red rices are strawhull, the blackhull types are a distant second, but there are also goldhull and brownhull or bronzehull types and variants in the blackhull group, e.g. dark blackhull, intermediate blackhull, faded blackhull, and greyhull (Constantin, 1960; Do Lago, 1982; Noldin, 1995). The red rices are mostly medium-grain types with a few short-grain and a few long-grain types, and the pericarp is always some shade of red.

In Viet Nam, some of the weedy rices (including red rices) belong to *Oryza sativa*, but others belong to other species. Recent surveys indicate that farmers recognize weedy rices at the booting stage by their taller stature, awned spikelets, dark coloured hulls, early and heavy shattering and smaller seeds – as compared with cultivated varieties – and by their usually having a red pericarp (Chin *et al.*, 1999).

Ferrero and Vidotto (1999) noted that while weedy rices in Italy are difficult to distinguish from the cultivated varieties in the seedling and young plant stage they can be identified rather easily after tillering is well established owing to many obvious morphological differences with the usual cultivated varieties. The weedy rice plants are usually taller, their tillers are more numerous, longer and slenderer, their leaves are pubescent, and several plant parts are often pigmented, particularly the pericarp.

In Central and South America, most weedy rices are weedy, red-pericarp ecotypes of *Oryza sativa*. The endemic species *O. latifolia* is also a problem in Central America and some of the countries bordering on the Caribbean (Lentini and Espinoza, 2005). In Costa Rica, *O. latifolia* is much taller (up to 2 m) than the cultivated varieties and the *O. sativa* red rices, has wider leaves, an erect growth habit like the cultivated rices but unlike the drooping and lax leaves and culms of the red rices, a white pericarp, and prominent awns like the red rices (Espitia, 1999). However, as noted by Valverde (2005) *O. latifolia*, called *arrozon*, has evolved some strains that closely “mimic” the cultivated varieties in height and maturity. Red rices in Nicaragua are also taller than varieties and generally flower before them (Fletes, 1999). Garcia de la Osa and Rivero (1999) cite a 1998 survey in Cuba that found 39 biotypes of red rices, 16 strawhulls, 10 goldhulls and 13 blackhulls. Twenty-seven percent of the population of red rices surveyed and collected exhibited some segregation when planted. In a summary of the weedy rice problem in Latin America, Fischer (1999) described red rices as having a pigmented aleurone pericarp and usually being taller, leafier, more tillered and more competitive than cultivated rice.

Weedy rices in SSA are very different from those in the Americas, Southern Europe, North Africa and some areas in Asia. The main weedy rices are the annual species *O. barthii* and *O. punctata* and the perennial *O. longistaminata* (Johnson *et al.*, 1999). These species are very vigorous and competitive and shatter the seeds produced early and heavily. *O. longistaminata* reproduces by rhizomes as well as seeds. In Senegal, some red-pericarp biotypes of *O. glaberrima*, the cultivated African rice, have a weedy habit (Diallo, 1999).

As stated above, recognition of the common weedy rices (including red rices) by farmers, extensionists, certification field inspectors, and seed analysts is the first requisite for implementation of any control strategy and/or tactic in a region. Farmers, advisors, inspectors and other rice specialists must be able to recognize the weedy rices common in their area. In addition, they must also be vigilant and always on the lookout for different ecotypes introduced from other areas and, especially, for segregates from the infrequent hybridization of cultivated and weedy rices and the new ecotypes naturally selected from the hybrid swarms. Plate 16 shows a small sample of the diversity of red rices in plant stature, form and panicle characteristics in comparison with several types of cultivated rice (also Plates 4 and 12).

PREVENTING INFESTATIONS

Importance of purity of planting seed

Weedy rices spread from an infested area to a clean area primarily as contaminants in planting seeds. Animals and farm equipment and machines (including vehicles) can also contribute to the spread of weedy rices. The primal role of contaminated seeds in the spread of the red rices was recognized more than 100 years ago and this recognition continues to the present:

- “Careful attention should be given to raising rice seed for planting. If the seed are purchased, a guarantee should be demanded that the seeds are free of red rice.” (Dodson, 1898). “Selecting pure seed is of utmost importance.” (Dodson, 1900).
- “Two things must be accomplished to keep the fields clear of red rice: First, seed planted must be free of red rice... (and)... Second, red rice must be prevented from producing seeds in the field if accidentally planted.” (Knapp, 1899).
- “In order to have red rice the seed must be planted. White rice does not turn into red as some farmers are inclined to believe. The principal means of propagation (of red rice) is that of planting the red seeds with white.” Quereau (1920).
- “Every precaution should be taken to avoid introducing these (red rice) and other weeds to clean land in the seed.” (Jones and Jenkins, 1938).
- “I think our problem with red rice is not ducks and geese moving it from one field to another. *The reason we have it is that we plant it and cultivate it.*” (Cox, 1978).
- “The first step in controlling red rice is to prevent infestations. This can be done by planting seed free of red rice.” (Huey and Baldwin, 1978)
- “The first measure to control red rice is to use good seed.” (Jorge and Barquin, 1980).
- “Preventive methods (of control) are planting rice seeds free of red rice seeds. To this end it is important to produce rice seeds completely clean and with no seed of red/weedy rice. In some countries there are tolerances admitting some seeds of red rice per kg of cultivated rice seeds. This practice has shown to be negative in long term.” (Labrada, 1999).

The above quotations are repetitious. However, some state and national seed laws still permit some weedy rice seeds even in certified rice seeds, e.g. the European Union (Vidotto and Ferrero, 2005), and some farmers still plant saved seed or seed bartered

from a neighbour or purchased from a trader that they know is contaminated or probably contaminated with weedy rice. This suggests that the appeals to plant clean seed have not been repeated often enough, loudly enough and to enough rice farmers.

The symposium held in Texas in 1978 was a response to an escalating red rice problem in the southern states of the United States of America. In large part, the problem was the result of a two-year or longer scramble by rice farmers to obtain enough seed rice in order to take advantage of the relaxation of strict government controls on the rice area planted and the release of some very superior new varieties. Supplies of clean seed of both the older and new varieties were insufficient to plant the expanded area, so farmers secured seeds for planting from almost any source, including grain rice destined for the mill (Huey and Baldwin, 1978; Do Lago, 1982). The consequences of this indiscriminate scramble for planting seeds ranged from substantial to enormous. Red rice infestations increased and spread to formerly clean areas in the major, long-time rice states, and red rice was introduced into states that had entered rice production more recently and served as prime sources of red rice free seed. The Global Workshop on Red Rice Control (FAO, 1999) recognized the rapid “globalization” of the red and weedy rice problem with “the shift from rice transplanting to direct seeding ... (and) ... the cultivation of weak, semi-dwarf ‘indica-type’ varieties” (Ferrero and Vidotto, 1999), the switch to “varieties of medium cycle that favour the multiplication of mixtures” (Garcia de la Osa and Rivero, 1999), “... the gradual change from the traditional system to an intensive agriculture with new and more demanding production objectives that require new technologies (new varieties, irrigation, mechanization.” (Diallo, 1999), and insufficient attention to the purity of planting seed and/or inadequate supplies of clean seed for planting as mentioned by all of the participants at the Global Workshop. Five of the 21 recommendations of the Global Workshop concerned the production and supply of clean seed free of weedy rices (including red rices).

Seed certification

The development and maintenance of adequate supplies of red-rice-free planting seeds requires a legally sanctioned, organized system of seed multiplication and production that operates in accord with well-tested protocols and procedures to assure the genetic integrity and purity of the seeds produced. Seed certification is the internationally recognized and accepted system for producing and supplying high-quality pure seed. Traditionally, seed certification is organized as an official agency of the government or a legally and officially sanctioned agency to conduct activities that are in the national interest. The original purpose of seed certification was to maintain the genetic integrity, i.e. varietal purity, of varieties. However, over time, it began to encompass other attributes of seed quality, such as physical purity, other crop and weed seeds, and seed-borne diseases. Seed certification is a responsibility of government at the national or lower government (e.g. state and province) levels. However, for many years in many countries, it has operated under the umbrella of and in accord with the protocols and standards of international organizations or associations. The main international organizations/associations are: the Organisation for Economic Co-operation and Development (OECD), Paris (variety certification units); and the Association of Official Seed Certifying Agencies (AOSCA), Moline, the United States of America. These two international organizations set minimum standards for genetic purity and for other seed qualities, such as seed-borne diseases and weed seed contaminants.

The organization, functions, standards and operational procedures of seed certification schemes are well known and available. Hence, there is little need for a detailed description and lengthy discussion of them in this report. However, some discussion and observations on aspects of key activities in producing pure seeds could

be useful. These aspects include field inspections, seed analysis or testing, and clean-up of seed stocks, which are especially relevant to preventing weedy rice contamination of any class of planting seeds (certified, non-certified, saved, etc.).

Field inspections and roguing

Effective field inspections of seed rice fields require: (i) that whoever makes the inspections (e.g. farmer, extension specialist, or certification inspector) be familiar to the point of expertise with the characteristics of the rice varieties planted in the area and with the off-types and variants including weedy rices (including red rices); and (ii) that the inspections be undertaken and executed in an objective, careful and serious manner. The inspection of flooded rice fields is difficult and exhausting, but there is no substitute for wading among the rice plants. Unless very small in area, fields cannot be inspected adequately by walking the levees or bunds or with binoculars from the bed of a cart or field vehicle. Field inspections are much easier in drilled rice plantings than in broadcast plantings. Sonnier (1978), one of the most experienced and expert red rice specialists in the United States of America, offered this advice on field inspections for red rice: "... you have to stand in one place (at a time) and look around. And when you see that tall plant out there, you can bet that two or three more are somewhere around, hiding in the rice. You have to get them all... Believe me, the red rice situation does not remain static. It either improves or it gets worse." Regarding roguing, Sonnier stated that roguing of red rice from rice fields at the time of or after inspections is very effective but very costly if done properly. Sonnier pointed out that substantial damage can be done to a broadcast field by a roguing crew, but then noted that in the case of a light and rogueable infestation of red rice in a field of seed rice, the producer must either rogue regardless of damage to the crop or divert the field to grain production.

The workers in the roguing crew must also be familiar with the weedy rices (including red rices) and other weeds and variants that are to be removed. Moreover, insofar as possible, roguing should be done before the weedy rices start shattering seeds. Roguing after shattering begins might prevent contamination of the harvested seeds but the soil and soil seed bank are repopulated with red rice. Workers should be taught how weedy rices need to be rogued in order to prevent scattering them further through shattering of the seeds. Cox (1978), a seeds expert from Arkansas, related an incident that contains a critical lesson for a roguing crew. He was visiting the farm of one of his contract seed producers when the farmer came out of the field waving a handful of red rice panicles he had rogued. With considerable irritation, Cox informed the farmer that he was not only wasting his time but making things worse because he had scattered more than half of the seeds through shattering as he walked about in the field looking for other red rices. He recommended: "If you spot a red rice plant in the field, look in all directions because there is always more than one. Ease up on it very gently, pull the head over into a bag and clip it off, and (only) then pull the root up and put it into another bag. That is the only way to get rid of it."

Seed inspections and testing

The seed-testing laboratory is the last place and seed analysis is the last chance for detecting weedy rice (including red rice) contaminants in planting seeds. Seeds of some weedy rice ecotypes are recognized easily, but the hulls should still be removed in order to view the pericarp for additional verification if red rice is the prohibited or severely restricted type. However, seeds of other weedy rice ecotypes mimic those of cultivated varieties so closely that identification is very difficult, time-consuming, and much less than 100-percent accurate. Therefore, laboratories should have a small



Plate 17
 A: Small rice huller used in seed testing for examining rice seed samples for the presence of RR. B: Seed sample with hulls on. C: Seed sample with hulls removed.

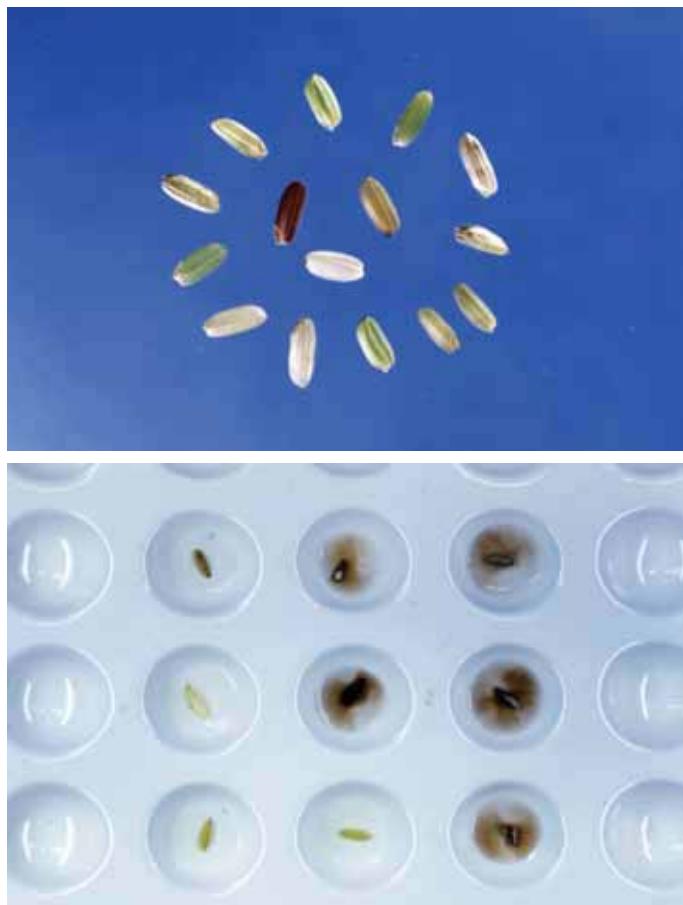
huller, such as used in breeding laboratories and in rice mills, to hull a specific quantity of the seeds for inspection for red pericarp seeds (Plate 17). The quantity of seeds to be hulled is usually specified in the certification standards, seed law or the laboratory protocols. However, this procedure is subject to error because the pericarps of some seeds, especially those gathered before maturity, are not red but about the same colour as similarly immature white rice, i.e. greenish, chalky white or some other off-colour that should arouse suspicion, but not always. Do Lago (1982) harvested seeds of four red rice types at 14, 16 and 18 days past anthesis and determined that the number of days required for the seeds to develop a visually detectable red colour varied with time of harvest, phenotype and storage conditions. Generally, the more immature the seeds are at harvest, the longer is the time taken for the red colour to develop, e.g. 36–59 days for seeds harvested at 18 days and stored under ambient conditions, and more than 100 days

for seeds of 3 of the 4 phenotypes harvested at 14 days. These suspect seeds should be tested individually in a test-tube or small glass or ceramic dish by placing several drops of 2.0-percent potassium hydroxide (KOH) solution on them (Rosta, 1975; Louisiana State Seed Testing Laboratory, 1980). Red rice seed will develop a deep red coloration within 5–10 minutes (up to 30 minutes for old seeds) while only a light or golden-yellow colour will develop for cultivated rices and any segregates or other weedy rices with a “white” pericarp. These procedures are shown in Plate 18.

Purification of contaminated seed stocks

Elite seed stocks, such as those of the basic or foundation multiplication classes, can become contaminated with weedy rices that mimic closely the variety, so that all the succeeding stages of multiplication and the fields used for multiplication become contaminated. Where the variety is a new and valuable one, something must be done to clean up the basic seed stock in order to avoid criticism and/or satisfy claims against the elite seed stocks unit. In one case, clean-up was accomplished by selecting four uniform areas in the field of about 0.1/ha each, with rigorous roguing of each plot to remove all suspect plants even those well behind in maturity. The seeds were harvested by hand with further discarding of any suspicious panicles. The panicles were threshed in a small thresher that had been cleaned and inspected thoroughly, and cleaned by sieving and aspiration. Two 0.5-kg samples from the cleaned seeds from each plot were hulled, aspirated to remove hulls, and checked under magnification for red or suspect pericarp colours. Suspect seeds were subjected to the KOH treatment for determining

red rice. Seeds from plots with no evidence of weedy rice (including red rice) seeds in the samples were combined, treated with a fungicide, and planted in an area that was more than 100 km from the nearest rice and had never been planted with rice. The seeds were planted in rows at a low density in order to maximize the multiplication. Many inspections were made; laggard and even slightly off-type plants were rogued. The seeds were harvested with clean machines never used to harvest rice, and then dried and cleaned. Tests on several 1-kg samples did not reveal any weedy rice (including red rice) seeds. The seed stock was certified clean of weedy rice seeds and multiplied as rapidly as possible in the same isolated area in order to prevent re-contamination. These rather laborious and time-consuming procedures delayed wide distribution of seeds of the much sought after variety for several years but restored the credibility of the foundation (basic) seeds unit and, very importantly, prevented additional claims and suits for damages.



J.C. DELOUCHÉ, 1993

Plate 18

Top: Immature caryopses (seeds) suspected of being RR but without any discernible pigmentation in pericarp (red and white pericarp seeds shown in centre for comparison). Bottom: The KOH test for positive identification of caryopses of RR.

Clean-up of contaminated seed lots

Most red rices produce medium-grain seeds that are wider and somewhat thicker than the longer and slender grains seeds of the long-grain rice varieties. These differences in physical dimensions of the seeds have long been taken advantage of by seed producers to remove red rice seeds from contaminated seed lots by cleaning the seed lots with special width separators. These width separators remove a lot of the red rice seeds from seed lots of long grain varieties but almost never all of them. Tests at Mississippi State University indicated that 98–99 percent of the seeds of a typical medium-grain SHR could be removed from seed lots of the long-grain Starbonnet variety with a loss of about 23 percent of the crop seeds, but the separation was not effective for lots of medium-grain crop seeds (Veras, 1984; Delouche, 1988). Clean-up of contaminated seed lots by mechanical or even optical separations should not be the first option for producers of certified seeds because of the high probability that some red rice seeds will remain with the crop seeds. However, the clean-up option has been used effectively to reduce the amount of red rice seeds in seed lots that have to be used for planting because certified seed is not available or for other reasons. In effect, removing red rice seeds in the seed-processing operation is a tactic in the depletion strategy – some of the red rice seeds that would have been planted are deleted from the potential red rice population. However, Vidotto and Ferrero (2005) emphasized that while a few weedy rice contaminants in planting seeds have a negligible influence on the weed rice

population dynamics where planted on substantially infested lands, they can lead to severe infestations in a few years where planted in clean fields.

The clean-up of seed lots is not possible where the red rices are of the long-grain type or the variety is medium-grain.

Other sources of infestations

Contaminated planting seeds are not the only source and ways that weedy rice seeds are spread among fields within a rice farm and from one farm to another. Other common sources of weedy rice infestations are:

- machinery, especially machinery used in harvesting including carts, tractors and other vehicles (Quereau, 1920; Huey and Baldwin, 1978; Smith, 1992);
- mud clinging to wheels and tyres;
- animals;
- land levelling and movement of soil;
- cultivation (De Souza, 1989; Garcia de la Osa and Rivero, 1999);
- flowing irrigation water (Manning, 1998).

Options for the small farmer

The purchase of certified seeds from a reliable seed dealer is the best way to avoid infesting or re-infesting rice production fields. However, in some countries, clean seed supplies are not available or the small farmers either want to continue with varieties no longer in the seed production system or they lack the resources to purchase the needed seed supplies. In such cases, two options are available the farmer:

- Rogue and save seed for planting from the best area in the field.
- Obtain seeds from a neighbour who has an exceptionally clean field – determined by close observation and inspection – of the variety wanted.

DEPLETION OF THE WEEDY RICE SOIL SEED BANK

The soil seed bank depletion strategy involves management decisions regarding cropping systems and employs a variety of cultural, mechanical and chemical practices and treatments. The management decisions relate to the sequence and intensity of cropping, e.g. rice monoculture, double-cropping, alternation of crops (rotation), multiple-year fallowing. In this section, the emphasis is on practices and treatments and their management during the interval between rice crops. This interval may be range from a few months to several years of fallowing in the case of especially heavy infestations. Crop rotation is considered in a later section. Vidotto and Ferrero (2005) have developed and tested a model of the population dynamics of weedy rice seeds and infestations as an aid for selecting and managing control measures. The model focuses on the dynamics of the soil seed bank in terms of inputs into the bank and measures that deplete the supply of seeds. Some of the more important measures in the model for depleting the seeds in the bank are included here.

The first post-harvest management decision should be to avoid deep ploughing or any but the very shallowest cultivation. This is in order to avoid burying weedy rice seeds in the soil seed bank, where they are very long-lived (Goss and Brown, 1939, 1940; Dishman, 1978; Do Lago, 1982; Teekachunhatean, 1985; Fischer, 1999). The first step should be destruction of the stubble to prevent ratooning of the rice – white or red – if there is an opportunity for reproduction before freezing or the onset of the dry season (Sonnier, 1978). Thereafter, the field should be managed in ways that cause the greatest depletion of weedy rice seeds on or in the soil at emergence depth.

Stale seed bed

One popular option is the stale seed bed (Baker, 1974). Essentially, a stale seed bed (frequently termed false seeding in Europe) is one that has received no preparatory tillage prior to planting (Heatherly, 1999). In the case of soybeans and similar crops, there might or might not be one or more tillage operations up to about 30 days before planting. However, for rice, little is done before sowing except possibly rolling the straw after harvest and keeping the field wet or flushing it with water one or more times in order to stimulate germination and/or rotting of the seeds (Huey and Baldwin, 1978). Leaving the field more-or-less undisturbed permits maximum depredation of the seeds by birds and field rodents. Some farmers in the Louisiana rice belt encourage the winter stop-over of wild ducks and geese to feed on shattered red and cultivated rice seeds by maintaining a suitable flood on the land by irrigation or natural rainfall (Fontenot, 1973). Smith and Sullivan (1980) conducted trials in Arkansas to determine the effectiveness of the winter feeding of ducks and geese in depleting the population of red rice seeds in infested fields and found that wild ducks consume large quantities of red rice seeds. They recommended that farmers attract wild ducks by keeping infested fields flooded after harvest until late winter.

The stale seed bed is rid of all green vegetation including weedy rice seedlings and plants before sowing by application of a non-selective systemic herbicide such as glyphosate, a contact and/or short-residual herbicide, or very light but thorough cultivation (Sonnier, 1978; Smith, 1992; Ferrero *et al.*, 1999; Fischer, 1999; Martinez, 1999; FAO, 2003). The seeds are then drill sown or broadcast in a relatively dry, wet or flooded seed bed depending on the type of water management used (Sonnier, 1978).

Minimum or no-tillage

Minimum tillage can be applied in the stale seed bed planting system. There does not appear to be much difference between them except that in the stale seed bed system there is no mechanical preparation for at least 30 days or so before sowing, i.e. the seed bed is not “freshly prepared.” The no-tillage system means just what it says, i.e. there is no tillage during the post-harvest, preplanting period – vegetation is killed by herbicide and the seeds are drilled or broadcast in the stubble. In some areas, minimum tillage is applied to the rice field several times during the post-harvest, preplanting period in order to destroy the flushes of weedy rice seedlings after rains or promoted by light irrigation (Sonnier, 1978; Martinez, 1999; Barreda *et al.*, 1999, Ferrero *et al.*, 1999). Tillage can be applied just before planting. However, this is not recommended because some weedy rice seeds germinate and emerge along with the cultivated rice. Minimum tillage is most often combined with some degree of water seeding, either drilling or broadcast into a flood, or drilling/broadcasting followed in a few days by flooding.

Fallowing

Fallowing is rather deep cultivation during the idle time between crops to turn up buried seeds of weeds and the crop (in the case of changing varieties to emergence depth), stimulate germination of weed seeds, and destroy all plants that emerge during the fallowing period. Fallowing is one of the oldest methods of weed control. It is often imposed on farmers by infestations with weeds to the point that crop production becomes uneconomic or impossible. Sonnier (1978) did much of the research on fallowing for red rice control in the United States of America and stated that with some reservations and qualifications it is an effective method. He found that fallowing only during the interval between rice crops had no effect on the level of red rice infestation and actually increased the problem by burial of the red rice seeds, i.e. planting them as

argued by Dishman (1978). The fallowing had to be continued for a 2–3 year period in order to significantly deplete the soil seed bank and reduce the red rice population in the rice crop following the fallow period. Idling cropland for long periods is not usually a feasible solution unless there is no alternative. The most economical and currently preferred solution is to fallow after the rice crop and through the winter, and then to rotate production into another crop that offers opportunities for destruction of emerged red rice plants by selective chemicals and cultivation while providing income from the alternative crop. Technically, rotation to another crop is not fallowing but it accomplishes some of the same things, mainly, depletion of the seed soil bank. Rotation for weedy rice control is considered below.

Burning of stubble and straw

Sonnier (1978) pointed out that burning of the stubble and straw in rice was once a very common practice in the Louisiana rice area because farmers believed that burning destroyed red rice seeds. However, the practice was eventually abandoned because of the smoke pollution problem and recognition that valuable organic matter was being destroyed, but mostly because it was not very effective except in areas where the straw was very dense. He also cited the “invention” of a burner designed to direct an intense flame onto the soil surface. The invention was soon abandoned owing to the destruction by burning of the equipment carrying the burner and the high consumption and cost of fuel for burning.

Other approaches

Several other approaches have been investigated with the aim of depleting weedy rice (including red rice) seeds in the soil seed bank. Eastin (1978) discussed efforts to find some way to release dormancy and induce germination in red rice seeds so that they could be destroyed by chemicals or mechanical means during the interval between rice crops. Many chemicals were evaluated in laboratory experiments, including gibberellin, ethephon, indole-3-acetic acid, kinetin, and hydrogen peroxide, but none was consistently effective. Based on the earlier laboratory studies at Mississippi State University (Delouche and Nguyen, 1964; Larinde, 1979; Do Lago, 1982), Teekachunhatean (1985) planted very dormant (germination < 5 percent) seeds of the Nato variety and three red rice types 2.5 cm deep in soil and drenched them with equal volumes of water, ethylene chlorhydrin and sodium hypochlorite solutions, flushed them with another equal volume of water, and counted emerged seedlings after 14 days. The water treatment had no effect on emergence, but 35–86 percent of the seeds drenched with 0.25-percent ethylene chlorhydrin and 0.50-percent sodium hypochlorite emerged, with the sodium hypochlorite drench stimulating the highest emergence. Garcia-Quiroga (1987) continued the drenching studies and found that the ethylene chlorhydrin drenches were generally more effective than sodium hypochlorite in stimulating emergence of an SHR and BHR ecotype, but that the effectiveness of both treatments varied widely among plots and times of treatment. Such treatments would need to be carefully screened for residual and pollution effects.

SUPPRESSION OF WEEDY RICE GERMINATION (WATER MANAGEMENT AND CHEMICALS)

The suppression of germination and emergence of weedy rices (including red rices) and other weeds by anoxia in wet and flooded soils has been practised for millennia in transplant rice culture. However, water management and sowing practices for producing anoxia in direct-seeded, irrigated rice culture have been developed only during the last

century. Smith (1972) conducted greenhouse studies on the effect of submergence in water on the germination and emergence of red rices. In these studies, submergence of the soil by 1.25–5 cm reduced emergence of red rice seeds 1–2.5 cm deep in the soil by 92 percent and emergence of seeds 5–10 cm in the soil by 100 percent. Other workers obtained similar results (Sonnier, 1978; Diarra, Smith and Talbert, 1985c). The most successful application of water seeding for control of red rices and other weedy grass species has been in California, the United States of America, which became an essentially red-rice-free production area through the use of red-rice-free certified seeds and the practice of water seeding (Fischer, 1999). California had the main requirements for water seeding, i.e. level fields, a dependable water supply, and a desert to semi-desert climate with few storms and heavy rains at sowing time. The suppression strategy maintains and extends both the short-term and long-term benefits of the weedy rice soil seed bank depletion strategy. Thus, it follows (or must be preceded by) the stale seed bed, minimum tillage, periodic flushing, smoothing and rolling practices used to stimulate the presowing germination of weedy rices and other weeds, and the mechanical or chemical destruction of all vegetation before sowing.

Water seeding (sowing in a flood)

There are several versions of water seeding in order to accommodate differences in field uniformity, levelling and climate. Most of them require use of pregerminated seeds, i.e. seeds soaked in water to full imbibition and held for a time in order to permit germination to commence. Some farmers like to leave the seed bed in a rough, cloddy condition in order to curtail movement of the seeds in the water film (Hill, 1978), while others smooth and roll it and still others puddle the soils (Garcia de la Osa and Rivero, 1999; Dominguez, 1999). According to Sonnier (1978), farmers have three water management options after water seeding:

- Maintain a continuous flood from planting until drainage preparatory to harvest. This is the best option for suppression of weedy rices but it has risks. Obtaining a satisfactorily stand of seedlings can be a problem in high organic soils that keep the water murky. Heavy rains and high winds can cause drifting of the seeds and uprooting of seedlings.
- Drain the fields after sowing and reflood only when the seedlings are established sufficiently to withstand a full flood. Obtaining a good stand of seedlings is not a problem but the stand is likely to include a good population of weedy rice seedlings.
- Drain the fields a few days after flooding and then reflood gradually as the cultivated rice seedlings set down roots. This option, a compromise between the other two options, is termed “pinpoint flooding.” Although the flood is drained, the soil is kept moist so that weedy rice germination and emergence is suppressed sufficiently for a “good” control rating. Stand establishment is favoured, and the seedlings set down roots quickly and resist drifting and uprooting.

Sonnier also stated that the continuous flooding option gave the best control of red rice but cautioned farmers about the risks of poor stands and drifting from rainy, windy weather. He noted that, while fewer red rice seeds emerge in continuous flooding, the plants are usually very robust and produce large quantities of seeds compared with the more numerous smaller plants that produce relatively few seeds in prolonged drainage systems. Overall, considering the suitability of fields for water seeding and climate conditions at sowing time, Sonnier and other specialists (Hill, 1978; Huey, 1978) generally considered the pinpoint flooding system as most suitable for the southern states of the United States of America and similar rice production areas.

Chemical suppression

Several herbicides are used in water-seeding rice culture for additional suppression of the germination of weedy rices and other “watergrasses”. The most widely used is the herbicide molinate incorporated preplant or in the water after seeding (Parker and Dean, 1976; Baker and Sonnier, 1982, 1983; Smith, 1981, 1992; Abud, 1986; Fischer, 1999). Application of 1, 8-naphthalic anhydride, a “herbicide antidote”, as a seed treatment has been used to enhance tolerance of rice to molinate and other thiocarbamate herbicides (Smith, 1972; Henry and Baker, 1972). However, water seeding and the use of chemicals such as molinate are changing the ecology of the direct-seeded, irrigated rice system to the extent that new weed problems have arisen. An increasing population of weeds are becoming well adapted to the water-seeding system and resistant. Goforth (2004) reported that the water-seeding system is losing its effectiveness and that in some cases growers are “taking a second look at drill seeding” in dry seed beds. He quotes Fischer: “Water-seeding has over the years selected for a specific set of weeds that are particularly adapted to this (water seeding) anaerobic system.. (and)... These weeds have developed resistance to many herbicides....Resistant biotypes of these weeds are distributed throughout the rice growing areas in California.” Fischer also noted that new herbicide chemistry is not a likely solution because of the high cost of development and the complex registration process and, moreover, that the herbicide molinate will be phased out in California within the next five years owing to regulatory restrictions and loss of effectiveness. After cautioning rice growers considering the dry-drill-seeding system to be on the lookout for new weed problems, Fischer concluded: “Although red rice has not yet become a problem in California, largely due to the water-seeding system and the use of certified seed, this weed may find favorable conditions in a continuous dry-seeding system.”

A variety of “antigermination” herbicides are used for the control of weedy rices in rotation crops such as soybeans, sorghum and sunflower. However, in rice culture, residual activity has limited their use to very-short-residual types. In European rice culture, the chemicals pretilachlor and dimethenamid, alone or in combination, applied preplant at least 25 days before rice sowing have enabled quite good control of the weedy rices (Ferrero and Vidotto, 1999).

Change to transplanting culture system

The transplant culture system is the traditional method for suppressing the germination and emergence of weeds in rice fields. It is always an option where available control methods used in direct-seeded rice systems fail to provide the level of control for economically viable rice production. This option is the next to last one – the last one being abandonment of rice production – and limited to small-scale operations managed largely with family labour. Nevertheless, it has been taken up in some areas in SSA (Johnson *et al.*, 1999), Asia (Chin *et al.*, 1999) and the Americas (Martinez, 1999).

DESTRUCTION OR REMOVAL OF WEEDY RICE PLANTS IN THE RICE CROP

Weedy rice seeds that germinate and emerge along with the rice crop will grow, develop, and produce seeds for infesting the next crop unless they are removed, killed or prevented from reproducing. However, the options available to most rice farmers for control of weedy rices in the growing rice crop have been limited, laborious and expensive. They have been limited because most weedy rices are strains of *Oryza sativa* or very close relatives, which precludes their control by selective herbicides as used for control of other weeds in rice and other crops. They have been further limited because the flood and broadcast seeding precluded the periodic cultivation traditionally used

for weed control in other crops. They were laborious because the only practice available to most rice growers was hand-weeding or roguing, or treatment of individual plants with herbicides. They were expensive because hand-weeding is expensive even when done by family labour. However, recent developments of a “biotechnology strategy” for control of weeds in a variety of crops (including weedy rices in the rice crop) have the potential to essentially eliminate these constraints and limitations for growers who can access and afford the technology. The biotechnology strategy is considered in a later section.

Hand-weeding of rice field (roguing)

Hand-weeding and/or roguing of volunteer, red and other weedy rices is a viable option only for small farmers and certified seed producers with relatively light infestations. Roguing of certified seed fields has been discussed above. The cautions and procedures described and discussed are equally applicable to small farmers using family labour. The main points are that roguing should be done as soon as the weedy rice plants can be identified, or at least before seed shattering. The panicles should be cut and placed in a bag before the rest of the plant is pulled for removal from the field.

Osborn and Faye (1991) and Chin *et al.* (1999) related for Senegal and Viet Nam, respectively, how small farmers could avail themselves of the relatively simple and readily available practice of planting rice in defined rows rather than by broadcast or other ill-defined planting systems. This greatly facilitates the early weeding between rows of the rice crop before flooding or during drainage periods by hand or with short hoes, with the added benefit of a substantial reduction in the amount of seeds required.

Mechanical and chemical control practices

Ferrero and Vidotto (1999) describe a cutter bar device from a combine harvester fitted with contra-rotating crushing rolls that is attached to the front of a tractor and used to cut and crush panicles of weedy rices (including red rices) and that are sufficiently taller than the crop. Two passes are made through the field – the first at the beginning of flowering, and the second 15 days later. An alternative to cutting and crushing is the use of a rope or sponge wick device wetted with an herbicide, such as glyphosate, to rub across the tops of taller weeds and weedy rices (Stroud and Kemper, 1989). In Brazil, maleic hydrazide, a plant growth regulator, has been labelled for the suppression of seed production in rice (Noldin and Cobucci, 1999; Saldan and Deambrosi, 2000). Use of maleic hydrazide, based on earlier work by Dunand (1996), requires that the weedy rice be at least 10–15 days later than the crop. Spraying the chemical on the weedy rice prior to or at the time of heading reduced the number of panicles, increased sterility and reduced viability. Agostinetto *et al.* (2002) reported similar suppression of weedy rice seed production by applications of the herbicides glyphosate, gluphosinate and paraquat as well as maleic hydrazide in rice fields planted to varieties substantially earlier than the weedy rices. Best results were obtained when flowering of the weedy rices had reached the basal spikelets in the panicles.

ALTERNATION OF RICE WITH OTHER CROPS OR FIELD USES TO CHANGE ENVIRONMENT

Rotation with other row crops

The disadvantages of monoculture and the advantages of crop rotation in terms of soil condition and conservation, disease and insect control, and control of weeds have long been recognized and practised. Baldwin (1978) related how the worsening red

rice situation in Arkansas led to the decision in 1969–1970 to focus research on crop rotation for control. Extension and research specialists in the state recognized that discovery of a selective herbicide for red rice control was highly improbable, that cultural practices were only slowing the increase in red rice infestations, and that some more effective control system other than multiple-year fallow was needed in order to maintain economically viable rice production. Soybean was the second crop in the grand prairie rice area of Arkansas and was already rotated with rice by some growers. Therefore, research attention focused on soybean–rice rotations and, to add another option, on sorghum–rice rotations. It was soon determined that a one-in-one-out rotation of rice and soybeans would not control red rices satisfactorily except in very lightly infested fields. Therefore, a two-out-one-in rotation (two successive years out of rice in a three-year period) became the minimum.

Rotating rice with soybeans, grain sorghum, sunflowers, maize and grain legumes other than soybeans has several crucial advantages. The sowing and cultural systems provide ideal conditions for the germination of red rice and the opportunity to deplete seriously the red rice soil seed bank by use of the full array of preplant incorporated, pre-emergence, post-emergence and over-the-top herbicides used for weed control in the alternate crop. More recently, the introduction of herbicide-resistant varieties of some of the rotation crops permits use of broad-spectrum herbicides. The equipment and facilities, e.g. storage bins and dryers, used for rice can also be used for the other “grain” crops with minimum modifications. The success of rotation for the control of weedy rices (including red rices) depends on how well weeds are controlled in the alternate crop in general and the specific attention given to preventing production of seeds by red rice plants in the crop from late-emerging seedlings or ratoon tillers. Rotation of rice with soybeans, sorghum or another suitable crop is currently the most successful practice for the control of weedy rices, especially severe infestations (Fischer, 1999; FAO, 2003). Moreover, rotation is becoming an even more critical component of weedy rice control programmes in the new era of herbicide-resistant rice as an essential tactic in strategies to reduce or prevent the development of herbicide-resistance in the weedy rices.

The main limitations on the rotation control system are the availability of a suitable crop, the drainage of the rice fields (poor drainage precludes the use of many row crops), and the need of rice for on-farm consumption, i.e. as in near-subsistence agriculture.

Rotations with green manure crops and pastures

Rice production is alternated with green manure crops in some countries, e.g. *Crotalaria* in Colombia (Carroza, 1999), and *Sesbania* in Cuba (Garcia de la Osa and Rivero, 1999). Moreover, it has long been rotated with pastures and cattle or hay operations. Sonnier (1978) stated that the prevailing rotation in the rice area in Louisiana before soybeans became a major crop in the same area was with improved or non-improved pastures. He then discussed some farmer perceptions and his station's findings on advantages and limitations of the rotation. Red rice plants readily volunteer in the pasture phase of the rotation and some reach maturity despite grazing pressure. Many farmers felt that the addition of one or two mowings and clippings to the grazing pressure destroyed most of the red rice plants that emerged and also prevented seed production. However, red rice plants in pastures mown to 5 cm regrew to 30 cm in 21 days and panicles were emerging from the boot. Red rice plants mown to 10 cm regrew to 35 cm in 21 days and were in head, while 28 days after mowing panicles were well developed and the seeds were nearly at the shattering stage. Based on the rapid regrowth and heading of red rices in pastures, Sonnier recommended that the pastures be grazed and mown to a

height of 7.5 cm or less at least twice in the warm season for rice at intervals of 28 days or less.

De Souza (1989) described a successful rice-improved pasture rotation in southern Brazil for the control of red rice and for additional income. Following the rice harvest, the annual pasture grass species *Lolium multiflorum* is established, grazed during the winter, then killed with a non-selective herbicide before drilling rice seed in the sod for the next rice crop. Beginning in the 1980s, Uruguay established a model rotation system of 2 years rice, 3 or 4 years pastures/cattle. This system brought red rice under control and permitted the development of Uruguay's premium quality rice export programme (Chapter 8).

BIOTECHNOLOGICAL STRATEGY – HERBICIDE-RESISTANT VARIETIES

Long before the release of the first herbicide-resistant rice variety in 2002, efforts had been made to identify a herbicide / herbicide-resistant-variety system that would permit easier, simpler and more effective control of weedy rices (including red rices) in the rice crop. Some varieties and lines were identified that were superior competitors and some exhibited tolerance to herbicides (Baker and Bourgeois, 1978; Wirjahardja and Parker, 1978; Wirjahardja and Susilo, 1979; Richard and Baker, 1979). However, the search for suitable herbicide-resistance sources was not very successful. The situation changed with the rapid progress in the development of herbicide-resistant and insect-resistant soybeans, cotton, maize and other crops. Several biotechnology companies and university research units began or accelerated work on the development of herbicide-resistant rice varieties that would permit the effective control of weedy rices (including red rices) and the increasing number of herbicide-resistant weedy species in rice with a single powerful, non-selective, environmentally “friendly” herbicide (as was also the goal in the work on herbicide resistance in other crops). In the mid-1980s, considerable progress was made in developing rice lines resistant or tolerant to the IMI herbicides, mainly by mass screening in tissue culture (Croughan *et al.*, 1984; Croughan, Pizzolatto and Trump, 1986; Croughan, 1994). Somewhat later, glufosinate resistance was transferred to rice lines by genetic engineering (Linscombe *et al.*, 1994; Braverman and Linscombe, 1994; Rathore, Rao and Hodges, 1994).

Apart from technical considerations, there were two main reasons why application of the herbicide resistance strategy for weed control in rice lagged behind that for soybean, maize, and cotton. First, rice is a minor rank crop in most of the countries with advanced agricultural research and agrichemical industries where it is direct seeded. Second, there was and is considerable apprehension that the resistance gene (or genes) would flow to weedy rices (including red rices) that cross with cultivated rice and produce herbicide-resistant populations of the weedy rices. However, by the late 1990s, rice varieties resistant to the broad-spectrum herbicides glufosinate, IMI, glyphosate and probably others had been or were being developed. Varieties resistant to IMI (so-called IMI rice) were introduced in 2001–02 in the rice-growing area of the south of the United States of America under the Clearfield trade name. The Clearfield varieties were not modified genetically by the insertion of foreign genes. They were selected as mutants and developed into varieties by classical breeding methods. Seeds of Clearfield varieties are marketed in a package with the Newpath® herbicide (imazethapyr). By 2005, Clearfield varieties had been planted to about 27 percent of the long-grain rice area in Arkansas, the leading rice-producing state in the United States of America (Horizon Ag, LLC, 2005). Farmers have generally obtained satisfactory results with the Clearfield varieties in terms of both weed control and production, especially after several years' learning process and the release of improved Clearfield varieties (Bennett, 2005). The area planted to herbicide-resistant varieties of rice in the

United States of America and other countries will probably continue to increase as it has for herbicide-resistant varieties of other crops.

In 2005, the rice trade magazine *Rice Farming* headlined a story under the headline “Red Flag Warning” (Boyd, 2005). The story related the first commercial case of Clearfield rice outcrossing with red rice in the 2004 crop in Arkansas. The field in which the hybrid was identified had been planted to the Clearfield variety for two successive years in “violation” of the Clearfield Stewardship Agreement. This agreement clearly states, among other things, that: “a Clearfield rice crop should not be followed by another Clearfield rice crop or a conventional rice crop in the same field; the rotation crop, e.g. soybean, should be treated with herbicides that have different modes of action than Newpath®; and red rice escapes in rice fields and adjacent areas should be carefully hand pulled and removed from the area.” Although the discovery of a herbicide-resistant red rice was indeed a warning it was not surprising. Olofsson, Valverde and Madsen (1999) has presented a thorough review and analysis of herbicide-resistant rice at the 1999 Global Workshop on Red Rice Control (FAO, 1999), while a year later, at the 3rd International Weed Science Congress, Valverde (2000) had pointed out that worldwide 19 weedy species in rice had developed resistance to herbicides and recommended that herbicide-resistant rice varieties be used rationally and in well-managed integrated weed control programmes (Gealy, 2005; Valverde, 2005). Moreover, university and USDA researchers, especially in Arkansas, had established outcrossing between Clearfield (IMI) rice and strawhull red rice with near synchronous flowering (Moore *et al.*, 2001; Estorninos *et al.*, 2001) with outcrossing rates estimated at 0.012 percent, and also between glufosinate-tolerant rice varieties and several red rice ecotypes (Wheeler and TeBeest, 2001). Methods have been and are being developed that permit rapid and accurate identification of hybrids between rice and red rice, with particular emphasis on hybrids from crosses of herbicide-resistant rice and red rice for use in close monitoring of developments by company representatives, extension specialists and consultants (Rajguru *et al.*, 2001; Gealy and Estorninos, 2004a, 2004b; Gealy, Mitten and Rutger, 2003; Estorninos, Gealy and Burgos, 2004). The hybridization of red rice with cultivated rice, including herbicide-resistant varieties, has been discussed in greater detail in Chapter 3, and reviewed comprehensively by Gealy (2005).

These recent events involving herbicide-resistant rice underline the importance of adherence to the agreement and other guidelines that have become an essential, even legal, part of the purchase order of proprietary varieties, both transgenic and non-transgenic. The terms of the agreement and guidelines have been determined by the owner of the technology, public scientists, extension specialists, and progressive growers. They are designed and intended both to protect the rights of the owner and, very importantly, to protect and sustain the integrity of the technology for use by all farmers who want to use it. There are risks associated with the use of herbicide- and insect-resistant varieties of any crop. Those related to herbicide-resistant rice varieties have been reviewed by Olofsson, Valverde and Madsen (1999) and, more recently, by Gealy (2005). However, there is a strong belief among knowledgeable scientists, specialists and farmer-users that the risks can be managed in ways that will protect the technology and preserve the very substantial benefits to the producers, the food supply, and the environment. However, it is generally recognized that the cost, complexity, and proprietary rights associated with most biotechnology products such as herbicide-resistant rices will limit access, at least in the initial stages, of the powerful and benefit-laden technology to large, mechanized and commercial rice production operations, and effectively exclude most of the smaller, lower input, resource-poor rice operations and producers.

REQUISITES FOR EFFECTIVE WEEDY RICE CONTROL PROGRAMMES

The development of a system for producing good-quality, weedy-rice-free seeds and the availability of supplies of clean seeds are essential first steps in the implementation of control programmes for weedy rices (including red rices). However, improvements will be limited unless and until all the stakeholders in the rice industry are persuaded that control is possible, that it is needed, that the control measures have to be integrated and comprehensive, and that the benefits will exceed the costs. Obtaining the attention of the stakeholders, especially the producers, is difficult to impossible in areas where rice is a subsistence and/or mainly an opportunistic market crop, crop yields are only slightly affected, and there is no market penalty for the presence of weedy rice grain, especially those with the red pericarp, in grain rice. Little can be done in such situations. However, such areas are vanishing as the urban and even rural markets in developing countries such as Senegal are becoming more discriminating in terms of quality, as noted by Diallo (1999).

Agreement by most of the stakeholders that the weedy rice problem is important and that action is needed does not improve things very much. What is needed is an imaginatively conceived, comprehensive, energetically led and sustained campaign that involves all the stakeholders. The campaign needs to be based on practical and doable measures, and have achievable goals. The critical requisites for a successful campaign are commitment, coordination, cooperation and comprehensiveness. Chapter 8 presents some examples of successful weedy rice control programmes/campaigns.

Chapter 8

Examples of weedy rice control campaigns

This chapter presents examples of actual weedy rice control campaigns in various countries in three geographical regions:

- South America: Uruguay;
- Central America and the Caribbean: Colombia, Costa Rica, Cuba, Nicaragua, Panama and Venezuela;
- North America: the United States of America.

SOUTH AMERICA – COMBAT AND CONTROL OF RED RICE IN URUGUAY

This case study analyses and discusses the main factors that allowed Uruguay to gain and maintain control of red rice with minimal impacts on yields and grain quality.

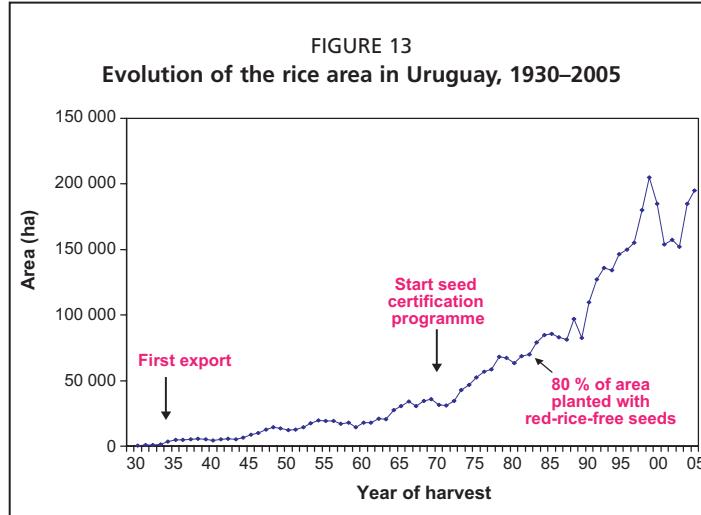
Background

Rice was first planted in Uruguay in about 1920 in the north of the country. In the 1930s, the first large rice farms started production activities in the east at the Laguna Merim basin, where rice cropping has mostly developed up to the present time. These rice production activities were initiated by national farmers and enterprises based on knowledge, technology and varieties introduced mostly from Brazil and Italy. Today, Uruguay has about 200 000 ha of rice managed under highly technical, mechanized systems (Figure 13).

Although documented data are lacking, it is assumed that red rice was introduced as contaminants in rice seeds imported by the pioneering rice farmers. In 1972, with a view to developing a rice seed certification programme, a survey was conducted on the varieties used by farmers and seed samples were collected and analysed (Jorge, 1972).

In 1972, about 26 800 ha of rice were planted, 70 percent with long-grain varieties and 30 percent with medium- and short-grain varieties. At that time, there was no organized seed programme and only 70 percent of the seed available for planting had been subjected to some degree of processing or cleaning. The rest of the seed used by farmers was home-saved.

Seed quality tests of the samples collected revealed that 38 percent of the seed lots being planted were contaminated with red rice. Of these red rice contaminated lots, 90 percent were from small farmers



Source: Zorrilla, 1998.

and 15 percent from large rice enterprises that were just starting the development of a seed programme. The seed lots of medium- and short-grain rice varieties had the highest levels of red rice contamination (about 400 red rice seeds per kilogram of rice seed). The results from the 1972 survey indicated that red rice was present in almost all of the rice cropping areas, a fact later corroborated by senior agronomists.

Basic elements to combat and control red rice

Development of a rice-exporting sector

Since 1935, Uruguay has had a positive rice production balance with a certain volume of grain available for export. For many years, these exports were mainly opportunistic and complementary to the national rice supply. However, by the mid-1960s, some changes in the rice sector had initiated activities that were the first steps in the successful campaign to combat and control red rice.

In 1965, some large seed producers involved in the export of rice introduced the variety Bluebelle, from the United States of America. This variety adapted well to the local conditions and played a crucial role in augmenting rice exports. In the 1970s and 1980s, more than 80 percent of the national rice production was of this variety, allowing Uruguayan producers to enter international markets with a fine-quality product. The rice sector subsequently developed into a major rice exporter, so that more than 90 percent of the rice production is now exported and Uruguay ranks seventh among the rice-exporting countries.

The need to survive and develop in a world rice market distorted by subsidies and numerous commercial barriers required a series of transformations in the rice sector in order to achieve and maintain a competitive position. Emphasis was placed on technological developments geared towards higher yields, greater efficiency in the use of resources, and higher quality and uniformity of the final product.

In this emerging rice production programme, it was soon recognized that lack of variety purity and red rice contamination were affecting not only rice yields but also the quality of the product, and that the development of a seed supply system to ensure varietal purity and the quality of the seeds as regards contaminants had to become an urgent priority. This seed supply and seed quality focus for development of the rice industry in Uruguay is fundamental for understanding and appreciating the successes obtained in the combat and control of red rice.

The national seed system as a basic component

The Estación Experimental del Este was created in 1970 with the objective of generating and adapting technology for rice production. Among its priorities were the development of a national rice breeding programme, the initiation of a rice seed certification scheme, and soil and crop improvement and management.

The certified rice seed programme has had a leading role in the combat of red rice. From the outset, it received strong support from the private sector and within a few years almost all the rice cropping area of the country was planted with rice seeds free of red rice.

In Uruguay, several categories of seed are recognized (foundation, registered and certified) with genealogical control at all stages by the Instituto Nacional de Semillas (INASE), which releases the seed labels. In addition, a category of commercial seeds is recognized. Commercial seeds do not require genealogical control but they have to meet all other standards similar to those of certified seeds. This category is guaranteed by the seed producer and is controlled, at market level, by the INASE.

In 1984, of a total planting area of 80 700 ha, 48 percent was planted with certified seeds and the balance with commercial seeds produced under strict quality control regulations (Zorrilla and Acevedo, 1985). The seed tests showed that all seed lots sampled were free of red rice contamination.

During the early implementation of the seed production scheme among the national rice producers (Figure 13), there was the opportunity to produce rice seeds in fields that had never been planted to rice. This was a major asset for the rice seed production system and made possible the early production of large volumes of red-rice-free rice seeds. The increase in the use of certified seeds has continued and now more than 85 percent of the national area is planted every year with certified seeds (Figure 14). The progress made in establishing a quality seed supply system and the very low use of farmer-saved seeds has been largely possible because of the strong support from the rice industry and its close relationship and cooperation with the rice farmers.

The rice-milling group developed into a highly technical industry with the consensus goal of producing the highest quality rice free of red rice. Seed production was and is considered an essential activity of the rice industry and not a profit-making business. Thus, the average cost of the red-rice-free rice seed is only 1.7 times the cost of rice grain, a fact that discourages the use of farmer-saved seeds.

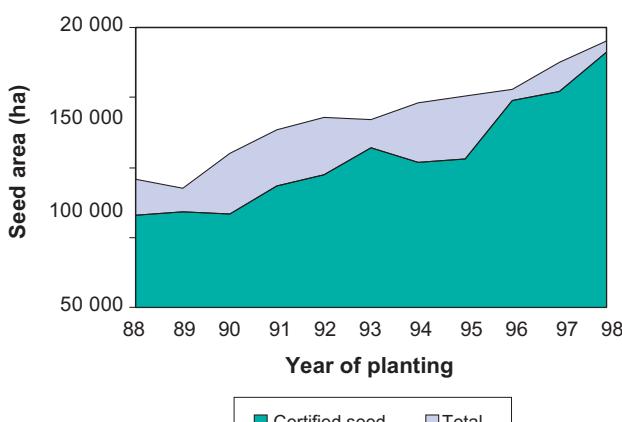
The contracting system used between rice farmers and the rice industry supports the expansion of the use of certified seeds, which is a specific requirement in the contracts. The rice producers of the Asociación de Cultivadores de Arroz have supported this system as they are convinced that this strategy is beneficial for the whole agroindustrial chain.

The governmental institutions have also supported the development of the rice production sector: the Estación Experimental – Instituto Nacional de Investigación Agropecuaria (INIA), Treinta y Tres, by generating and maintaining new varieties and producing the foundation seeds of the new varieties, and the INASE as the institution responsible for the whole system (Figure 15).

Among the elements that were adjusted in the improvement and development of the red-rice-free seed production process, some significant changes were made in the rice seed certification standards. In 1989, a zero tolerance of red rice was included for the category of certified seeds. In 1993, this was extended to all seed categories (Table 31).

The establishment of large-scale rice seed production free of red rice before the rapid expansion

FIGURE 14
Evolution of the total planted area and the area planted with certified seeds in Uruguay, 1988–1998

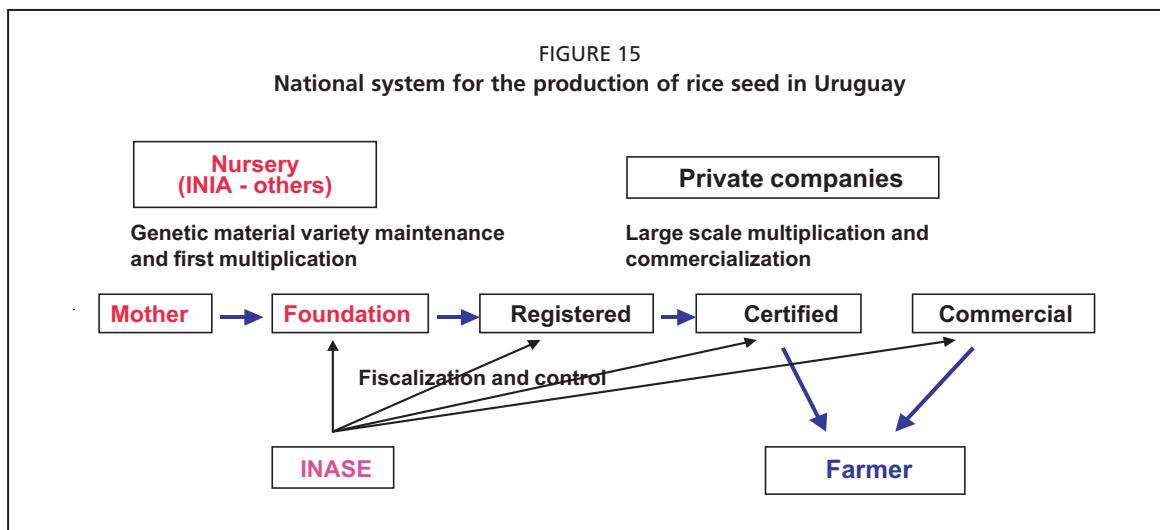


Source: G. Sanguinetti, personal communication.

TABLE 31
Seed testing laboratory standards for red rice in Uruguay

Year	Tolerance of red rice seeds per 2 kg rice seed			
	Foundation	Registered	Certified	Commercial
Before 1989	0	0	1	4
1989	0	0	0	4
1990	0	0	0	2
1993	0	0	0	0

Source: Zorrilla, 1998.



of the rice-producing sector in the country, and the recognition by rice farmers of the importance of buying quality rice seeds every year were critical steps in the implementation of an effective and efficient programme for the control of red rice.

Rotation of rice and livestock

The limiting factor for increasing the rice production area in Uruguay has not been the availability of land, but the availability of irrigation water and the necessary investments. For these reasons, from the outset, the rice sector developed a rotation system of rice and pastures with 2–3 years of rice followed by several years of fallow and pastures for livestock. Since the start of the national rice research activities in 1970, the improvement of this rotation system has been a main priority.

In the 1980s, the Estación Experimental del Este – INIA, Treinta y Tres, promoted and obtained the massive adoption of a rice–pastures–livestock rotation system with two years of rice cropping followed immediately after harvest by aerial seeding of pastures. The pastures were used for four years for fattening cattle before the land was returned again to rice (Bonilla and Grierson, 1982). More recently, considering the needs of the producers, the INIA, Treinta y Tres has been developing a more intensive rotation system that includes 2 years of rice and 3 years of pasture. Rice is planted directly, and the livestock includes bovines and sheep (Bonilla and Zorrilla, 2000). This strategy of integrating rice with livestock production has many advantages, including:

- increased sustainability of rice production by having lower costs and higher yields;
- diversification of livestock production;
- sustainable management of the natural resources;
- reduced impact on the environment.

Ongoing research means that the rotation system is being improved.

Although red rice control was not the primary reason for adopting the rotation system, it was soon learned that the rice–livestock rotation was a very effective measure for combating and controlling red rice. One of the main traits of red rice that contributes to its success as a weed is the longevity of its seed in the soil. In a long-term trial installed at the INIA, Treinta y Tres, viable red rice seeds have been found after 11 years of burial on the soil (Zorrilla, personal communication, 2004). The interruption of rice cropping for several years obtained by the rotation with pastures and livestock avoids the multiplication of the weed and reduces the red rice soil seed

bank. Thus, the low-intensity system of rice production has been a significant factor in the effectiveness of measures used to combat red rice.

Diffusion and knowledge – complementary measures

The organizations linked to the rice system considered the need to implement measures complementary to the availability of red-rice-free seed rice in order to offer an efficient and coherent control strategy. The population dynamics of red rice calls for a permanent and active state of alert for its combat and control by making farmers aware of the red rice problem and its importance in maintaining a good export market.

In the 1980s and 1990s, extension and educational campaigns were implemented by all the institutions among all the stakeholders participating in the rice-related agroindustrial chain: the INIA, INASE, the Asociación de Cultivadores de Arroz (ACA) and the Gremial de Molinos Arroceros (GMA). These campaigns included:

- specific publications;
- press and magazines articles;
- field visits and workshops for producers, technicians and field staff of the rice firms.
- The most important messages disseminated in the campaigns were:
- Better knowledge of the different forms of red rice and the need for permanent vigilance and combat are very important.
- The best strategy is to prevent the entry of red rice into a field.
- Rice seed free of red rice is the first and most crucial control measure.
- Avoid other means of contamination, in particular by machinery, tools and harvesters.
- Implement specific control measures for primary infestations: manual control, localized herbicide application, others as available and appropriate.
- Reduce cropping intensity of rice by including rotations with pasture.

Results of the integrated strategy

The widespread distribution of red rice in the rice-producing area in the 1960s was reduced slowly. In the 1980s and 1990s, red rice was a sporadic weed in fields with many years of continuous rice cropping, but usually absent in new fields. In the early 1990s, studies were made to evaluate the actual incidence in the final product, that is, in the grain for industrial processing.

The majority of rice farmers in Uruguay produce under contracts with the industrial sector. The contract specifies, among other things, a price and penalty system for the quality of the grain delivered, and every truckload of rice reaching the mill is sampled and analysed. With the collaboration of the main rice millers, harvests for several years were collected and studied (Zorrilla, 1998). Table 32 shows that about 90 percent of the production of 3 years was surveyed and that red rice was detected in less than 1.5 percent of the samples.

These results confirmed the success of the red rice control programme and campaigns, and the nil or minimal impact of the very low incidence of the weed seeds on the quality of the final product and on the industrial costs. However, these results do not show directly the incidence of the weed in the field

TABLE 32
Survey of analyses of incoming rice received by the main rice mills of Uruguay

	1986	1991	1992
Total surveyed tests (no.)	21 124	18 524	20 320
Analysis with red rice (no.)	228	262	295
Analysis with red rice (%)	1.08	1.41	1.45
National production surveyed (%)	90	90	85

Source: Zorrilla, 1998.

as it shatters early and heavily and only a small fraction of the seeds is taken in the harvest. The analysis of the incoming rice also identified the location of the production represented by the sample. The results confirmed that, in spite of the low incidence of red rice in the grain, it was still present in all the rice production areas of the country.

The present situation

In the latter part of 1990s and up to 2000, there was a significant increase in the rice-cropping area. This was in part as a consequence of the expansion of the agricultural frontier and of the intensification of the rotations (with fewer years devoted to pasture between rice crops). This increased the presence of red rice in the fields, especially in the traditional rice-growing areas. In the same period, there was a significant increase in the number of new producers of Brazilian origin. They brought with them the habit of using their own seed, as is common in Rio Grande do Sul in southern Brazil. This situation has resulted in an increase in red rice infestations in the new fields and clean areas. The national institutions are now increasing their efforts to avoid the deterioration of the existing favourable situation. Emphasis is maintained on the national red-rice-free seed production system and the rotations. The INIA has now moved from the diffusion and prevention strategies emphasized in the past to the support of specific projects on red rice management and control.

There are studies in progress on the variability of biotypes present in the country and its possible genetic origin (Federici *et al.*, 2001). There are ongoing trials and recommendations on systems for soil preparation, types of planting and strategies for the use of herbicides that could enable economically viable production on heavily infested soils (Castillo, Gauna and Saldain, 2004), and applications of herbicides at the end of the weed cycle to avoid seed formation (Saldain and Deambrosi, 2003).

Although the problem continues to be a minor one at field level, in milling and in the quality of the final product, there is concern about the trend of increasing weed populations. Discussions with the officers of the main milling industries of the country indicate that the percentage of red rice in the rice received by the mills between 1986 and 1992 was less than 2 percent (Table 32) but that it was close to 5 percent in the 2004 harvest. Nevertheless, this is not yet considered a serious problem.

The Clearfield technology of mutant varieties (not transgenic) that are resistant to herbicides of the IMI family (Croughan *et al.*, 1990) is arriving in the country at the right moment and could become a very efficient and effective tool if managed properly. For the 2005 planting season, a recently introduced American variety will be available for farmers. In the next few years, the INIA expects to release national varieties obtained by the INIA plant-breeding programme under an agreement with BASF. If the technological package is applied as directed to avoid the flux of genes to the red rice, it may become the ideal tool to consolidate the control of the weeds and especially red rice in Uruguay just at the moment when an increasing trend in red rice infestations has been detected.

Lessons learned

The experience gathered from 35 years of combating red rice in Uruguay allows the identification of the most important factors that have contributed to the development of a successful national strategy for red rice control:

- An effective strategy to combat red rice requires the participation and commitment of all the stakeholders in the rice chain: farmers, millers and public institutions on research and seeds. This team of actors must achieve a fair distribution of costs and benefits for all the actions performed.

- Rice seed free of red rice accessible to all farmers is fundamental but it must be complemented by other actions taken in the comprehensive combat and control plan.
- It is necessary to develop and maintain education and extension programmes in order to ensure that farmers, millers, technicians and workers in the rice industry are aware of the problems caused by red rice and combat it vigorously, following the motto that “the best control is not to have red rice in the field”. In this regard, a basic element is the development and extension of a set of measures to combat primary infestations. These measures need to be applied by farmers in a systematic way when the problem is still relatively easy to resolve.

Rice farmers always need to be attentive and ready to apply at once the technological advances that the national research confirms as effective in combating red rice.

CENTRAL AMERICA AND THE CARIBBEAN – MANAGEMENT AND CONTROL OF WEEDY RICES

Background

Recognizing the importance of the problem of weedy rices, particularly in countries practising direct seeding, FAO started some activities in order to assist developing countries with ways to reduce weedy rice infestations in rice. The first activity in this context was to organize an FAO global workshop on the subject, which was held in Varadero, Cuba, (FAO, 1999) with the participation of specialists from 17 countries. The workshop concluded that the high weedy/red rice incidences in many rice-producing countries are the result of using contaminated seeds, continuous monocropping and inappropriate cultural practices during the crop cycle. The need for an integrated management approach was emphasized with the critical first step of reducing the weedy rice seed sources.

Based on many suggestions and recommendations, a subregional project was implemented by FAO jointly with relevant national institutions. Six countries affected by weedy rices participated in the subregional project: Colombia, Costa Rica, Cuba, Nicaragua, Panama and Venezuela. All field activities were conducted through the development of the so-called farmers field schools (FFS). At these schools, farmers learned about:

- control procedures;
- elements of the ecology of weedy rice;
- the soil seed bank;
- identification of the main biotypes of weed rices and their cycle;
- the importance of cleaning the equipment and machinery coming from infested areas.

Weedy rice problems in the participating countries

Rice is grown on 320 000 ha in Colombia, where the first constraint on its production is weedy rice infestations in the fields. There are usually two crops a year and monocropping is the normal practice. The use of uncertified rice seeds of low quality is also common in areas with limited-resource farmers.

In Costa Rica, the rice area is about 40 000 ha, distributed in five regions of the country (Chorotega, Brunca, North Huetar, Central Pacific, and Atlantic). The area infested by weedy rice is about 19 500 ha. The major weedy rice species are *Oryza sativa* L. and *O. latifolia* Desv. (known locally as “arrozón”). Their major incidence is in fields where rice is cropped twice each year. The presence of weedy rices can reduce rice yields by up to 65 percent in some areas. In such cases, rice is usually abandoned and replaced by sugar cane or pasture. Many farmers do not pay the necessary attention

to the use of certified rice seeds that are free of weedy rice seeds, and they ignore the importance of depleting the seeds in the soil seed bank.

In Cuba, rice is the major staple food in the country. Most of the rice consumed is imported as the national production provides only 30 percent of the needs. The crop is grown in an area of slightly less than 200 000 ha, and 35 percent of it is severely infested by weedy rices. In some heavily infested areas, rice yield losses reach 89 percent. The problem is aggravated by insufficient supplies of certified rice seed and/or the use of low-quality seeds contaminated with weedy rice seeds.

Weedy rices also affect rice production in Nicaragua. The weeds are present in all rice-producing areas of the country with infestations of more than 80 panicles/m². The main weedy rice species are *Oryza sativa* and *O. latifolia*, with infestations of up to 40 percent in rice fields. Farmers do not use certified seeds and no specific methods are practised to control the weeds. Normally, farmers either apply glyphosate preplanting over the weeds that have emerged or simply rogue the plants.

In Panama, rice is grown on more than 75 000 ha, mainly in the provinces of Chiriquí (54 percent), Coclé (14 percent), Panama (Chepo) (11 percent) and Veraguas (9 percent). Rice yields are not high owing to the use of non-certified seeds with low germination level, and high incidences of weedy rices. In addition to reducing crop yields, the weedy rices increase the consumption of herbicides for their control as well as the costs associated with applications (including fuel). In some cases, heavy infestations of weedy rices increase the costs of rice production to the extent that farmers have to abandon the rice crop.

Venezuela has a rice-producing area of about 140 000 ha. The main rice-producing states are Portuguesa, Guárico, Cojedes and Barinas. In contrast to the other countries, there is a high level of mechanization and irrigation for the production of rice with average rice yields of 3.8 tonnes/ha. Weedy rices are a major constraint on rice production, with about 88 percent of the crop area infested with up to 17–18 plants/m². The main species of weedy rices in Venezuela are *Oryza sativa* L., *O. rufipogon* Griff., and *O. latifolia* Desv. The certified seed category permits up to three seeds of weedy rices per kilogram of rice seeds as well as one plant of weedy rice per hectare in areas for production of certified seeds (Gaceta Oficial-Venezuela, 1986). These tolerances have favoured the proliferation of weed rices, affecting the yields and the quality of harvested rice.

Some of the countries are aware of and concerned about the losses caused by the weedy rices and implement some control methods, while others simply coexist with or ignore the weedy rices and continue with conventional cropping practices.

FAO project on weedy rice in Latin America

Several Latin American countries affected by weedy rices requested technical assistance from FAO in order to reduce infestations. The main objective of the project developed was to strengthen national capabilities on methods for the prevention and control of weedy rices through the implementation of a comprehensive training process for relevant technical bodies and farmers. The project included activities for educating pilot groups of farmers on problems caused by weedy rices and on the best methods for their control. For this purpose, FFSs were implemented, where farmers learned by doing and observing the results of the practices they implement. This participatory approach allowed the farmers to meet every two weeks in order to observe and discuss the results of their activities in the field. Generally, the farmers assessed the number of all weeds, the health and density of rice plants, and other related matters for a plot they shared. Technicians acting as facilitators usually added the explanations of related topics of interest to the farmers.

The first things for farmers to learn were the sources of weedy rice infestations and the importance of using certified seeds as well as ways to reduce the weedy rice soil seed bank. In nearly all the countries, farmers collected the weedy rice biotypes and gave names to each of them. In some cases, they studied the germination of seeds of these biotypes. Another activity carried out was the estimation of viable weed seeds in the soil seed bank using the methodology proposed by Forcella, Webster and Cardina (2003). Taking into account their observations and discussions regarding the sources of weedy rice infestations, the farmers designed control procedures to prevent early competition of the weed in the crop. The use of clean rice seeds was adopted as one of the main strategies, together with the preplanting control of weedy rice infestations.

Land preparation in some areas started in dry soils, followed by: fast irrigation to promote weed seed germination, puddling, draining the field to permit the emergence of new weed flushes, application of glyphosate, flooding, and rice seeding into a shallow water layer. In other areas, land preparation started with puddling, draining the field, glyphosate application, flooding and seeding as above. In some areas, control of weed flushes was also done mechanically immediately after draining. Promoting the early emergence and control of weedy rices increased the cost of the production slightly but yields increased by up to 25 percent, and grain quality was much improved. In the case of Nicaragua, farmers used this type of production system in the model plot for seed purposes.

In one area in Venezuela, after harvest of an infested field, crop residues were burned in order to encourage germination of weedy rice seeds remaining at the soil surface. Soil moisture was maintained for a period of 85 days, and weedy rice populations reached the level of 130 plants/m². Land preparation was then started. The field was flooded, drained and left for another 15 days to promote a new weed flush. The same operation was then repeated for another flush of weeds, after which the area was flooded for 8 days and the herbicide oxadiargyl was applied (1.15 litre/ha). Finally, the field was drained and two days later pregerminated rice seeds were planted. Weedy rice plants escaping from these control measures were later controlled by direct application of glyphosate or removed manually.

Several other control strategies were practised or discussed with the farmers. One was the possibility of short crop rotations with “smothering” cover crops, e.g. for 40–45 days, in order to reduce the weedy rice infestation. The leguminous plant *Sesbania rostrata* Brem. is used for this purpose in Cuba. Other cover plants with fast growing habits should also be considered. This practice would also enable the soil to recover part of its fertility.

Roguing and using glyphosate shortly before harvest is another useful method to prevent further weedy rice seed germination in soil. Inflorescences of weedy rice plants that have survived are simply soaked with glyphosate before crop harvesting.

In Venezuela, farmers were very well trained in procedures for cleaning the machinery coming from rice fields infested by weedy rice.

In general, the process of farmer training went well in all cases when working with groups of low-income farmers who expressed the need for such a participatory approach for training on all the problems affecting rice production. The participatory approach also changed the way of thinking of the technicians involved as facilitators. Both parties noted that this approach was much better than traditional technology transfer methods. However, FFS was not a suitable procedure in the case of wealthy farmers with large areas in rice production. However, as they all have technicians working on their farms, training of trainers (TOT), which is the training applicable for

the facilitators, can be implemented for their technical staff combined with some field days for the farmers themselves.

The training and the results of the methods proposed and practised by the farmers in their plots demonstrated the importance of using clean, good-quality rice seeds. In some countries, farmers evaluated the number of weedy rice seeds present in rice seeds marketed as “certified”, and having learned the importance of even one weedy rice seed in the seeds planted, concluded that it is best to demand totally clean seeds and/or even to pay more in order to obtain the quality seeds they need.

Farmers also acknowledged the importance of early weedy rice control. Preplanting, stale seed bed procedures, and eliminating the first weed flushes with glyphosate or mechanically clearly showed that avoiding early competition of weedy rice with the crop increases the yields as well as quality of the produce. Although not always enthusiastic about assessing the soil weed seed bank, farmers became convinced of the need to control those weedy rice plants escaping from the early control operations either with direct application of a chemical over the plant or by removing them manually in order to prevent them from depositing more seeds in the soil seed bank.

NORTH AMERICA

The two case summaries in this section are shorter than the cases presented above. However, these cases from Arkansas and California in the United States of America are significant. Indeed, the California case represents the most successful control programme for red rice anywhere, while the Arkansas case illustrates how innovative a campaign can be when weedy rice begins to have a serious impact on farm income.

California – clean seed and water seeding

California is a long-term producer of rice. The bulk of its production is destined for export to Asian countries, such as Japan, that have strict market standards. There is no record of red rice in California before about 1920, but, in 1932, Bellue (1932) noted that red rice was present in about 28 percent of the seed samples submitted for testing and concluded that it must have been introduced into the state from other states in the 1920s. In 1950, Randall (1950) stated that red rice was the second most important weed in rice after *Echinochloa crus-galli*. However, beginning in the 1960s, red rices have been brought under almost complete control by good extension and industry-backed campaigns based on the production and use of clean seed and the water-seeding system combined with appropriate herbicides.

Arkansas – “Get the red out”

Arkansas is the leading rice producer in the United States of America. Production is on a commercial scale, technologically advanced and fully mechanized. Red rice has been present in Arkansas rice fields since at least 1908. Long a problem, it became a rather alarming one in the late 1970s when difficulties were encountered in marketing the grain because of too much contamination with red rice. The rice area had expanded so rapidly in the mid-1970s as a result of good prices and the relaxation of controls that the supplies of certified seeds were exhausted and farmers turned to less reliable sources for seeds. The marketing difficulties and heavy discounts drew the attention of the rice producers, millers, the agrochemical industry, the experiment station researchers and extension personnel. Increased emphasis began to be given to the production and use of certified seeds, rotations with other crops, and the use of effective herbicides. This emphasis developed into an imaginative and well-organized campaign by the

extension service and its clients and cooperators under the slogan: “Get the red out”. Meetings were held with farmer-producers and the rice mills. Demonstrations were carried out in all of the 42 rice-producing counties, and colourful posters with cartoon characters carried the message “Get the red out”. The programme and technological developments have brought red rice under control although it remains a problem that requires constant attention.

Chapter 9

Conclusions

Weedy rices (including red rices) have long been important weeds in direct-seeded production areas. However, in the past 25 years or so, they have increased in importance in the long-established direct-seeded areas and have spread worldwide with the adoption of direct-seeding systems in some of the traditional transplant culture areas. Currently, infestations by weedy rices (including red rices) are considered one of the most troublesome, difficult-to-manage and economically damaging weed problems by stakeholders in the rice industry from production through to marketing. Infestations increase labour requirement and production costs while reducing the yield and market quality of the crop.

Botanically, red rices in the Americas, Europe and North Africa are mostly weedy biotypes of *Oryza sativa*. In West Africa and SSA, the weedy rices are *O. barthii*, *O. longistaminata*, *O. punctata*, and weedy biotypes of *O. glaberrima* and *O. sativa*. In Asia, the area where *O. sativa* originated, *O. rufipogon* and other *Oryza* spp. are the sources of the weedy rices. Agronomically, the weedy rices (including red rices) consist of weedy populations of *Oryza sativa* and/or other *Oryza* spp. that are phenotypically and genotypically diverse, changeable, very vigorous and competitive, exceedingly difficult to control, and able to spread rapidly. In most areas, the diversity of the populations and their changeability are the result of introductions from other areas and natural crossing of the weedy biotypes and cultivated varieties. The weedy rices (including red rices) have been and still are spread from infested areas to non-infested areas primarily as contaminants in planting seeds.

Weedy rices (including red rices) are very successful as weeds because they have most of the traits and characteristics that contribute to the success of weeds in general plus some that are unique. The traits they share with other important weeds are: excellent adaptation to most rice cultural systems; a life cycle closely synchronized with rice; abundant production of seeds that are dispersed widely by early and heavy shattering; rapid emergence followed by vigorous growth and reproductive development; and intense and prolonged dormancy (which maintains the viability of the shattered seeds in the soil seed bank during adverse climate conditions). The unique traits that contribute to their success as weeds include: morphological and phenological similarity of the plants and seed to those of the rice crop (which makes them difficult to recognize and separate); and their close genetic relationship to cultivated rice (which precludes the use of most selective herbicides). Among these traits, four are critical to their success: the diversity and changeability of the populations produced by natural crossing of the weed and crop; early and heavy shattering; intense and prolonged seed dormancy; and superior vigour and competitiveness as compared with cultivated varieties.

Natural crossing of weedy rices (including red rices) and cultivated rice provides variability that can be and has been naturally selected to produce ecotypes adapted to changes in cropping systems and varieties. Early and heavy shattering ensures that most of the weedy rice seeds (including red rice seeds) are scattered and dispersed to the surface of the field rather than gathered with the grain for consumption or marketing. Intense and prolonged dormancy maintains the viability of the seeds during the adverse climate conditions that occur between harvest and the next planting season and permits the establishment of a soil seed bank that can be drawn on for several to many years.

The superior vigour and competitiveness of weedy rices (including red rices) ensures that they will produce seeds in the midst of the rice crop. The general and unique traits of the weedy rices (including red rices) make them multidimensioned weeds that produce multidimensioned problems in direct-seeded rice cultural systems.

Satisfactory control of weedy rices (including red rices) requires an approach that fully integrates informed management decisions, control practices and methods. Successful integrated control programmes involve the implementation of combinations of tactics from five long-time, well-tested control strategies and the judicious exploitation of powerful new technology.

Infestations of weedy rices (including red rices) are prevented or kept from spreading through the use of quality seeds that are not contaminated with red rice seeds, i.e. red-rice-free seeds.

Cultural practices such as the stale seed bed and minimum or no-tillage systems are employed to deplete the population of seeds of weedy rices (including red rices) on the soil by bird and rodent predation, stimulation of germination, and mechanical or chemical destruction of the seedlings before sowing the next crop. Where practical and feasible, fallowing for two or more years is an effective way of depleting the deposit of seeds in the soil seed bank.

Flooding and water are managed in ways to take advantage of the suppression of germination and emergence of weedy rices (including red rices) by anoxia in wet and/or flooded soils. The main systems are seeding in a water film maintained until harvest, and the “pinpoint flooding” method of seeding in a water film followed by draining for a few days to establish the seedlings and return of the flood until harvest time. The herbicide molinate is used effectively in the water-seeding systems to suppress and control other weedy grasses as well as the weedy rices (including red rices).

The methods and practices for control of weedy rice plants (including red rice plants) in the rice crop are limited. Hand weeding is the most common method. However, the application of non-selective herbicides directly to tall weedy plants or clumps of weedy plants and the mechanical clipping or crushing of weedy rice panicles that stand above the rice crop are used effectively in some areas.

Rotation of rice with other crops is one of the most effective and economical methods of maintaining satisfactory control of weedy rices (including red rices). The cultural practices used for the alternate crop stimulate the germination of weedy rices (including red rices), which can then be controlled by a variety of selective herbicides. The most effective rotations are one year of rice followed by two or three years of the alternate crop. Alternate crops include soybeans, sorghum, green manure crops, sunflower, and pastures (and cattle).

Herbicide-resistant varieties of rice have been and are being developed. They permit the use of specific non-selective or broad-spectrum herbicides to control weedy rices (including red rices) as well as the other weeds in the rice crop. The biotechnological strategy has been used successfully in soybeans, maize, cotton and other crops for some years now with no technical problems, albeit with considerable controversy. However, the situation with rice is different because the crossing of cultivated varieties and the weedy rices (including red rices) could transfer the herbicide-resistance genes to the weed. The companies and scientists involved in the development of herbicide-resistant varieties are aware of the risks and have established protocols for use of the technology that should minimize if not eliminate them. These protocols involve the adoption of integrated control systems that use many of the time-tested control measures, such as rotation of rice with other crops, rotation of herbicides, and the destruction of escaped weeds by roguing, mechanical and chemical means.

In conclusion, in the last 25 years or so, much information has been developed on the diversity, incidence of outcrossing, phenology, and ecology of weedy rices (including red rices), particularly of the *Oryza sativa* red rices. Biotechnological developments and potentials are providing powerful incentives and resources for finally and fully understanding the ecophysiology of the *O. sativa* red rices and, perhaps, other weedy rices in the shorter rather than the longer term.

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This publication presents a compilation of information from literature reviews on the body of knowledge available from ongoing unpublished research, research reports and symposia carried out on various aspects of the importance, ecology, biology and control of weedy rices. It also highlights global economic and environmental problems created by weedy rices. This document is a result of FAO partnership arrangements with institutions of excellence to generate information that will be for general public use in an attempt to fulfill the goal of food security. Since this publication will interest a wide range of stakeholders – policy-makers, scientists, technicians and producers – including those interested in rice crop research, production, rice milling for commerce, quarantine regulations and seed trade, an attempt has been made to define *weedy*, *wild* and *red* rice so as to engender a common understanding of various aspects of these weeds. The information provided will contribute to the better knowledge of weedy rices throughout the world.

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