ISSN 0259 2517

Weedy rices – origin, biology, ecology and control

FAO PLANT PRODUCTION AND PROTECTION PAPER

188

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by
James C. Delouche
Nilda R. Burgos
David R. Gealy
Gonzalo Zorrilla de San Martín
and
Ricardo Labrada
with the collaboration of
Michael Larinde
and
Cadmo Rosell

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 2007

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ISBN 978-92-5-105676-9

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Acknowledgments

The FAO Plant Production and Protection Division (AGP) wishes to acknowledge James Curt Delouche, Professor Emeritus of the University (Mississippi State University, United States of America), the main author of this publication for his interest and availability to lead in the collection and collation of information, as well as, writing and preparing the publication. AGP also express sincere thanks to the Co-authors Professor Nilda R. Burgos (University of Arkansas, United States of America), David R. Gealy (United States Department of Agriculture, Agricultural Research Services, United States of America), Gonzalo Zorrilla de San Martín (*Instituto Nacional de Investigación Agropecuaria*, Uruguay), Ricardo Labrada (FAO Plant Protection Service) and Michael Larinde (FAO Seed and Plant Genetic Resources Service), who gave many hours of their time to provide updated and comprehensive information on the subject. Their dedication, knowledge and experience have been critical to make this publication a reality.

The critical contributions of largely unpublished dissertations and theses of graduate students of Mississippi State University on research they undertook and completed are also appreciated. In particular, we gratefully aknowledge the works of A.C.S.A. Barros, M.J. Constantin, A.A. Do Lago, E.F. Eastin, E. García-Quiroga, L.G. H oward-Kandakai, M.A. Larinde, O.J. Moreno, J.A. Noldin, K. Paquiot, N. Pitty, V.K. Shrivain, E.N. Stiers, T. Teekachunhatean, R.D. Veras and K. Wague. The assistance of K.D. Gordon for the computer elaboration of most of the tables, figures and photographic material is also gratefully acknowledged.

This document was circulated for peer review to Nguu Nguyen and Elcio Guimaraes, (FAO/AGPC), Tom Osborn and Robert Guei (FAO/AGPS) whose comments are greatly appreciated.

We also wish to thank Shrivaji Pandey, Director, Plant Production and Protection Division and Arturo Martinez, Chief, Seed and Plant Genetic Resources Service (AGPS) for their continuous support.

Finally, we wish to recognize the edition made by Julian Plummer, the preparation and formatting of the final text by Lynette Chalk and the administrative assistance of Liliana Lazzerini.

Preface

Weedy rices, especially types with a red pericarp, are globally well known as a problem in the rice industry. The economic and environmental problems they pose include those related to rice crop production, rice milling for commerce, quarantine regulations and seed trade. Each stakeholder in the rice industry has a different perception of the problem posed by weedy rice. For instance, red kernels of red rice detract from market value of marketed rice. Red rice is a Plant Quarantine object in many countries and various seed certification programmes, including the OECD seed scheme.

Various national and international stakeholders, including public and private institutions recognize weedy rices as serious pests that need concerted and coordinated efforts to bring it under control. In this context, the 21st Session of the International Rice Commission (IRC) observed *inter alia* in 2004 that: i) weedy rice, which is a product of the natural hybridization between cultivated varieties and wild rice relatives, has become a serious problem due to wider adoption of direct seeding as a result of the labour shortages and high costs in several countries; and, ii) weedy rice is not easy to control since it is a weed which has the same genome as cultivated rice. Normally the best way to combat weedy rice is through the use of clean rice seeds and pre-planting treatment - for example stale seed bed preparation, removing the germinated weedy rice mechanically or in some cases using a suitable herbicide before rice planting.

On the control of weedy rices, the IRC noted that the major issues related to weed management are resistance to herbicides/species shifts; mitigation of gene flow from cultivated rice with enhanced traits to weedy rice; herbicide drift; water scarcity (the most serious issue); emerging aquatic weed complex including invasive species; and input costs. In conclusion, the Commission recommended that *Integrated and diversified strategies for weed management should be urgently developed for sustainable rice production under the changing environment of high labour costs, increased adoption of direct seeding in crop establishment and water scarcity*.

This publication is proposed by FAO's Plant Production and Protection Division (AGP) as commitment to tasks aimed at meeting the mandate of FAO as it relates to diffusion of valuable technical information on agriculture, using its diverse expertise and partnership arrangements. It provides the latest information on the origin, biology, ecology and control of weedy rices with the hope of providing a basis for strategies to control this problem. AGP is using its partnership with outstanding experts, academics from renowned universities and collaborators of the FAO network to collect valuable information which will enhance the capability of stakeholders to deal with the problems created by weedy rice and thereby help them to meet the high standards of the global rice trade.

We are grateful to the senior author, James C. Delouche, Professor Emeritus of the Mississippi State University, for his outstanding contribution to this publication based on his over 40 years experience in the area of seed technology and his pioneer work on detailed studies of red rice species. Equally, we express our sincere thanks to Nilda Burgos, Associate Professor, Weed Physiology of the University of Arkansas and

her colleague David R. Gealy for their invaluable contribution to this publication. We also recognize the inputs of Gonzallo Zorilla de San Martin.

Shivaji Pandey
Director
Plant Production and Protection Division

List of acronyms

ACA	*Asociación de Cultivadores de Arroz*
AOSA	Association of Official Seed Analysts
AOSCA	Association of Official Seed Certifying Agencies
BHR	Blackhull red rice
BLKH	Blackhull
BrHR	Brownhull (or bronzehull) red rice
DAP	Days after planting
DNA	Deoxyribonucleic acid
FFS	Farmers field school
GA	*Gibberellic* acid
GD	Genetic distance
GMA	*Gremial de Molinos Arroceros*
HYV	High yielding variety
IMI	Imidazolinone
INASE	*Instituto Nacional de Semillas*
INIA	*Instituto Nacional de Investigación Agropecuaria*
IRRI	International Rice Research Institute
KOH	Potassium hydroxide
N	Nitrogen
NRRC	National Rice Research Center
OECD	Organisation for Economic Co-operation and Development
PP	Pentose phosphate
PVC	Polyvinyl chloride
RAPD	Random amplified polymorphic DNA
RR	Red rice
SHA	Strawhull awnless
SHA+	Strawhull short-awned
SHR	Strawhull red rice
SSA	Sub-Saharan Africa
SSR	Simple sequence repeat
TOT	Training of trainers
USDA	United States Department of Agriculture

Chapter 1
Introduction

Although weedy rices of several *Oryza* species have been in existence for many years in the vast areas of rice culture in Asia, they have been kept under satisfactory control in the transplant flooded culture system. However, these weedy rices and others introduced as contaminants with high-yielding varieties (HYVs) of *Oryza sativa* (or produced by crossing with them) are becoming serious problems in countries where direct seeding is replacing the transplant culture for all or for one or more of the rice crops in multicropping systems. As these trends continue and accelerate, the problem of weedy rices becomes more pervasive and serious. Similarly, in Africa, the second-oldest rice culture, several endemic species of *Oryza* (i.e. *O. barthii*, *O. longistaminata* and *O. punctata*) have long been a weed in the production of *O. glaberrima*, Africa's cultivated rice. However, as in Asia, they are becoming a very serious problem and nearly impossible to control in the mechanized, direct-seeded rice schemes in various countries in West Africa and sub-Saharan Africa (SSA). Furthermore, *O. sativa* is replacing *O. glaberrima* as the main cultivated rice in many of the countries and additional weedy rices are emerging as contaminants in introduced seeds or from the crossing of cultivated and weedy types.

In the Americas and Europe, where rice culture began in historically recent times, weedy rices were introduced as contaminants in seed, and new or different types then developed as a consequence of crossing with cultivated types. In areas where direct seeding has been the main practice since the beginning, as in the United States of America and other countries in the Americas, or has become dominant in the last 30–40 years, as in Southern Europe and the Mediterranean, the most important and damaging types of weedy rices are red rices, varieties of *O. sativa* with weedy traits and grains that have a red pericarp. In these and other rice production areas where the crop is direct seeded, rice farmers, millers and extension and research workers view weedy red rice infestations as one of the most troublesome, difficult-to-manage and economically damaging weed problems. However, selected rice strains with a red pericarp are maintained and produced in some Asian countries as a special food for ceremonial occasions (Vivekanandan *et al.*, 1979). In Vallee de l'Artibonite, Haiti, red rice selections have been cultivated for use as a "weaning" food for children (Delouche and Dougherty, 1973).

Against the background of a rapidly spreading and increasingly serious weed problem in one of the world's most important food crops, the Global Workshop on Red Rice Control was convened in Varadero, Cuba, 30 August – 3 September 1999, under the sponsorship and guidance of the Food and Agriculture Organization of the United Nations (FAO). Thirty-three participants from 19 countries met to present reviews of the weedy rice situation in their countries, discuss the effectiveness of various control measures, and exchange information in formal and informal gatherings. The workshop group formulated 21 conclusions and recommendations, some technical, some economic and social, and some relating to the lack of educational and informational resources on the weedy rice problem. This report addresses the constraints on educational and informational resources highlighted by the workshop participants and by many other rice specialists around the world.

Chapter 2
The weedy rice problem

Rice (*Oryza sativa* L.) is an Asian species. China is thought to be its centre of diversity (Vaughan *et al.*, 2005). Weedy and cultivated rices both evolved from wild *Oryza* species. Of the 21 wild species in the genus *Oryza*, 9 are tetraploid (BBCC, CCDD) and the rest are diploid (Khush, 1997). Diversification into the different groups of *Oryza* probably occurred in China about 8 000 years ago. The wild species *O. rufipogon*, *O. nivara*, *O. glumaepatula*, *O. meridionalis*, *O. breviligulata*, *O. longistaminata* and the cultivated species *O. sativa* and *O. glaberrima* belong to the diploid gene pool (AA genome) and, therefore, can hybridize with each other. *O. sativa* is believed to have evolved from *O. nivara*, which in turn evolved from the wild species *O. rufipogon.* The cultivated *O. sativa* evolved into three main types: *indica*, *japonica* and *javanica*. Domestication in various climate regions in Asia resulted in the evolution of two types of *japonica*, a tropical *japonica* (such as the type now grown in the south of the United States of America) and a temperate *japonica* (such as the types grown in Japan and in California, the United States of America). *O. glaberrima,* the other cultivated species of *Oryza*, is native to Africa, and remains a crop of importance in West Africa.

Weedy rices, especially types with a red pericarp, are well known to rice farmers, suppliers of production inputs (including credit), millers, marketers of rough and milled rice, agronomists and other specialists involved in the rice industry in direct seeded areas where they are a problem. There are substantial differences in the meaning and significance of weedy rice among these participants and stakeholders in the industry, especially in the case of the dominant red-pericarp types. For farmers, weedy rice is a difficult-to-control, aggressive weed that increases the costs of production, reduces yield, lowers the market value of their rice crop and, where not controlled properly, can render the infested cropland unfit for rice production. Marketers and millers view it as a quality factor that can have a significant effect on costs and erode profits and reputation severely where it is not recognized and taken into account in buying and milling decisions. Suppliers of production inputs have to take special precautions to produce and market rice seeds that are not contaminated with those of weedy rice. For agronomists and other specialists involved in rice extension, research and other services, weedy rices represent a problem that is exceedingly difficult to resolve but easy to cause. These differing stakeholder perceptions are essentially one-dimensional views of a multidimensioned weed that produces a multidimensioned problem.

WHAT WEEDY RICES ARE

Weedy rices can be defined broadly and generically as plants of the genus *Oryza* that infest and compete with rice and other crops. Of these weedy rices, red rice is the dominant and most damaging type. It can be defined more narrowly and restrictively according to its common meaning to the miller, marketer, and consumer as a type of weedy rice that produces grains with a distinctly red or rouge pericarp (bran) rather than the tan or beige pericarp of cultivated varieties (Cragmiles, 1978). The red bran or pericarp is the critical characteristic that distinguishes red rice from other weedy rices and makes it a more troublesome and costly problem because of the heavy discounting of contaminated grain. Botanically, most specialists now classify weedy types (including red rices) as *Oryza sativa*, the most important cultivated rice. Some specialists, especially in the past, have considered red rice to be *O. rufipogon* (Knapp, 1899; Stubbs, Dodson and Brown, 1904; Quereau, 1920; Kennedy, 1923) or *O. sativa* var. *rufipogon* (Dodson, 1900; Nelson, 1907, 1908). It is believed that red rice originated from *O. rufipogon*, an Asian perennial species of wild rice (Watt, 1891), which was the progenitor of *O. nivara*, an annual species, which, in turn, became the progenitor of *Oryza sativa* (Singh and Khush, 2000). Vaughan *et al.* (2001) collected red rice ecotypes from across the rice area of the south of the United States of America for analysis with simple sequence repeat (SSR) markers. They found that, while most of the red rice types were related closely to either *O. sativa indica* type or *O. sativa japonica* type, some were rather closely related to *O. rufipogon* and perhaps *O. nivara*. As previously noted, *O. rufipogon*, *O. nivara*, a few other *Oryza* spp., and weedy rices of *O. sativa* with the AA genome, i.e. diploids with 12 pairs of chromosomes, can intercross with cultivated *O. sativa* (Sitch, 1990). Thus, although *O. sativa* varieties are considered self-pollinating, they are genetically compatible and there is some outcrossing among them. This natural hybridization is responsible for the wide diversity of red rice populations worldwide. The development of herbicide-resistant rice varieties has provided a powerful technology for very effective and economical control of red rice. However, this technology also provides the opportunity for further diversification of red rice with herbicide-resistant types. This very current and important issue is reviewed and discussed in Chapters 3 and 7.

Some other species of *Oryza* are important weeds in the various rice-growing regions. The endemic species *O. latifolia* is a troublesome rice-field weed in Central America and other countries along the Gulf of Mexico and Caribbean Sea. In Italy and other Mediterranean areas, red rice is generally classified as *O. sativa* var. *sylvatica* (Ferrero and Vidotto, 1999; Vidotto and Ferrero, 2005). The weedy rices in West Africa, some with the red pericarp, belong to *O. barthii*, *O. longistaminata* (a perennial), *O. punctata*, *O. glaberrima* (the endemic African cultivated species), and the introduced *O. sativa.*

Agronomically, weedy rices are best defined in descriptive terms that are or should be meaningful to rice producers, rice millers and production specialists, for example:

- Weedy rices consist of weedy populations of the genus *Oryza*, mainly of *O. sativa* and with a predominance of the red pericarp, that are: phenotypically and genotypically diverse and changeable; very vigorous and competitive; exceedingly difficult to control; able to spread rapidly; and able to reduce both grain yield and the value of the grain (Sonnier, 1978; Huey and Baldwin, 1978). Most of the populations, variously termed ecotypes, biotypes or phenotypes, are as stable as cultivated varieties. However, a few are essentially hybrid swarms from weedy or weedy red and cultivated rice crosses from which most new weedy rice biotypes arise (Do Lago, 1982; Delouche, 1988).

In the distant past, different types of weedy rice were generated primarily through natural crossing between wild and cultivated rice species in areas where they grew (or still grow) sympatrically (Vaughan and Morishima, 2003; Australian Government, 2004). While this type of crossing is still important in a few areas in Africa and Asia, most types of weedy rice elsewhere now arise from much closer crosses between the plants of cultivated varieties and those of the weedy rices that infest the crop.

Definitions

In summary, this report makes use of the following definitions:

- Weedy rices: plants of the genus *Oryza*, mainly *O. sativa*, that infest and compete with rice and alternate crops.

- Red rice: a type of weedy rice, mainly *O. sativa*, that has a red-pigmented pericarp. It is the most dominant, troublesome and economically damaging type of weedy rice.
- Wild rice: species of the genus *Oryza*, including the progenitors of the two cultivated rices, that grow in largely undisturbed areas. However, some wild rices, particularly those of the *O. sativa* (AA) complex (i.e. *O. rufipogon*, *O. barthii* and *O. longistaminata*) and three species of the *O. officinalis* complex (i.e. *O. punctata*, *O. latifolia* and *O. officinalis*) have become invasive and very troublesome weeds in rice and other cropped areas.
- Feral rice: a type of rice produced by a de-domestication process from the cultivated species that may have weedy traits.

WHERE WEEDY RICES ARE A PROBLEM

The weedy rice problem is pervasive. Weedy rices have long been, are now or are becoming a major problem throughout the world where rice crops are direct seeded.

The Americas

Direct seeding has long been the dominant planting method in the Americas.

In the United States of America, red rice infestations were reported as early as 1846 (Allston, 1846). It is generally believed that red rice was introduced into the United States of America at a much earlier date as contaminants in imported seed rice. Anecdotal information indicates that the first rice variety was introduced into what are now the states of North Carolina and South Carolina in 1698 from the India subcontinent. A subsequent introduction of a different rice variety or type is believed to have come from Madagascar (Stubbs, Dodson and Brown, 1904; Cragmiles, 1978). As rice cultivation expanded, seeds were imported from several other countries including Japan in a search for better varieties. Rice production moved gradually westward from the eastern tidal lands and wetlands into the southern area and, much later, into California. By 1899, the states of South Carolina, North Carolina, Georgia, Louisiana and Arkansas were producing rice, and weedy red rice was already a major problem. Dodson (1898) published the earliest and most detailed information on weedy red rice in the United States of America in an illustrated technical bulletin. In the first two sentences of the bulletin, he summarized the weedy red rice problem in terms that are as meaningful to most rice farmers today as they were to those in Louisiana more than a century ago: “All the rice planters in Louisiana are familiar with ‘red rice’ as it grows in the field. In many instances, to their sorrow, they are too frequently confronted with the annoying grain, and it often occurs that rice cultivation has to be abandoned for a period on account of its predominance.”

As there are no naturally occurring wild relatives of rice in North America, the only plausible explanation for the existence of weedy rices in production fields in the mid-1800s and earlier is that they were introduced as contaminants in imported seed, probably from India, Japan or both. Indeed, weedy rice strains from Brazil, China (upper Yangtze River area), Japan and the United States of America belong to the same group called crop “mimics” with *indica* characteristics (Tang and Morishima, 1996). While the majority of present-day red rices in the United States of America fall into the mimics category, recent studies (Vaughan *et al.*, 2001) suggest that *japonica* type weedy rices are also present. For many years, more than 100 years in some important cases, red rice has been an important weed in all of the main rice-growing states in the United States of America except California, i.e. Arkansas, Louisiana, Mississippi, Missouri and Texas. Red rice was a rice field weed in California from the 1920s (Kennedy, 1923;

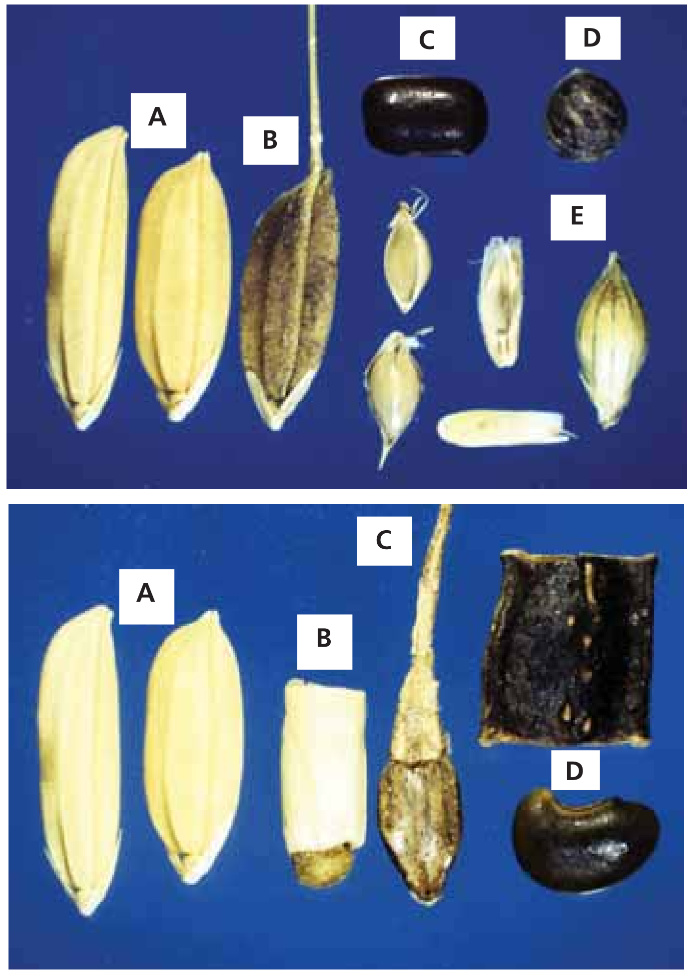
J.C. DELOUCHE, 1986

Plate 1
Typical strawhull-red (SHR) and blackhull-red (BHR) rices collected in Mississippi in 1978 and 1979. Note lax and loose panicle branches and spikelets (seeds) lined up like beads on the branches. Seeds are shown in inserted photos.

Bellue, 1932) at least into the 1950s, at which time it was considered the second most important weed in rice after *Echinochloa crus-galli* (Randall, 1950). Since then, red rice has apparently been virtually eliminated from the rice crop in California through the adoption of the water-seeding system, the use of appropriate herbicides and red-rice-free certified seeds. Plate 1 shows plants and seeds of typical strawhull-red and blackhull-red rice types in the rice area of the south of the United States of America. Seeds of common weeds (including red rices) in rice fields of the United States of America that are also difficult to separate from rice seed and, thus, occur as contaminants in rice seed are compared with those of medium- and long-grain cultivated varieties in Plate 2.

Rice was introduced to the Caribbean area earlier than to the North American mainland. The first reference to successful rice production is from Puerto Rico in 1535 (Lentini and Espinoza, 2005). Rice was also introduced into Mexico and Peru by the Spanish colonizers in about 1549. Weedy rices (including red rices) have been present in the Caribbean and the rest of the Americas for a long period, beginning soon after rice culture became significant and planting seeds began to be imported from other countries (including the United States of America). Red rice was apparently introduced into Venezuela from the United States of America in the mid-1940s in imported rice seed stocks (Dominguez, 1999). In Cuba, it was probably introduced in rice seeds from the United States of America during the intensification of rice cultivation beginning in 1927, or perhaps even earlier from Spain during the colonial period (Garcia de la Osa and Rivero, 1999). The extent and severity of the red rice problem in the reports from countries of the Americas in the Global Workshop on Red Rice Control (FAO, 1999) ranged from light to heavy between areas within a country and between countries with substantial rice cultivation. Noldin and Cobucci (1999) stated that red rice infestation is a critical problem in the state of Rio Grande do Sul, the most important rice production area in Brazil. They cited the use of red rice contaminated seeds as the main factor contributing to the initial spread of infestations and re-infestations. Fischer (1999) pointed out that the red rice problem is most serious in the tropical areas in Latin America where rice fields have to be drained after direct seeding, thus, precluding the establishment of the anaerobic seed bed conditions that are so effective in preventing germination of red rice, e.g. the transplant and water seeding systems. Monoculture and double-cropping of rice and the use of red rice contaminated seeds “results in perpetual field infestations”, which increase progressively to the extent that fields have to be abandoned in some cases.

While weedy red rice is not yet the most damaging weed in many of the countries, it has increased steadily in importance with the adoption of shorter-maturity, semi-dwarf varieties. It now ranks among the three or four worst weeds in most of the countries. Moreover, the nature of the weed problem and the difficulties of control have had or are having a profound influence on cultural practices, especially planting and water management after planting. Some countries, e.g. Costa Rica, Nicaragua and Venezuela, have reported problems with the endemic wild rice species *O. latifolia*, a white-pericarp type, often called *arrozon*, while *O. rufipogon* is claimed to be present as a weedy rice in Venezuela and Colombia.



J.C. DELOUCHE, 1988

Plate 2
Common weed seed contaminants in machine-harvested rice seed in the USA. Top: A: long-grain and medium-grain rices, B BHR, C: Sesbania exaltata, D: Caperonia castaneifolia, E weedy species of Poaceae. Bottom: A: long-grain and medium-grain rices, B: Rottboelia cochinchinensis, C Rhynchospora spp., D: Aeschynomene virginica, in hull and hulled.

Southern Europe and the Mediterranean

Southern European and other Mediterranean countries have not escaped the weedy rice problem. According to Vidotto and Ferrero (2005), shattering types of weedy rices were reported in Italian paddy fields early in the nineteenth century. Since then, weedy rices have spread and have become a major constraint on rice cultivation. The adoption of the transplant culture from about 1920 to 1960 retarded the spread of weedy rices considerably and reduced damage to the crop.

Since the beginning of the twentieth century, weedy rices in Europe have been classified as *O. sativa* var. *sylvatica.* According to Ferrero and Vidotto (1999), red-grain weedy rices began to be considered a significant problem when direct seeding replaced transplanting about 50 years ago. References cited in Eastin (1979) indicate that red rice was a problem in some Eastern European countries as early as the 1960s, e.g. Hungary and Bulgaria. However, it is in the last 25–30 years that they have become a major problem in European rice-growing countries with the adoption of “weak” semi-dwarf “*indica*-type” rice varieties and rice monoculture. Crop losses from weedy red rice infestations in Portugal can be as high as 50 percent, while in Spain weedy rice infestations range from very little to very severe in the main production areas (Barreda *et al.*, 1999).

There are about 20 000 ha under rice in the Rhone Delta in southeast France (Mouret, 1999). Weeds are the main constraint on production, and among them red rice can be the most damaging, e.g. up to 50-percent reduction in yield. Strategies employed by farmers to control red rice infestations are diverse and range from traditional weed control practices to the use of chemicals and crop rotations.

Asia

Oryza rufipogon, a wild perennial rice with a red pericarp, is endemic to South and Southeast Asia. As previously noted, it is considered to be an ancestor of the *sativa* (AA) group of cultivated rices, i.e. *indica*, *japonica* and *javanica* types, and the likely donor of the red pericarp that is the common characteristic of the weedy red rices as well as selected red-pericarp lines of rice that have been and still are cultivated for ceremonial and other special occasions. However, in the context of the huge rice crop in Asia, weedy rices have not been among the more important weed problems in rice production because of the dominance of the flooded, transplant culture. The transplant culture was designed and adopted millennia ago in order to access important benefits including weed control. Puddling of the soil with retention of a film of water on the surface destroys weed seedlings that have emerged and results in anaerobic conditions that are unfavourable for germination of weed seeds. In addition, the use of relatively well-developed seedlings for transplanting provides a competitive advantage to the rice crop and facilitates the identification of weedy rice and other weed seedlings that do emerge for removal during post-transplant weeding operations.

However, in recent times, weedy rices have been increasingly reported among the major weed problems in some Asian countries, such as Malaysia, Sri Lanka, Thailand, India, Republic of Korea, philippines and Viet Nam. The weedy rices are morphologically similar to the cultivated rices in plant and seed characteristics. They share a common gene pool with cultivated rice, and they have the early and heavy seed shattering and dormancy traits that make them so difficult to control wherever they become established. The reported losses caused by infestations of weedy rices range from reductions in yield (by from 5 to 86 percent) to the abandonment of paddy fields by farmers facing the most severe infestations. The incidence and spread of the weedy rices in the affected countries is associated closely with the increase in direct seeding. The strong and growing trend in many Asian countries towards the practice of direct seeding for part or all of the annual rice crop (because of the shortage and high costs of labour) is extending the areas infested with weedy rices and increasing the severity of the infestations.

The extent of the areas affected by weedy rices varies among the countries. In Thailand, more than 2 million ha are seriously affected by weedy rices, while more than 500 000 ha are also infested in the Mekong River Delta in Viet Nam. Malaysia, Sri Lanka and the Philippines also have substantial areas of paddy production infested with weedy rices. It is probable that the increase in direct seeding in the huge paddy areas of Asia will result in the rise of the weedy rices to the top ranks of the most troublesome weeds in rice production.

The rapid emergence of weedy rice, "padi angina", in northwest Malaysia following the adoption of direct seeding in the 1980s is a case in point (Vaughan *et al.*, 2005). In Viet Nam, the transplant culture is popular and dominant in the north, while in the south more than 90 percent of the sown area is direct seeded (Chin *et al.*, 1999). Only two crops of rice can be produced in the north owing to the cool winter season. However, triple-cropping is rather common in the south, and even quadruple-cropping is possible in some areas. In the case of triple-cropping, one or more of the crops might be transplanted. Infestation with weedy rices is lowest in transplanted rice and most severe in the "dry seeding" type of direct seeding. Most of the weedy rice types in Viet Nam have a red pericarp. Losses in infested areas average about 15 percent but can approach 70 percent in some cases. Surveys of farmers' perceptions about the sources of weedy rices reveal that 36.5 percent believe that they evolve from cultivated rice, 32.3 percent that they emerge from the soil seed bank, and 13.7 percent that they are introduced as contaminants in planting seeds.

Africa

Weedy rices are important weeds in the rice-producing areas in West Africa and south of the Sahel. Observations indicate that about 50 percent of the area sown to rice in Senegal is infested with biotypes of weedy rice (Diallo, 1999). Although weedy rices have been known in Senegal for a very long time, they have become an important problem only rather recently with the expansion, intensification and commercialization of rice culture and the replacement of traditional practices with those that invariably accompany such a transition, e.g. new varieties, irrigation, mechanization, and, very importantly, the concept of product quality in marketing. Some of the red-pericarp weedy rice biotypes in Senegal and other rice-producing areas in West Africa are different from those in other parts of the world. The annual species, *O. barthii*, and weedy biotypes of cultivated *O. glaberrima* are important there. During a 1970 visit to the Bumba area along the Congo River, then an important rice production and milling centre in the Democratic Republic of the Congo (formerly Zaire), Delouche (1970) determined that seed supplies and grain of R66, an important variety developed during the colonial period, were highly contaminated (10–35 percent) with red rice. Heavy infestations of red rice were also observed in the slash-and-burn dryland rice fields. Examination of milling records indicated that the high rates of contamination with red rice combined with inexperience and poor maintenance of essentially obsolete milling equipment reduced mill turnout considerably, especially head rice (whole grain) yield (which averaged only about 3 percent). In Egypt, an important North Africa rice producer, the types of weedy rice (including red rices) appear to be more similar to those in the Americas and Asia than to those in West Africa and SSA.

Johnson *et al*. (1999) reported that the main wild/weedy rice species in Africa south of the Sahel are biotypes of the annuals *O. barthii*, *O. glaberrima*, *O. punctata*, and the perennial *O. longistaminata*, which reproduces mainly from rhizomes. Two of these weedy species, the annual *O. barthii* and the perennial *O. longistaminata*, are among the four most important weeds in West Africa and the Sahel (Labrada, 1999). Overall, the wild rice / red rice situation in Africa differs considerably from that in other rice areas. Johnson *et al*. (1999) pointed out that the dominant lowland, mangrove and deep-water production systems that cover about 60 percent of the rice area in West Africa vary greatly in terms of the level of land development, water control and management, while relatively modern irrigated production systems have been developed in most of the countries. This diversity of production systems combined with "the uncertain genesis and identity of wild rices, the extent of gene introgression with crop cultivars and the degree of morphological and genetic variation further complicate the development of management strategies for these weeds." (Johnson *et al.*, 1999).

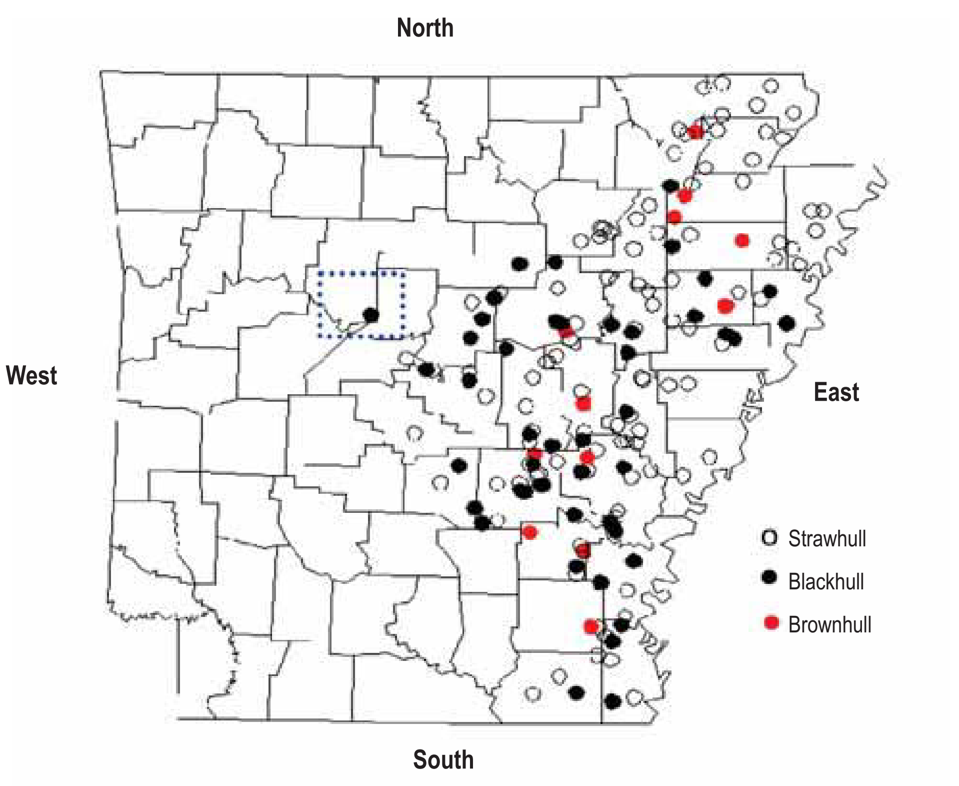
THE ORIGINS AND SOURCES OF WEEDY RICES

The most generally accepted views and ideas about the origin and/or genesis and evolution of weedy rices (including red rices) have been outlined above. Olofsdotter, Valverde and Madsen (1999) prepared a comprehensive review of the genetic relationships among red, weedy, cultivated and wild rices for the Global Workshop on Red Rice (FAO, 1999). Chang (2003) and Vaughan and Morishima (2003) provide recent authoritative reviews of the origin and taxonomic relationships of weedy rices. However, the origins and/or sources of weedy red rice are well known.

Contaminated seed stocks

Allston (1846) documented the presence of three distinct phenotypes of red rice in rice fields in North Carolina and South Carolina, the United States of America, in 1846. In 1850, the United States Department of Agriculture (USDA) agriculturists identified four distinct red rice phenotypes in the same area (USDA, 1850). These early observers and most later rice specialists concluded that red rice must have been introduced into the United States of America as a contaminant in imported rice seed, probably much earlier than 1846, since rice cultivation began in the colony of South Carolina in 1698 or even earlier with imported seeds, possibly from Madagascar (Dodson, 1898, 1900; Knapp, 1899; Jones and Jenkins, 1938). Cragmiles (1978) stated without qualification that: "red rice was definitely present in the rice fields of the American colonists long before rice cultivation began on a commercial scale in Texas, Louisiana, and Arkansas." The presence of red rice in California in the early 1900s is powerful evidence of its introduction as contaminants in seeds obtained from the southern states of the United States of America (Bellue, 1932). While red rices have been essentially eliminated from California, they have persisted in the other rice-producing states for various reasons, perhaps the most important being the continued and periodic infestation with red rice contaminated seeds. Recent surveys in Arkansas illustrate the importance of contaminated rice seeds as the main vehicle for the spread of the weedy rices (Figure 1). Red rices were found in rice-growing areas of Conway and Pope counties in the Arkansas River Valley, which are geographically isolated from the other rice-growing counties in the state. The only link between the isolated counties and the rest of the rice area is seed exchange.

FIGURE 1
Red rice distribution by hull colour in commercial fields in Arkansas, United States of America, summer 2002 and 2003



Source: Shivrain and Burgos, unpublished.

The original sources of red rice in Latin America and the Caribbean are believed to be rice seeds imported from the United States of America (Dominguez, 1999; Garcia de la Osa and Rivero, 1999), Spain or through Spain, The Netherlands, France and Portugal from Asian suppliers for cultivation in their "New World" colonies. After introduction, red rice spread to other areas through the exchange of seeds.

In Asia and West Africa, the origins of weedy rices were different from in the Americas or Europe because they are the sites of the evolution and domestication of the two cultivated rice species, *O. sativa* in Asia and *O. glaberrima* in Africa, where there are other wild rice species, many of which are troublesome weeds, and where rice has been cultivated for thousands of years. However, the present initial and recurring sources of weedy rice appear to be essentially the same as in the Americas. For example, farmers and specialists in Viet Nam recognize the importance of contaminated rice seeds as a source of weedy rice infestations and re-infestations (Chin *et al.*, 1999). Similarly, weedy rice contaminated seed (either purchased or exchanged) is considered to be the main means of infestation of new rice lands in Africa and of re-infestation of areas that have been largely freed of weedy rices (including red rices) (Johnson *et al.*, 1999).

Other means of distribution

Several "delivery systems" other than seed stocks have been implicated in the spread of weedy rice. Harvesting equipment is a significant source of contamination of rice seed lots and rice fields with seeds of weedy rice, other rice field weeds, and other varieties, i.e. "volunteers" (De Souza, 1989; Smith, 1992). Weedy rice seeds are also spread within fields and to other fields in mud adhering to the hooves and legs of animals, the wheels of carts, trucks and similar vehicles and in the movement of rice straw (Quereau, 1920; Garcia de la Osa and Rivero, 1999). Very rigorous procedures are specified and used for cleaning harvesting equipment used in certified seed production. Alert and conscientious rice farmers use similar procedures in grain operations in order to lessen the chances of spreading weedy rice within and among their rice fields.

J.C. DELOUCHE, 1980

Plate 3
Top, left to right: Starbonnet long-grain, Nato medium-grain, BHR, and SHR rices; note typical pubescence on hulls of the RR. Bottom, left to right: SHR and BHR rices with and without hulls. The SHR is a short-grain type.

Because the spikelets (grains) of many of the weedy rice phenotypes are pubescent and some have long, hispid awns (Plate 3), the seeds can be spread by adhering to the fur of domestic and wild animals and even the clothing of field workers. One of the most persistent beliefs regarding the spread of weedy red rices is that they are spread by waterfowl, mainly ducks that frequent rice fields for feeding after harvest. However, data collected from intestinal analyses of hunter harvested ducks of many species and in controlled feeding experiments refute this belief. Some very small seeds, e.g. *Leptochloa fascicularis*, and very hard seeds, e.g. *Polygonum* spp., pass intact through the digestive system of ducks but red and cultivated rice seeds do not (Powers, Noble and Chabreck, 1978; R.M. Kaminski, personal communication, 1993). Indeed, an article in *Rice Journal* in 1973 proposed ways to encourage wild ducks to stop over in rice fields in order to eat and deplete the red rice seeds in the top zone of the soil (Fontenot, 1973).

Hybridization of weedy and cultivated rices

Contaminated planting seed stocks are the main source and means of distribution of weedy rices in all the areas where they are a problem. However, there is another very important source of weedy rice types that has been documented conclusively for the weedy red rices. It is the source of the red rice types that arise to mimic the types of cultivated varieties produced in the area in terms of phenology, morphology and adaptation. These weedy types evolve from crosses of red and cultivated rices that result in the hybrid swarms from which, over time, types with high weedy potential and enhanced or special adaptability are selected under the pressure of natural forces and human activities involved in rice culture. Hybridization of a red rice with cultivated rice in the rice fields in North Carolina and South Carolina in the early nineteenth century (or earlier) was the most probable source of one or more of the three to four distinct biotypes of red rice described by Allston (1846) and the USDA (1850).

Even relatively recently, some authors of papers on the weedy red rices have become equivocal discussing the cause or origin of their great diversity. The earliest investigators recognized considerable diversity in red rice, a diversity that they attributed without reservation to hybridization of red and cultivated rices (Dodson, 1898; Knapp, 1898; Quereau, 1920). Furthermore, Beachell *et al.* (1938) published definitive work demonstrating that significant natural crossing occurs in rice, and Jodon (1959) published a widely quoted paper on the extent of natural crossing in rice (about 1 percent). It has been suggested that at least in the past the gene flow in the natural crossing between cultivated and weedy rices (including red rices) has been from the cultivated varieties to the weedy rices because the latter are more receptive to "non-self" pollen (Vaughan and Morishima, 2003; Australian Government, 2004). The significance of natural crossing in the persistence, spread and adaptability of red rice is discussed in detail in Chapters 3 and 4.

Early myths, speculations and conclusions

In earlier times (e.g. before the rediscovery of Mendelian genetics about 1900), the appearance of weedy red rices in rice fields stimulated much speculation, resurrected some old but enduring myths and generated some new ones about their origin or source. Many early lay observers of the weedy red rices believed that they were the result of the reversion, or conversion, of cultivated rices to wild forms. In the Louisiana rice area of the United States of America in the late 1800s, the common belief among rice farmers was that white rice seeds shattered onto the ground during harvest and exposed to winter conditions were changed irreversibly in some way so that those that survived the winter and emerged the following spring produced plants that had red rice characteristics and produced red grains. Once changed from white to red, the seeds continued to produce red rice in later generations, thus, causing the rapid increase in weedy red rice infestations. Other farmers thought that injuries to the young rice plants or tramping of the field by animals and wagon wheels induced injury responses that resulted in the production of red grains that produced red rice plants and grains the next generation, and so on. These beliefs and others about the origins and sources of red rice and complaints to the Director of the Louisiana Agricultural Experiment Station led to the assignment of W.R. Dodson, Station Botanist, to investigate the "cause of the development of the red grain" in Louisiana rice fields and the publication of his 20-page illustrated bulletin (Dodson, 1898). In this publication, Dodson refuted all of the beliefs and myths about the environmentally- or injury-induced and/or seemingly spontaneous one-way and one-time change of white cultivated rice to red rice through close observations, rigorous logical reasoning, and field experiments.

Reading this century-old bulletin can be a most instructive exercise for present-day students of the red rice problem because it identifies and describes most of the traits and ecological aspects that make the red rice problem so interesting and challenging even though the author was unaware of Mendel's laws of inheritance. Dodson's conclusions from his investigations of red rice in Louisiana were: "I. Red rice is a different variety from the white (*rice*). II. White rice will not produce red seeds when the seeds have been exposed to the weather all winter, as is commonly believed by planters. *(The white pericarp trait does not spontaneously mutate to red; white is the recessive allele.)* III. The two varieties will cross, producing hybrids, and these hybrids tend to revert to one of the parental forms, red rice being the stronger. *(Most of the obvious red rice traits are genetically dominant over their alleles in white rice.)* IV. The red rice, being dependent upon self preservation is hardier than the white rice, and also has a special device for preserving the seeds shattered to the ground in early fall. *(Red rice seeds are very dormant and survive the winter.)* V. The proper methods to be adopted *(for managing red rice infestations)* are to use clean seed and prevent red rice from seeding *(on late emerging plants or ratoons)* after the general harvest." (Italics in parentheses added for clarity, explanation or the modern interpretation.)

WHY WEEDY RICES ARE SO SUCCESSFUL AS WEEDS

Weeds are plants growing where they are not wanted. "Volunteer" maize plants in a soybean crop following maize are troublesome weeds to a soybean seed producer. The volunteer plants have to be rogued (removed) from the field before the final field inspection and harvest, which adds to the cost of production. Similarly, rice seed producers have to take special precautions when they change variety in order to prevent contamination of the new rice variety with volunteers of the previous variety. Producers who change from a medium-grain to a long-grain rice variety sometimes experience discounts in marketing owing to mixtures of grain types caused by volunteers. Volunteers of these types from different crops (maize and soybean) or different varieties of a crop (e.g. rice) are weeds and can be troublesome, especially to seed producers, but they do not pose serious problems. They are managed easily and are usually self-eliminating even where no specific control measures are taken. They are usually not even marginally successful as weeds.

Weedy traits shared with other weeds

Most of the weedy rice types are essentially varieties or strains of rice that are highly successful as weeds. They cross, albeit infrequently, with cultivated rice varieties.

While it may seem that their success as weeds is related to the red pericarp because most of them are red, there is essentially no evidence that the red pericarp per se has an effect on the weedy habit. However, the possibility that the red-pericarp characteristic has an indirect effect through linkage with important weedy traits, such as intense and prolonged seed dormancy, should not be dismissed. Red rice is a highly successful weed because it possesses essentially all of the traits that contribute to the success of weedy plants and some that are unique to weedy strains of cultivated species. Some of the more important traits that red rice shares with other very troublesome weeds are:

- excellent adaptation to the agronomic practices and ecological conditions favoured for the crop that it infests;
- a life cycle that is closely synchronized with the crop;
- abundant production of seeds that develop a capacity for germination relatively early and are dispersed fully and widely through early, easy and heavy shattering;
- rapid emergence followed by vigorous, competitive vegetative growth and reproductive development;
- intense and prolonged seed dormancy that maintains the germinability of shattered seeds on or in the soil through the cold or dry season until the next crop and those incorporated in the soil seed bank for multiple years;
- the seeds commonly occur as contaminants in planting seeds, which is a major means of widespread distribution of the weed.

Special weedy traits

Weedy rices, especially the ubiquitous weedy red-pericarp types, share a number of characteristics with other successful weeds. However, they also possess some rather unique characteristics derived from their botanical identity as strains or biotypes of the cultivated rice species they infest, mainly *O. sativa*, but also of *O. glaberrima* in some areas in West Africa and the Sahel. These unique and relatively rare characteristics contribute greatly to the complexity and difficulty of weedy rice control and to the losses resulting from infestations. These characteristics are:

- Most weedy rice ecotypes are so phenologically and morphologically similar to cultivated rice varieties from the seedling to the reproductive stage that they are difficult to recognize during the periodic weeding of the crop.
- Weedy rice seeds are difficult to distinguish and essentially impossible to separate from those of some cultivated varieties, especially medium-grain varieties. They are readily and often unknowingly distributed in planting seeds and in rice-harvesting equipment.
- As most of the weedy rice types belong to the same species as cultivated rice, the "selective" herbicide strategies that are used widely and effectively for control of other important weeds that are genetically dissimilar from the crop cannot be employed.
- Weedy rice contaminants in rice grain are difficult or impossible to remove. The red pericarp (bran) of weedy red rice is very objectionable to consumers and reduces the market grade and value of the grain. "Overmilling" to remove the objectionable red bran results in breakage and reduced mill turnout and grade. Thus, the losses from weedy red rice are not limited to the added costs of production for weeding and losses in yield but extend through milling to the final product.

Critical weedy traits of weedy rices

Each of the traits and characteristics of the weedy rices described above contributes to the complexity and severity of the problem in direct-seeded rice culture. However, four traits are critical for the establishment and continuation of weedy rice as a serious weed problem. The absence of any one of these traits would change it into a lesser, more easily managed weed, while the absence of any two of the traits would reduce it to the weedy status of a volunteer. The critical characteristics or traits are:

- diversity and changeability of weedy red rice populations produced by natural crossing with cultivated varieties;
- heavy seed production with early and heavy shattering;
- intense and prolonged seed dormancy as compared with cultivated rice varieties;
- superior vigour and competitiveness from emergence to the reproductive stage compared with cultivated varieties.

The first characteristic, i.e. diversity and changeability, sets weedy rice apart from most other serious weeds. However, it is, perhaps, the least understood and appreciated. It is reviewed and discussed in detail in Chapter 3, while the nature and interrelationships of the other three traits are considered in Chapters 4 and 5.

Chapter 3
Diversity of weedy rice populations

Four distinct types of red rice were documented in the United States of America as early as 1850 (USDA, 1850), and at least 7 different types were reported in the literature between 1846 and 1956. A review of the relatively recent literature reveals widespread recognition of the diversity and changeability of weedy rices (including red rices), and the reports in *Global Workshop on Red Rice Control* (FAO, 1999) are replete with references to the different types, variously termed biotypes, ecotypes, phenotypes or morphoforms, of weedy rices (including red rices) identified in various countries:

- Brazil: two distinct types recognized in 1971 (Mariot, 1971);
- Colombia: much morphological diversity (Montealegre and Vargas, 1992), and 30 types of red rice that fall into four groups (Carroza, 1999);
- Cuba: 38 red rice biotypes (Garcia de la Osa and Rivero, 1999);
- Guyana: "short" and "tall" red rice types recognized (Small, 1999);
- Mexico: seven distinct types of red rice (Aragon, 1969);
- Senegal: red rice biotypes of *O. glaberrima* and *O. barthii* (Diallo, 1999);
- Spain: biotypes of weedy rice some with red pericarp, some with white pericarp (Barreda *et al.*, 1999);
- Suriname: "179 different weedy rices", some with the red pericarp, some with the white pericarp (Khodabaks, 1999);
- Viet Nam: ten distinct and described ecotypes of red rice (Chin *et al.*, 1999).

The United States of America is used as the geo-ecological location and database for this chapter on the diversity and changeability of weedy rice, especially the weedy red rices, for two reasons: (i) it has been a problem in the direct-seeded rice culture of the United States of America for more than 200 years; and (ii) research studies and observations by researchers and extension workers in the rice-growing area of the south of the United States of America in the last 100 years and more constitute the most important and accessible database on red rice. Furthermore, weedy rices (including red rices) in Central and South America, Europe and Oceania, and in direct-seeded rice cultures in Asia and even Africa appear to be similarly diverse and changeable. In 2006, the total harvested rice area in the United States of America was 1.14 million ha, with an average production of 7.7 tonnes/ha. For reference, Figure 2 shows the present distribution of rice production areas in the United States of America.

Much of the diversity of weedy rices (including red rices) has been and continues to be camouflaged semantically in the common use of the singular or, more properly, generic names red rice or weedy rice, just as enormous diversity is submerged in the generic names wheat, rice or even weed. While the use of such generic names and terms is so common and accepted as to be unavoidable, the seemingly awkward plural terms weedy rices or red rices are generally used in this report in the plural form in order to convey a clearer image and better understanding of the diversity of weedy rices (including red rices). Weedy rices (including red rices) are not one specific weed. Rather, they are a variety of weeds that share a common assemblage of "weedy" traits but differ morphologically and phenologically from place to place and time to time. The diversity and polymorphism of red rice has been characteristic of red rice in North

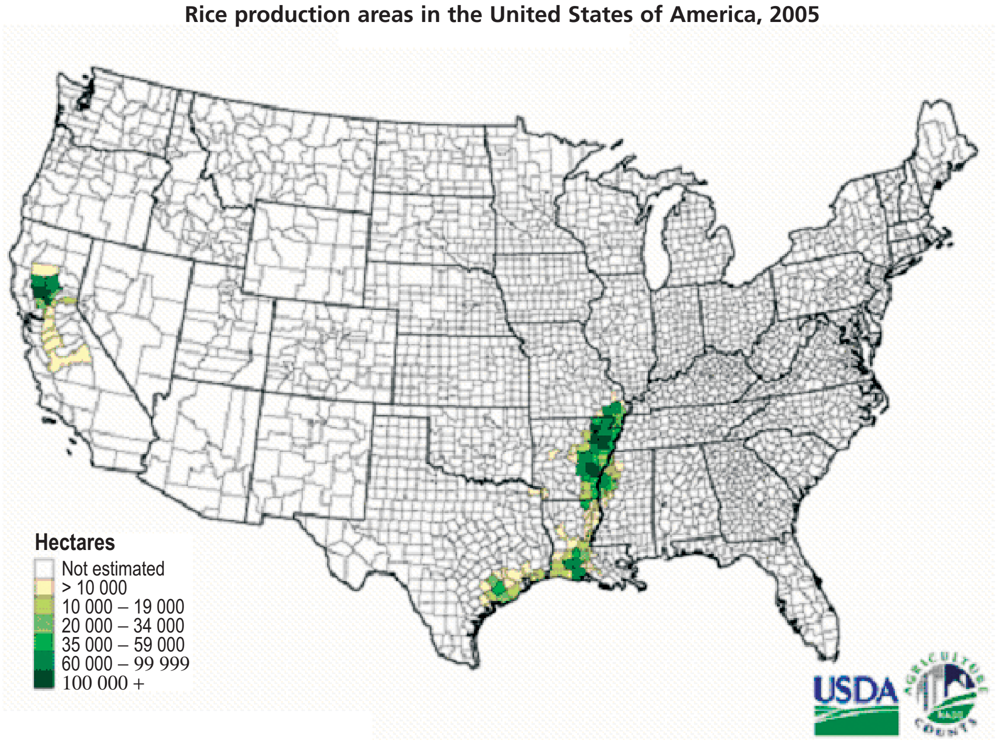
America since it became established as a type of weedy rice in rice fields more than 200 years ago.

EARLY AND GENERAL OBSERVATIONS ON THE DIVERSITY AND VARIABILITY OF RED RICE

Early studies of red rice in the United States of America described the plants as: generally shorter than the cultivated rice (Dodson, 1900); growing in "clumps" because of numerous tillers, up to 60/plant (Nelson, 1908); having an open growth habit (Quereau, 1920) with culms growing at an angle about 65° from the vertical rather than essentially erect like the cultivated rice (Dodson, 1900). In these early times, tall rice varieties were grown, hence the emphasis on the difference in height. However, by the mid-twentieth century, rice breeders were giving much more attention to plant stature in order to better adapt varieties to mechanization and higher rates of fertilizer; this culminated in the development of (and near global shift to) semi-dwarf varieties in the latter half of the century. Therefore, more recently, red rice plants have begun to be described as generally taller than cultivated rice with long, pale, rough, droopy leaves and more, wider-angle tillers or culms. This latter trait gives the red rices a more "clumpy" open canopy in contrast to the rather compact and near vertical cultivated rices.

Early observers also emphasized differences in panicle morphology and structure between red and cultivated rices. The red rice panicle was described as longer and with fewer and shorter grains than that of the long-grain rice varieties then cultivated. Hence, it did not droop as much as did the panicle of cultivated rice. The red rice panicle was also described as more open than that of cultivated rice. The "openness" of the red rice panicle is associated with a distinctive pattern of curves of the main panicle branches in

FIGURE 2
Rice production areas in the United States of America, 2005



Source: National Agricultural Statistics Service (NASS), USDA.

contrast to the rather straight branches of cultivated rice (Dodson 1898). In addition, red rice grains have red pigmentation, which was generally described as limited to the pericarp (Chambliss, 1920; Quereau, 1920; Kennedy, 1923), but sometimes as infusing the whole endosperm (Dodson, 1898). Red rice grains had pubescent hulls and were generally shorter and wider than cultivated rice grains, except those of medium-grain or short-grain varieties. These early comparative descriptors of red rice are generalizations of the situation in the last years of the nineteenth century and the early years of the twentieth century. Since then, the ecological landscape for rice in the United States of America, the varieties cultivated and the rice field weeds including weedy rices have changed considerably, and they continue to do so. The red rice types that now infest rice fields in the southern states of the United States of America display great variability in height, panicle morphology, tillering, culm and leaf angle, pubescence, grain size, hull colour, and phenology.

LOUISIANA – AN EARLY STUDY OF VARIABILITY IN RED RICE

In 1958, Constantin (1960) made one of the earliest and most comprehensive studies of variability in red rice in the United States of America. He surveyed and analysed the weedy rices in maturing rice fields in the southwest Louisiana rice area, one of the oldest rice production areas in the United States of America. The incidence of weedy red rice plants was estimated in 21 fields. Nine of the 21 fields had fewer than 200 red rice plants per acre (500 plants/ha; 1 acre = 0.405 ha), 8 fields had 200–1 000 plants/acre (500–2 500 plants/ha), and 4 fields had more than 1 000 plants/acre (2 500 plants/ha), with an estimated 25 000 plants/acre (62 500 plants/ha) in one of the fields. In a second survey, the proportions of strawhull and blackhull red rice types were estimated in 65 fields (the synonymy of colour descriptors is: white hull with strawhull; dark hull with blackhull; grey hull with "faded blackhull", brownhull with bronzehull, while goldhull has no synonym). Both strawhull and blackhull red rices were found in all the fields surveyed, but the proportions of each varied widely. Strawhull and blackhull types were present in about equal proportions in 21 of the 65 fields, while 19 fields had predominantly blackhull types and 25 fields had predominantly strawhull types. In order to examine the variability of the red rices in the area surveyed, Constantin collected 1 084 panicles from weedy and "off-type" rice plants in 44 randomly selected fields of maturing rice for laboratory study of the variation in panicle, spikelet and grain characteristics (Table 1). Although grain colour was not determined at the time of collection and was not a specific criterion for collection, subsequent analysis determined that the grain in every panicle collected had a red pericarp. No weedy or off-type rices with a white pericarp were collected. Pericarp colour ranged from light red to dark red but most of the panicles in each hull colour group had intermediate red pericarps although the greyhull group had a somewhat higher incidence of light red pericarps. While there was wide variation in the combinations of these and other characteristics among the panicles collected, there was no variation in grain shattering and hull pubescence. Every panicle shattered easily and heavily and had grain with pubescent hulls.

TABLE 1
Major characteristics of the spikelets and grains in 1 084 panicles

Hull colour	Of total	Awn status			Mean grain length	Shattering	Pubescence
		All	Partial	None			
	(%)		(%)		(mm)	(%)	(%)
Black	25	94	6	0	8.1	100	100
Grey	14	74	24	2	8.2	100	100
Straw	61	9	33	58	7.9	100	100

Source: Constantin, 1960.

Constantin's review of available records suggested that the blackhull red rice was a relatively recent introduction as none of the descriptions of red rice published up until 1920 mentioned black-coloured hulls, whereas strawhull red rices were mentioned in the earliest descriptions published in the mid-1800s. He cited an undated and unconfirmed report that a blackhull type of rice had been introduced into Vermillion Parish as a potential cultivated variety but abandoned because of its early and heavy shattering characteristic. There was some evidence to support this report. Blackhull red rices were more concentrated in Vermillion Parish than in other locations in the rice area and were popularly called Vermillion rice. Constantin's review of the historical data available and his findings led to the conclusion that the original source of red rice in the southwest Louisiana rice area was most probably contaminated seed from the southeast, i.e. North Carolina and South Carolina. However, he pointed out that contaminated seed stocks would at most account for only a limited portion of the wide variability determined in his 1958–1960 studies, and, thus, attributed most of the variation to hybridization of cultivated and red rices. More specifically, he contended that red rice was the probable seed parent for new red rice segregates because its shattering trait ensured that most of the hybrid seeds, would be left in the field to infest the next crop rather than be removed with the harvested seeds as would have been the case with the reciprocal cross. In addition, he asserted that classification of the red rices according to hull colour is genetically valid and that the blackhull and strawhull red rices were genotypically distinct and probably distant. His assertion has been upheld by recent molecular evidence obtained by Gealy, Tai and Sneller (2002) and Vaughan *et al.* (2001) that strawhull and blackhull red rices are distinctive genotypes and that there is greater genetic diversity among the blackhull group, with an average genetic distance (GD) of 0.33 compared with an average GD of 0.20 among the strawhull group.

MISSISSIPPI – A CASE STUDY OF DIVERSITY AND VARIABILITY IN RED RICE

Rice production in the State of Mississippi, the United States of America, began relatively recently compared with the traditional rice states (Louisiana, Texas, Arkansas and California) and did not expand much for several decades owing to tight government controls on area planted. In the late 1960s, about 20 000 ha were planted to mainly Starbonnet, a fine-quality, long-grain variety that was replacing Bluebonnet 50, the long-time favourite. The foundation seed of Starbonnet was maintained by one company that was also the main producer of registered and certified class seeds. Farmers planted certified seeds or saved seeds for planting from a crop produced from certified seeds one to several generations removed. Red rice was not a problem. There had been some red rice in the state in the 1940s but it had been essentially eliminated by rotating rice with other crops and pastures, rigorous roguing of rice fields and the production and use of red-rice-free seeds.

In the early 1970s, the federal government relaxed controls on the area planted to rice and the area planted in Mississippi more than doubled within two years. Because the rapid expansion in the rice area greatly exceeded the supply of high-quality certified rice seed produced in the state, some farmers had to obtain seed supplies of Starbonnet and other varieties from various sources in other states. Within a couple of years farmers began to complain about red rice in their fields, seed inspectors encountered red rice plants in certified seed production fields, and some lots of seed had to be rejected for certification owing to contamination with red rice. Alarmed by the introduction and rapid spread of red rice in the state, the rice producers requested that the seed technology laboratory of Mississippi State University undertake studies to obtain information on the extent and nature of the red rice problem for use in certified seed production and weed control research and development.

Initial study

The first study of red rice in Mississippi was undertaken by Larinde (1979). He compared the patterns of development, seed maturation and intensity and release of dormancy in two red rices, a "strawhull awnless" phenotype (here, the term phenotype is used as essentially synonymous with ecotype) and a "blackhull, long-awned" phenotype, with those of Nato, a medium-grain variety with unusually intense seed dormancy, and several other varieties. The two red rice phenotypes had thinner, more lax, pubescent leaves, more tillers, and shattered early and heavily as compared with Nato, which had erect, glabrous leaves, relatively few tillers and did not shatter. Anthesis and maturation for the strawhull phenotype was nearly two weeks earlier than that of the blackhull phenotype and about the same time as that of four of the five cultivated varieties with which they were compared. Larinde noted some variation in the two red rice phenotypes. Some of the blackhull plants had red rather than black awns, and a few of the strawhull plants had short awns while the rest were awnless. He hypothesized that these variants might be the result of segregation after natural crossing and recommended additional studies on this aspect.

Phenological and morphological variability

Comprehensive follow-up studies of red rice phenotypes in Mississippi were undertaken by Do Lago (1982). Panicles from red rice plants were collected from rice seed fields by certification inspectors during field inspections in 1978 and 1979 and examined closely in order to eliminate obvious duplications. Ten rather distinct phenotypes collected in 1978, 15 collected in 1979 and 3 collected in 1980 were compared in uniform controlled plantings along with the "blackhull" (BLKH), "strawhull awnless" (SHA-), and "strawhull short-awned" (SHA+) phenotypes from Larinde's studies, and three popular varieties. Twenty-two or 44 10–12-day-old seedlings from each entry were transplanted into a fumigated, irrigated field plot in April of each trial year (the usual time for planting rice), at spacings of 30 cm between plants and 60 cm between rows. Table 2 compares phenological data and morphological traits for 29 of the 31 red rice entries and 3 varieties along with those from subsequent plantings of five additional red rice types collected from 1986 to 1990, the semi-dwarf Lemont variety, and some entries from Texas (coded with a T), for observation and comparison.

There was a very considerable diversity among the red rice populations in Mississippi within 5–6 years after the apparent re-introduction of red rice into the state in seed rice from other states during the great expansion of rice production in 1972–74. The 34 red rice entries fell into two major phenotypic groups plus one unique phenotype.

The red rice phenotypes in the Mississippi studies are hereafter generally referred to as RR, while the red rices with straw coloured hulls are termed SHRs, those with black hulls as BHRs, and the brown or bronze hull types as BrHRs in the remainder of the paper.

Strawhull reds

Twenty-six RR phenotypes had straw-coloured hulls, but otherwise exhibited great diversity and variation in phenology and morphology:

- Plant height ranged from 68 to 169 cm.
- Time to 50-percent anthesis ranged from 89 to 109 days.
- Number of tillers per plant ranged from 24 to 54.
- Two phenotypes had short grains, 5 had long grains, and 19 had medium grains.
- Twenty-three phenotypes were awnless (no awns), 3 had short awns.

TABLE 2

Characteristics of 42 red rice contaminants from commercial rice fields in Mississippi and Texas, USA, 1978–1990 as compared with four cultivated varieties

Variety/ecotype	No.	Plant height (cm)	50% anthesis (days)	Tillers		Leaves		Shatter	Hulls		Grain type	Grain colour	Awns (length)
				No.	Angle	PUB	Angle		Colour	PUB			
Cult. varieties													
Starbonnet	1	118	105	27	ERT	GLB	ERT	None	STW	GLB	Long	WHT	None
Lebonnet	1	111	102	18	ERT	GLB	ERT	None	STW	GLB	Long	WHT	None
Labelle	1	103	92	20	ERT	GLB	ERT	None	STW	GLB	Long	WHT	None
Lemont	1	74	90	22	ERT	GLB	ERT	None	STW	GLB	Long	WHT	None
STW hull reds													
SHA-	1	157	99	50	INT	PUB	DRP	Heavy	STW	PUB	Short	DRE	None
79/11	1	153	`89	37	INT	PUB	INT	Heavy	STW	PUB	Short	DRE	None
79/6, 79/3	2	154–158	90–92	48–54	INT	PUB	INT	Heavy	STW	PUB	Medium	IRE–DRE	None
79/8, 79/7, 79/2, 78/2, 78/19, 78/3, 78/9, 80/2	8	137–161	91–103	40–53	INT	PUB	DRP	Heavy	STW	PUB	Medium	IRE	None
79/9, 79/14, 78/1, 79/17, 78/7, 80/3	6	145–169	91–99	46–51	INT	PUB	DRP	Heavy	STW	PUB	Medium	DRE	None
SHA+	1	144	108	54	INT	PUB	INT	Heavy	STW	PUB	Medium	DRE	AWN–SRT
79/1	1	162	97	24	ERT	GLB	ERT	Moderate	STW	GLB	Long	DRE	None
80/1	1	169	109	25	ERT	GLB	ERT	Moderate	STW	GLB	Long	IRE	None
86/1, 88/1	2	84–95	95–103	38–44	ERT	PUB	ERT	Heavy	STW	GLB	Medium	IRE	None
89/1	1	68	86	33	INT	PUB	ERT	Heavy	STW	PUB	Long	IRE	AWN–SRT
90/1	1	72	98	51	INT	GLB	ERT	Moderate	STW	GLB	Long	IRE	None
90/2	1	66	95	30	INT	GLB	ERT	Moderate	STW	GLB	Long	IRE	AWN–SRT
T/9	1	131	101	52	INT	PUB	INT	Heavy	STW	PUB	Short	IRE	None
T/5/2	1	151	108	40	INT	PUB	ERT	Heavy	STW	PUB	Medium	LRE	AWN–LNG
Gold hull red													
T/2/5	1	153	102	33	INT	PUB	DRP	Heavy	GLD	PUB	Medium	LRE	None
Brown hull red:													
78/8	1	152	112	60	INT	PUB	ERT	Heavy	DBR	PUB	Medium	IRE	AWN–MED
Black hull reds													
BLKH	1	171	109	77	INT	PUB	INT	Heavy	DBL	PUB	Medium	LRE	AWN–LNG
79/13	1	184	93	62	INT	PUB	INT	Heavy	DBL	PUB	Medium	IRE	AWN–LNG
79/4	1	180	103	85	INT	PUB	INT	Heavy	DBL	PUB	Medium	IRE	AWN–LNG
79-5, 79-10, 78-4, 79-15, 78-6	5	173–179	104–110	67–76	INT	PUB	ERT	Heavy	DBL	PUB	Medium	LRE	AWN–LNG
78-5	1	150	104	52	INT	PUB	DRP	Heavy	DBL	PUB	Medium	LRE	AWN–LNG
T/4/1	1	I72	97	46	INT	PUB	INT	Heavy	IBL	PUB	Medium	LRE	AWN–LNG
T/8/2	1	162	115	97	INT	PUB	INT	Heavy	DBL	PUB	Medium	LRE	AWN–LNG
T/4/4	1	173	98	64	INT	PUB	INT	Heavy	IBL	PUB	Long	LRE	AWN–LNG

Note: Abbreviations: ERT = erect; INT = intermediate; DRP = drooping; PUB = pubescence or pubescent; GLB = glabrous; STW = straw (hull colour); STW- = straw hull awnless genotype; STW+ = straw hull awned genotype; BLKH = black hull genotype; DBL = dark black; IBL = intermediate black; FBL = faded black; DBR = dark brown or bronze; GLD = golden colour; WHT = white; LRE = light red; IRE = intermediate red; DRE = dark red; SRT = short; MED = medium; LNG = long. T/entries are accessions from Texas for comparison.

Source: Data from Do Lago (1982) and colleagues.

- Twenty phenotypes were pubescent, 6 were glabrous.
- Twenty-two phenotypes shattered early and heavily, 4 shattered a bit later and moderately.
- Twenty-two phenotypes had intermediate angle tillers, 4 had erect tillers.
- Fifteen phenotypes had drooping leaves, 4 had intermediate angle leaves, and 7 had erect leaves.

Compared with Starbonnet and Lebonnet (the two most widely planted varieties in Mississippi in the 1970s and early 1980s), the SHRs collected up to 1980 were taller, earlier in terms of 50-percent anthesis, and more vigorous, i.e. had twice as many tillers. The most unique of the SHRs collected in 1980 or earlier were entries 79/1 and 80/1 – very tall, glabrous, long-grain RR with erect leaves, comparatively few tillers, and moderate shattering. Although very similar morphologically, there was a difference of about 12 days between the two entries in reaching the 50-percent anthesis stage, and the apicula of the grains were very different in curvature and colour. Beginning in 1986, short RR phenotypes with erect, glabrous leaves and long grains that mimicked the semi-dwarf Lemont variety began to be collected in the state. The uniqueness of some of the entries and the appearance of the semi-dwarf mimics are discussed in detail below.

Blackhull reds

Nine phenotypes had black hulls and were somewhat less morphologically diverse than the SHRs:

- Plant height ranged from 150 to 184 cm.
- Time to 50-percent anthesis ranged from 93 to 110 days.
- The number of tillers ranged from 52 to 85.
- All the phenotypes had medium grains with long awns, were pubescent, bore tillers at the intermediate angle, and shattered early and heavily.
- Five of the 9 phenotypes had erect leaves, 3 had intermediate angle leaves, while 1 phenotype had distinctly droopy leaves.

Overall, the BHRs were taller, later in maturity, and had more tillers not only than the cultivated varieties but also the SHRs. No different BHRs were collected after 1980.

Brownhull red

A unique phenotype with brown or bronze-coloured hulls was collected in 1978. It had the latest maturity of the entries, 112 days to 50-percent anthesis, erect pubescent leaves, medium-pubescent grains with medium-length awns, and shattered earlier and more completely than any other RR. It was also the most dormant of the RR phenotypes.

A comparison of the RR phenotypes collected through to 1980 with the cultivated varieties, excluding the semi-dwarf Lemont, in terms of mean values for three traits that influence competitiveness is summarized in Table 3.

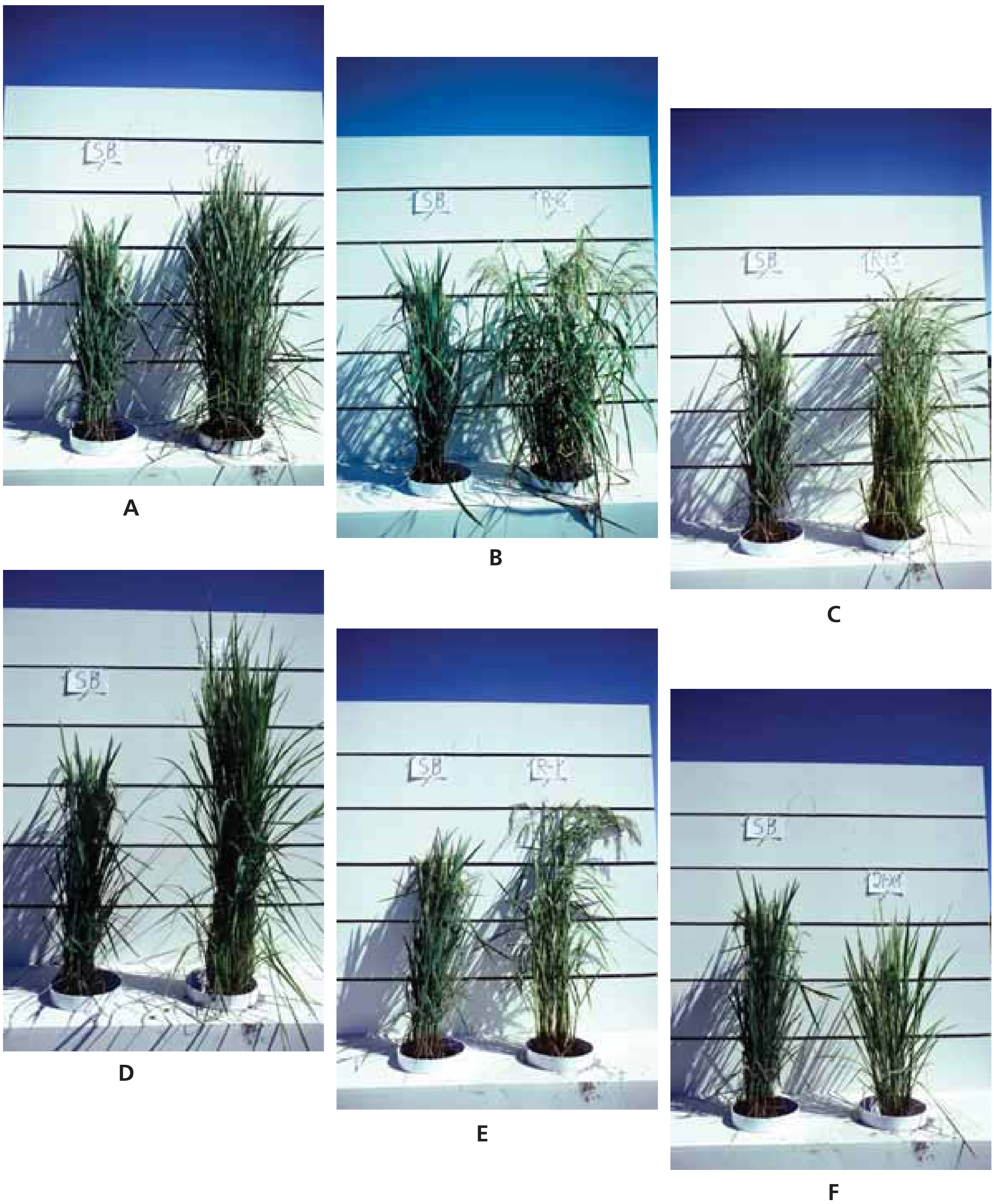
The mean height of the RR phenotypes was 40 percent (SHR) to 57 percent (BHR) greater than that of the cultivated varieties, and the mean number of tillers was 2–3 times greater. However, maturity, as indicated by days to 50-percent anthesis, was very similar with the SHR averaging about 2 days earlier and the BHR about 6 days later than the cultivated varieties. As all the RR phenotypes shattered early and heavily, a substantial portion of the seeds produced would have been dispersed to the soil surface before mechanical or hand harvest of any one of the three cultivated varieties. Plates 4 and 5 show the plant and spikelet types of some of the entries.

TABLE 3
Mean values for three traits influencing competitiveness

Trait	All varieties*	All RR	SHR	BHR
Plant height (cm)	110	160	154	173
50% anthesis (days)	98	99	96	104
No. of tillers	22	55	48	72

* Excludes semi-dwarf Lemont variety.

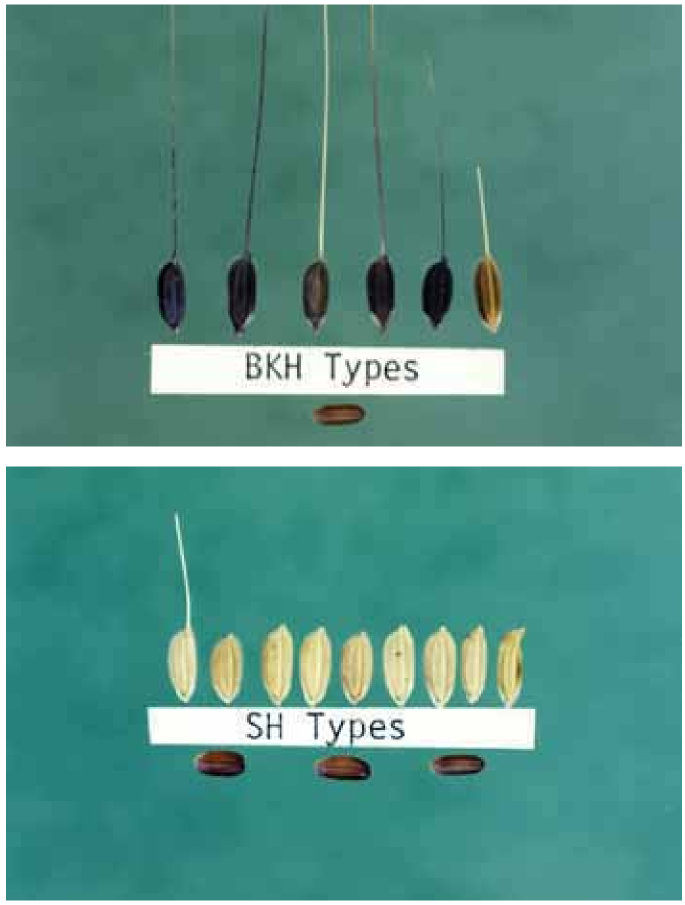
Although all entries except two that were not included in Table 2 were uniform and stable in several field plantings, it is unlikely that each was a distinctive "pure line" RR. The most common phenotypes, SHA- and BLKH, for example, were collected



J.C. DELOUCHE, 1982

Plate 4
Variation in RR phenotypes as compared with the variety Starbonnet. The variety Starbonnet (SB) is on the left and an RR is on the right in each picture. A: SHR, 79/8; B: SHR, R-6; C: BHR, R-13; D: BHR, R-1; E and F: RR segregates.

many times in many fields. The other entries were collected and entered into the uniform field plantings because they appeared to be different. However, some of these, especially some of the SHRs, turned out to be very similar and probably were not different or differed only in terms of a few days' maturity. Nevertheless, most of the lines appeared distinctive and became more distinctive to the workers during the nearly 5 years of field plantings (just as commercial varieties become more and more distinctive to field inspectors as they gain experience over time). If some of the new "finger-printing" methods had been in general use at the time, it would have been possible to establish identity and examine relationships in a more definitive way.



J.C. DELOUCHE, 1988

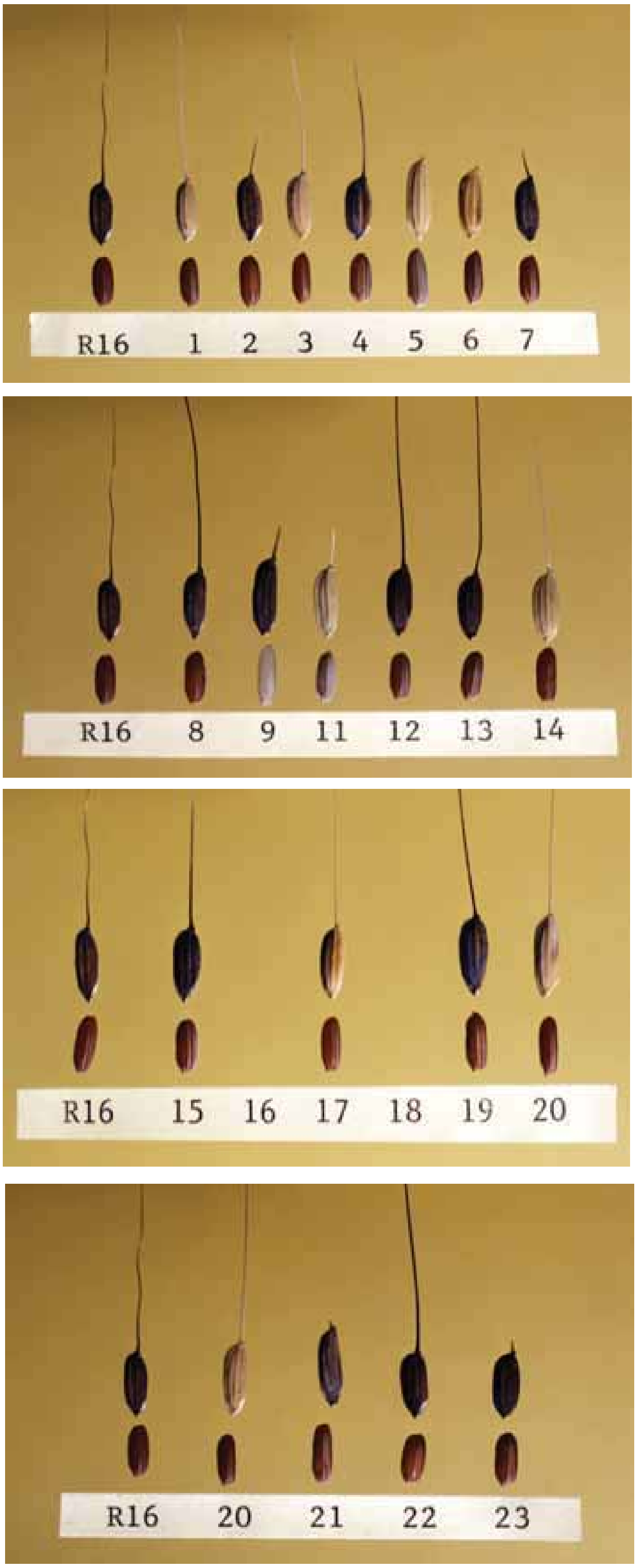
Plate 5
Typical variation in spikelet (seed) type among BHR (top) and SHR (bottom) phenotypes.

Source of diversity and variation in red rices

The main question concerning the great diversity in the phenology and morphology of the RR phenotypes in Mississippi within just a few years of red rice being re-introduced into the state in the early 1970s was where it had come from. One answer to this question was suggested by the two entries in the uniform plantings that were not included in Table 2: one collected in 1978 and coded 78/21, and one collected in 1979 coded 79/16.

Entry 78/21

This entry (collected from a seed field of Starbonnet rice) had long, slender grains with a dark-red pericarp, straw-coloured hulls and partial tip-awns. The collector's note indicated that the plant from which the panicle had been collected was slightly taller than Starbonnet. Early observations of the 22 plants from entry 78/21 revealed so much variability that not much attention was given to them until it was realized that they were a segregating population. Some morphological traits were recorded and seeds collected from the 15 plants that produced seeds within the time frame of the other RR entries. The remaining 7 plants of the 22 plants either flowered very late, exhibited sterility, or had very few and weak culms. Selected morphological traits for the 15 segregates are given in Table 4. Thirteen of the 15 progeny had strawhulls, 2 had light-brown or light-gold hulls; 7 of the plants produced medium grains, 8 produced long grains; 10 plants had white grains, 5 had red grains; 8 plants were glabrous, 7 were pubescent; only one plant was awnless, the rest had long, short or tip-awns; tiller angle ranged from open to erect; and seeds of two of the plants has distinctive black apicula. General observations of the entire 22-plant segregating population revealed considerable variation in plant



J.C. DELOUCHE, 1982

Plate 6
Variation in spikelet (seed) characteristics of 21 of the progeny produced by the 79/16 (R-16) segregate collected in 1979.

height, time of flowering and maturity, sterility and tiller density as well as in the traits recorded in Table 4.

Entry 79/16

This entry, also collected from a seed field of Starbonnet a year later in 1979, had slender, pubescent medium grains with a red pericarp, faded black or greyish hulls and long awns. It became evident within a few weeks after transplanting that the 25 surviving plants were another segregating population. Observations and measurements of selected traits for 16 of the plants are given in Table 5. Of the remaining 9 of the 25 surviving plants, 5 were either very late or very sterile and 4 were not included in the measurements for various reasons. Fifteen of the 16 plants had red pericarps (the other one was white). Most of the plants were relatively tall compared with Starbonnet (118 cm), but 3 plants were about the same height or a bit shorter. Time to 50-percent anthesis ranged from 102 to 111 days compared with 105 days for Starbonnet. Tiller numbers ranged from 21 to 61 and the tiller angle was erect for 5 plants, intermediate for 8 plants and open for 3 plants. Nine of the plants had purplish leaves while the other 7 had "normal" green leaves. Seven plants were glabrous, and 9 plants were pubescent. Hull colour varied considerately: 5 plants had strawhulls, 6 had intermediate (colour) black hulls, 1 had faded black or grey hulls like the parent 79/16, 2 had dark-black hulls and 2 had dark-brown hulls. All plants had awns ranging from tip-awns to long awns. Grain type was mostly medium but there were several long-grain types (including the one with a white pericarp). Dormancy varied from very intense to essentially none for the white-pericarp type. Only 1

TABLE 4
Characteristics of progeny from the 78/21 red rice segregate collected in a field of Starbonnet rice in Mississippi, USA, in 1978

Collection No.	Hull colour	Grain type	Grain colour	Pubescence	Awns	Additional observations
78-21	Straw	Long	Red	–	None	Slightly taller than Starbonnet
Progeny						
21-I	Brown	Medium	White	Pubescent	Tip-awned	Sparsely awned
21-II	Straw	Medium	Red	Glabrous	None	Tiller angle erect
21-III	Straw	Long	White	Pubescent	Long	Tiller angle open
21-IV	Straw	Long	Red	Glabrous	Long	Tiller angle open
21-V	Straw	Medium	White	Glabrous	Short	
21-VI	Straw	Long	White	Glabrous	Tip-awned	Tiller angle intermediate
21-VII	Straw	Long	Red	Pubescent	Long	Very late in flowering
21-VIII	Brown	Medium	Red	Pubescent	Short	Tiller angle erect
21-IX	Straw	Medium	White	Glabrous	Long	Tiller angle intermediate
21-X	Straw	Long	White	Glabrous	Long-red	Black apicula
21-XI	Straw	Medium	White	Pubescent	Long	Tiller angle erect
21-XII	Straw	Long	Red	Glabrous	Long	Tiller angle intermediate
21-XIII	Straw	Medium	White	Pubescent	Long	Tiller angle intermediate
21-XIV	Straw	Long	White	Pubescent	Short	Tiller angle erect
21-XV	Straw	Long	White	Glabrous	Long-red	Black apicula

Source: Data from Do Lago (1982).

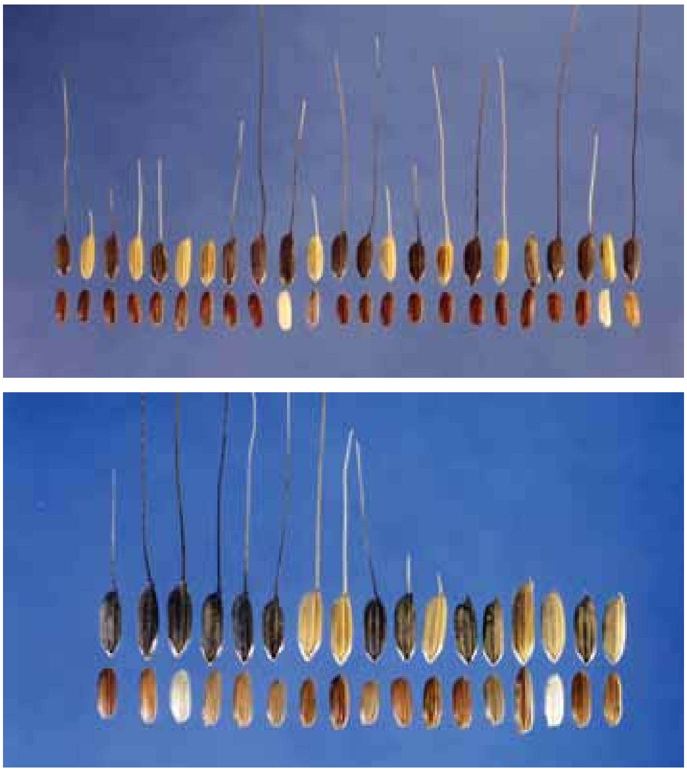
of the 7 plants with glabrous leaves also had glabrous grain. Plate 6 shows seeds from the 21 plants that produced seeds.

On the basis of observations of the segregates produced by entry 78/21, the strawhull, long-grain segregate (Table 4), during the initial and subsequent generations, it appeared to be a relatively early generation segregate of a cross between the Starbonnet variety and one of the common SHRs, possibly the short-awned SHR (SHA+). The entry was collected in a field of Starbonnet, which occupied probably as much as 75 percent of the area planted to rice in the state in the late 1970s. This conclusion was supported by the selection of multiple lines of red rices that were very uniform and stable and nearly identical to (i.e. "essentially derived from") Starbonnet after five or six generations so that even experienced field inspectors had difficulty in distinguishing them from Starbonnet (Plate 7).

It is more difficult to speculate on the parentage of the 79/16 blackhull (faded), awned, medium slender

J.C. DELOUCHE, 1993

Plate 7
Starbonnet (SB) type RR lines developed by selection from progeny of the 78/21 segregate. Top, left to right: non-shattering panicles of two RR lines and SB. Bottom, left to right: SB, two RR glabrous lines, one RR pubescent line.



J.C. DELOUCHE, 1986

Plate 8
Variation in spikelet characteristics of progeny from the 78/21 and 79/16 segregates collected in Mississippi Starbonnet rice fields in 1978 and 1979. Note variation in grain length, hull colour, and awns.

J.C. DELOUCHE, 1986

Plate 9
Variation in grain length, awns, and awn colour in white-pericarp blackhull rices from segregating populations.

grain segregate. It too was collected from a field of Starbonnet, and the common black hull, long-awned RR (BLKH) is one of the likely parents. Some of the segregates produced by entry 79/16 in subsequent generations were as tall or taller than BLKH and were similar to it in leaf, tillering and grain characteristics. However, many of the segregates had the pronounced purple leaf sheath character with the purple coloration extending in some cases into the leaf blades, which was not present in the Starbonnet and BLKH populations. However, the purple leaf sheath character was observed in a few white-pericarp variants collected from certified rice fields and planted for observation.

Examples of the variability in spikelet (grain) and caryopsis characteristics in segregates from the 78/21 and 79/16 populations in subsequent generations are shown in Plates 8–10.

At about the time of the work of Larinde (1979) and Do Lago (1982) in Mississippi and Helpert (1981) in Texas in the United States of America, workers in Brazil were also looking at the diversity of red rices. Marques and co-workers (Marques *et al.*, 1983) were cataloguing the variability in red and blackhull rice in Brazil and its effects on seed production, while another Brazilian team (Galli, Terres and Him, 1982) were examining first-generation hybrids from cultivated and red rice crosses.

TEXAS – COMPARATIVE STUDY OF DIVERSITY IN RED RICES FROM FOUR STATES

Noldin (1995) compared and characterized 19 ecotypes of RR obtained from researchers in Arkansas (4 ecotypes), Louisiana (5 ecotypes), Mississippi (6 ecotypes

– 5 of which were collected in the late 1970s for Do Lago's study) and Texas (4 ecotypes). The ecotypes represented essentially all the hull colours: 11 strawhull, 5 blackhull, 2 goldhull and 1 brownhull. Comparison plantings including several popular cultivated varieties were made on the Texas A&M Research Farm, College Station, Texas, the United States of America, and 46 different plant and seed traits were observed and/or evaluated. The results can be summarized as follows:

- Most ecotypes were uniform and stable although there was considerable variability within ecotypes.
- On average, compared with the cultivated varieties, the RR ecotypes were taller, had pubescent, lighter-green leaves, more tillers, panicles and seeds/panicle, larger flag leaf and leaf area/plant, and shattered heavily.
- Most of the RR ecotypes had traits associated with high

J.C. DELOUCHE, 1990

Plate 10
Variation in grain length, awns, spikelet type, and pericarp colour of progeny from the 78/21 segregate collected in a Mississippi Starbonnet rice field in 1978. Note variation in grain length from short to extra long.

TABLE 5
Characteristics of progeny from the 79/16 red rice segregate collected in a field of the Starbonnet rice in Mississippi, USA, in 1979

Collection No.	Plant height	50% anthesis	Tillers		Leaves		Hulls		Grain colour	Awns	Germ
			No.	Angle	Colour	PUB	Colour	PUB			
	(cm)	(days)									(%)
79/16	–	–	–	–	–	–	BLK	PUB	Red	–	–
Progeny											
16-1	110	109	35	INT	PPL	GLB	STW	PUB	Red	Awns	12
16-2	114	100	35	INT	PPL	PUB	IBL	PUB	Red	Awns	–
16-3	140	112	33	OPN	PPL	PUB	STW	PUB	Red	Awns	–
16-4	131	113	51	INT	GRN	PUB	IBL	PUB	Red	Awns	3
16-5	114	110	22	ERT	GRN	GLB	STW	GLB	Red	None	27
16-6	141	110	42	INT	PPL	GLB	DBR	PUB	Red	None	2
16-7	149	103	21	ERT	GRN	PUB	IBL	PUB	Red	Awns	12
16-8	147	103	47	OPN	GRN	GLB	IBL	PUB	Red	Awns	19
16-9	145	102	43	ERT	GRN	PUB	IBL	PUB	White	Awns	96
16-12	135	111	61	OPN	GRN	PUB	DBL	PUB	Red	Awns	15
16-14	138	111	39	INT	PPL	PUB	STW	PUB	Red	Awns	–
16-17	149	107	49	INT	PPL	PUB	DBR	PUB	Red	Awns	–
16-19	159	103	35	INT	PPL	GLB	DBL	PUB	Red	Awns	11
16-20	152	101	41	INT	GRN	GLB	STW	PUB	Red	Awns	47
16-21	146	103	32	ERT	PPL	PUB	FBL	PUB	Red	Awns	9
16-22	156	102	40	ERT	PPL	GLB	IBL	PUB	Red	Awns	4

Note: Abbreviations: ERT = erect; INT = intermediate; PPL = purplish; GRN = green; PUB = pubescence or pubescent; GLB = glabrous; STW = straw (hull colour); STW- = straw hull awnless genotype; STW+ = straw hull awned genotype; BLK = black; DBL = dark black; IBL = intermediate black; DBR = dark brown or bronze.
Source: Data from Do Lago (1982).

competitive ability – they were taller than the cultivated varieties and produced more biomass/area (tillers/plant × aboveground weight/plant).

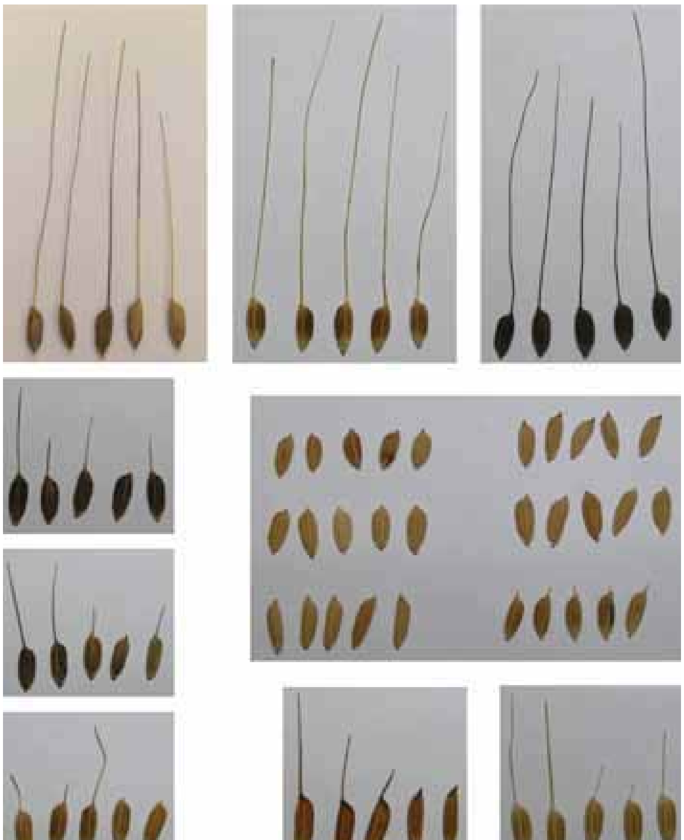
- On average, the RR ecotypes flowered 3–5 days earlier than the semi-dwarf variety Lemont, but 12 of the 19 ecotypes reached 50-percent anthesis at the same time as the Lemont.

Several of the ecotypes had plant and seed characteristics similar to commercial varieties, viz. erect, glabrous leaves, erect tillers, relative resistance to shattering, and long, slender grains.

ARKANSAS – PHENOTYPIC AND GENETIC DIVERSITY OF RED RICE

Phenotypic diversity

Arkansas is the leading state in terms of rice production in the United States of America, producing about 50 percent of the nation's rice. Researchers from the Dale Bumpers National Rice Research Center (NRRC) at Stuttgart in Arkansas and from the University of Arkansas have conducted the most recent and comprehensive survey of red rices in the southern rice area (Figure 1). The 136 accessions obtained in Arkansas between 2002 and 2004 confirmed that the majority (76 percent) of red rices were SHRs and that about 95 percent of these were awnless (Table 6). BHR rices comprised 15 percent of the accessions, and 95 percent of them were awned. Thus, a few awned SHR and a few awnless BHR rices have evolved. BrHR rices constituted a very minor group, all of which were awned. Awn lengths ranged from a few millimetres to about 10 cm (Plate 11). The widest variation in plant height was in the BHR group, where the shortest accession was 110 cm and the tallest was 170 cm. Some BrHR rices were as tall as the BHRs but there were no short accessions. SHR rices had the narrowest range in plant height (120–150 cm). On average, the BHR accessions were the tallest plants. Although plant height is an environmentally influenced trait, tall genotypes are almost invariably tall relative to medium and short, e.g. semi-dwarf, genotypes under similar environmental conditions. While tall plants usually have a competitive advantage, short-stature red rices also have distinct advantages for establishment, survival and spread in rice fields. Red rice plants about the size of those of the cultivated variety, especially with erect culms and leaves, are frequently not recognized during casual and even more rigorous field inspections. They reproduce and shatter seeds into the soil seed bank in that season and perhaps in subsequent seasons. In contrast, a red rice plant taller than the variety is spotted



N.R. BURGOS, 2005

Plate 11
Types of grains from weedy (red rice) plants in Arkansas, USA, collected between 2002 and 2003.

rather easily in rice fields and can be rogued before reproduction.

Plate 12 shows representative plant types of various heights and canopy structure. The large, tall plants are top heavy and generally lodge at maturity, especially where growing at high densities. When the red rice lodges, the infested rice crop also lodges owing to the weight of the red rice biomass, which makes harvesting difficult. Tiller production in the absence of competition can vary by 50–60 tillers and generally ranges from 70 to 140 tillers per plant. The canopy structure of red rice plants varies widely from closed (or erect) to wide open (spreading) culm structure. While the majority of plants of all hull types have an intermediate canopy structure (culm angle = 20–45 °), a higher proportion (28 percent) of BHR rices have erect culms, while only 10 percent of the SHR rices are erect.

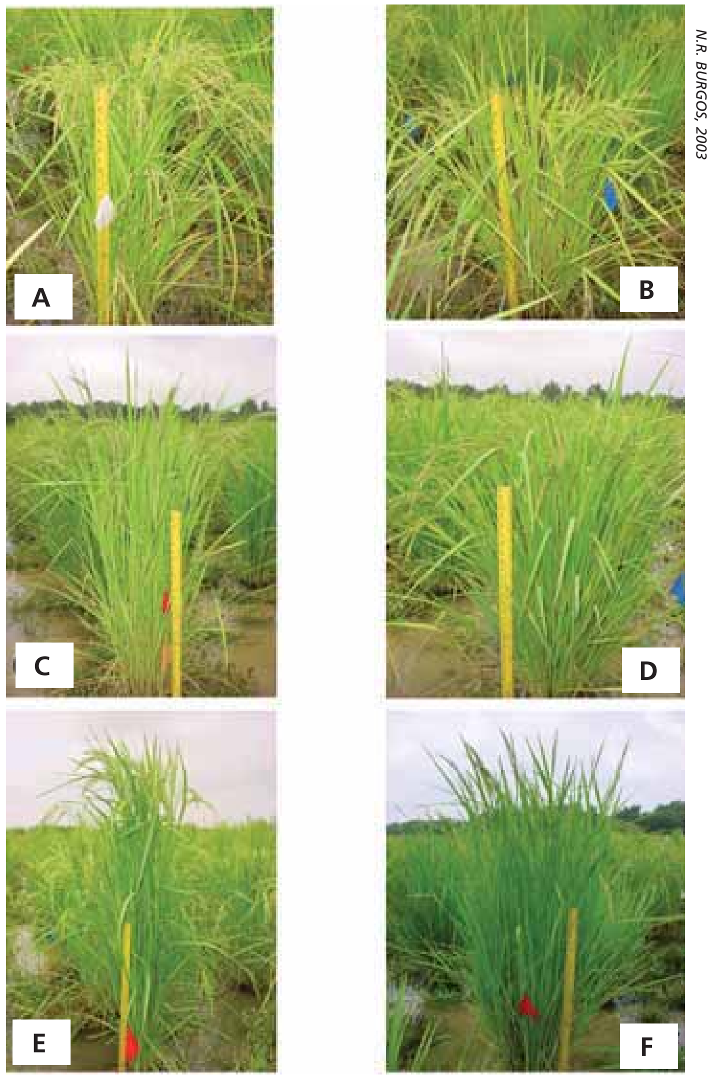


Plate 12
Representative weedy rice types in Arkansas, USA. A: short, compact; B: short, open; C: intermediate height, compact; D: intermediate height, open; E: tall, compact; F: tall, open canopy.

This recent characterization of red rice populations in Arkansas does not deviate significantly from the morphological characterization of red rices in Louisiana about half a century earlier, the more detailed characterization of red rice populations in Mississippi in the early 1980s or the Texas comparative studies of red rices from four states in the mid-1990s. It is probable that current surveys in Louisiana, Mississippi and Texas would find that the awnless SHR rices are still the dominant group, the long-awned BHR rices are of secondary importance, while the BrHR and greyhull red rices are still distinct minor groups. However, it is also probable that the diversity within each hull colour group would have increased, especially from the 1960 base, owing to outcrossing with shorter-stature and more erect varieties. The rarest type of red rice is goldhull, which was found in only one location in Arkansas and a few other locations in Louisiana and Texas. Of the Arkansas collection, goldhull red rice is also the most morphologically distinct, with long (42 cm), wide (19 mm) flag leaves, purple basal leaf sheath and leaf margins, dark-green leaves, longer grains (8.6 mm) than the other red rice types, and negligible seed shattering. Although this population is stable, its low seed-shattering characteristic may eventually cause its elimination from the plant community as most of its seed would be harvested along with the crop grain.

The red rice cultivated in Vallee de l'Artibonite, Haiti, had goldhulls (above). There was speculation that it was derived from a cross with Century Patna, a goldhull variety that had been widely grown in the country.

Phenological diversity

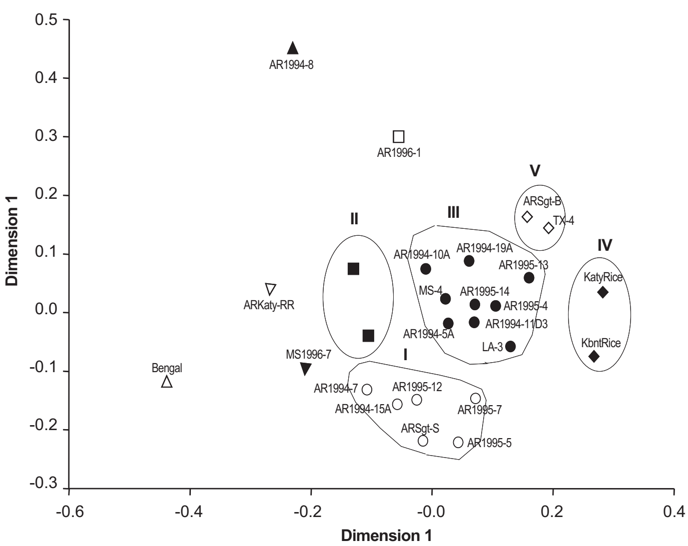
It is commonly reported that red rice flowers earlier than cultivated rice. This is true for the majority of SHR types. However, within the SHR category, the onset of flowering can vary for weeks depending on the latitude of origin of the accession (Shivrain, 2004). The greatest variation in onset of flowering existed among the SHRs at 942–1 401 cumulative heat units (Table 6). The earliest and latest plants to flower were SHR types. When they were planted at Stuttgart, located in the central region of the state, the length of time from planting to the onset of flowering increased with decreasing latitude of origin. However, latitude of origin had no effect on the phenology of the BHR and BrHR rices. The great variability in time of flowering has significant implications for gene flow between cultivated rice and red rice.

Genetic diversity

Genetic fingerprinting experiments with deoxyribonucleic acid (DNA) and using microsatellite markers (Vaughan *et al.*, 2001; Gealy, Tai and Sneller, 2002) and random amplified polymorphic DNA (RAPD) markers (Estorninos *et al.*, 2006) showed that, generally, SHR and BHR rices are distinct genotypes (Figure 3). Therefore, the major grouping of red rices according to hull colour is genetically valid. There are also variants of these two groups that belong to different, albeit smaller, genotypic clusters. Others do not belong to any particular genotypic cluster. This supports earlier contentions that several intermediate genotypes have evolved from the SHR and BHR groups, which is also apparent in their morphological traits. These intermediate plant types are either the result of interbreeding between SHR and BHR rices or the products of genetic introgression from cultivated rice. However, it is not known whether these intermediate types are more genetically compatible with cultivated rice (thus, with a higher outcrossing rate) than the typical SHR and BHR types.

Red rice samples were collected from red rice contaminated grain rice from all over Arkansas at 11 dryer installations. Because each dryer processes grain rice from the immediate surrounding areas, a dryer can be equated to a subregion generally comprised of two or three rice-growing counties. A total of 55 samples (5/dryer) were genetically fingerprinted using SSR markers together with eight rice varieties, all of which were planted at the same time in fields where the samples originated (Rajguru *et al.*, 2001). The rice varieties were: Bengal, Cypress, Drew, Jefferson, Kaybonnet, LaGrue, Leah and Lemont. As expected, the average GD among rice varieties was lower (0.28) compared with that among red rice samples (0.46). Genetic distance is a measure of genetic variability, with values ranging from 0 to 1. As the GD approaches 0, individuals become closer to being genetically identical. Thus, rice varieties grown in the south of the United States of America are more genetically homogeneous,

FIGURE 3
Multidimensional scale diagram (using GD values derived from RAPD markers) of genotypic clustering of red rice accessions and cultivated rice (Bengal – medium grain; Katy and Kaybonnet rice – long grain)



Source: Estorninos *et al.*, 2006.

TABLE 6
Characterization of red rice in Arkansas, USA

Characteristic	Blackhull	Brownhull	Strawhull
Occurrence (% of total)	15	8	76
Average grain length (mm)	7.9	8.2	7.7
Average grain thickness (mm)	2.0	2.0	2.3
Presence of awn [1]		% of each hull type	
Awned	95	100	6
Awn colour		% of awned type	
Black	100	0	0
Straw	0	100	50
Pink	0	0	50
Average awn length (cm)	5	6	6
Seed production (g/plant)	75–250	150–225	100–275
Predominant seed yield (g/plant)	175–200	150–175	200–225
Panicle length (cm)	22–30	24–30	24–32
Predominant panicle length (cm)	28	28	26–28
Tiller number	80–140	70–130	70–120
Predominant tiller number	120	120	90–100
Plant height (cm)	110–170	120–170	120–150
Predominant plant height (cm)	160	150	140
Canopy structure		**% of each hull type**	
Closed or erect (< 20 °)	28	9	10
Intermediate (20–45 °)	43	64	79
Open (> 45 °)	28	27	12
Flag leaf length (cm)	30–45	35–45	20–55
Predominant flag leaf length (cm)	35	35–40	40
Heat units required to flower	1 042–1 389	1 047–1 307	942–1 401

Notes:
Single plants were grown between May and October 2003 at the Rice Research and Extension Center, Stuttgart, Arkansas, USA.
Data from 136 accessions, with up to ten plants per accession, planted 1 m by 1 m apart. Accessions were collected from the northernmost to the southernmost part of the state with latitudes between 33 and 36.5 °N.
[1] Some panicles have 100 percent of grains with awns while others have grains only at the upper portion of the panicle with awn. Awn length also varies within a panicle.
Source: Shivrain, 2004.

while the red rice populations maintained a high degree of genetic variability. The county or origin (or dryer) had the strongest contribution ($R^2 = 54$) to genetic variability among the red rice samples. In general, red rices were more genetically homogeneous within rather than among locations. Thus, it appears that genotype evolution of red rices is influenced strongly by geographical location, as is commonly known in other species. This localized evolution is manifested to a certain extent by the latitudinal influence on days to maturity of the red rice accessions.

The great diversity in the characteristics of red rices described for Arkansas and the several other adjacent states supports the hypothesis that not all the weedy rices in the United States of America are of the *indica* type, some are probably *japonica* types. Regardless of the subspecies of *O. sativa* to which the red rices are most closely related, it is apparent, as Constantin (1960) noted, that the great diversity of the red rices cannot be accounted for only in terms of contaminated seed rice imported from other countries or exchanged domestically among the rice-producing states. Therefore, the greatest portion of the diversity must derive from natural hybridization between the weedy types, and between them and the continuing succession of rice varieties of different stature, canopy structure, maturity, grain type, etc. The possibility of some of the diversity in red rices emanating from hybridization with entirely different species, i.e. *O. nivara* or *O. rufipogon*, cannot be discounted but it requires more rigorous verification. The practical lesson to learn from the studies on the diversity of red rices is that not all SHR or BHR rices are the same. The populations within each group differ sufficiently to affect management strategies for the control of weedy red rices.

HYBRID SWARMS

The natural crossing of weedy red rices with cultivated varieties is the source of the multiple phenotypes, ecotypes and biotypes observed and reported for more than 100 years. Hybrid swarms segregating for many characters that emerge from the natural white and red crosses could generate hundreds of distinctive troublesome weedy rices with red and white pericarps. However, the fact that this has not occurred raises the questions as to what happens to the hybrid swarms. To put this another way, the question could be posed as to why the common and well-known SHR and BHR complexes have maintained their dominant position for such a long time in the United States of America against the considerable pressures of multiple hybrid swarms produced by the natural crosses. It would seem reasonable to expect that either a great number of distinctive and stable types would arise or that a type or types very similar to the cultivated varieties of rice except in shattering, dormancy, tillering and competitiveness would come to dominance as a result of natural selection aided by unconscious and indirect selection incidental in rice production, e.g. roguing, mechanical harvesting, removal of some types of red rice contaminants during seed conditioning, crop rotation, etc. Another issue relates to why there are not any white-pericarp rices with the typical weedy red rice characteristics infesting rice fields.

Selection pressures on segregates

Definitive answers to most of the questions posed above have not yet emerged. However, the observations made and the data collected in the past 50–60 years provide a basis for speculation. A partial answer may be available to the question as to why selection pressures, direct and indirect, do not produce red rice types that are very similar to the cultivated varieties they infest. They apparently do to a considerable extent, as is evident in the observations and data from the studies of diversity and variability of the red rices in Louisiana, Mississippi and Arkansas. The dominant red rice phenotypes infesting Louisiana rice fields in the 1950s were, first, the SHR types (61 percent) and, second, the BHR types (25 percent). In the Mississippi study 20 years later, 69 percent of the red rices collected were of the SHR group and 25 percent were BHR types. In the most recent and comprehensive survey in Arkansas in 2002–04, 76 percent of the red rices collected were of the SHR group while only 15 percent were of the BHR group. Most of the dominant SHR rices surveyed in the three states in the nearly 60-year period were awnless, while essentially all of the BHR types were conspicuously awned. Overall, the dominant awnless SHR types are much more similar in general appearance to the cultivated varieties and, thus, less noticeable during inspections and roguing than are the generally taller, more erect BHR awned types. Furthermore, there is some indication in the results of the three surveys that the dominance of the SHR type is increasing, up from 61 percent in the 1960 survey to 76 percent in the 2002–04 studies. On the other hand, the more distinctive and easily recognized BHR types appear to be diminishing, down from 25 percent in the 1960 and 1982 studies to 15 percent in the 2002–04 studies. Therefore, these results suggest that the SHR rices are dominant because of direct, indirect and unconscious selection towards the cultivated varieties without loss of the crucial weedy traits of seed shattering, dormancy, vegetative vigour and competitiveness. On the other hand, the two rather distinctive SHR rices in the 1982 Mississippi studies that mimicked the cultivated rice except for conspicuous height (above), e.g. they had glabrous leaves, erect stems, compact panicles, and long awnless grain, were apparently not very successful as weeds because they did not retain the crucial weedy traits. They produced relatively few tillers, were relatively resistant to shattering, seed dormancy was not very intense or persistent, and they were conspicuously tall, which would attract the attention of inspectors and roguing crews.

Among the most interesting and revealing red rice phenotypes in the Mississippi studies were the 86/1, 88/1, 89/1, 90/1 and 90/2 entries collected in the period 1986–1990 (Table 2). These five entries, collected 7–12 years later than the basic collections in the late 1970s, were uniform and stable with erect leaves and strawhull grains, 3 entries had long grains and 2 had medium grains, 2 entries had short awns and 3 were awnless, 3 entries shattered early and heavily, 2 shattered moderately, 4 were glabrous and 1 was pubescent, and all were 95 cm or shorter in height with 3 of the lines the same height as the new (in the 1980s) semi-dwarf varieties, represented by the variety Lemont. These five red rice lines probably originated from crosses between a common red rice, probably the most common SHR phenotype, and one of the semi-dwarf varieties that began to replace the Starbonnet stature varieties in the mid-1970s. They were probably imported in seeds of the Lemont variety from another state, where natural and unconscious indirect pressures associated with cultural practices had produced some red rice phenotypes that mimicked the new semi-dwarf varieties with three of the phenotypes very similar to the semi-dwarf Lemont. Mimics are not restricted to intraspecific variants. A herbicide-resistant watergrass, *Echinochloa phyllopogon*, that infests rice fields in California, is referred to as "mimic" grass because it resembles rice both in appearance and ability to detoxify certain herbicides (Katz, 2005).

Cragmiles (1978) pointed out that most of the main morphological and physiological traits that distinguish red rices from cultivated rices, e.g. the red pericarp, pubescence, early and heavy shattering, intense and persistent dormancy, tallness, later maturity, vegetative vigour, and lighter green colour, are genetically dominant over their alleles in cultivated rice. Thus, it is not surprising that new red rice types can and do arise as a result of natural crossing.

Other ideas on the hybrid populations

There are several ideas, hypotheses and beliefs that relate to the hybrid populations from cultivated and red or wild rice and the fate of segregates. One set of ideas based on the work of Oka and Chang (1959), De Wet and Harlan (1975) and the studies of competition in rice by Jennings and Aquino (1968) was summarized by Noldin (1995): "... hybridization between rice and red rice would produce a population with large genetic diversity, but this variability would be reduced by natural selection, including the cultivation pressure. … ecotypes (of red rices) resembling rice cultivars are at a selective disadvantage in competition with rice cultivars. The natural selection for adaptability to the environment leads to reduced fitness, and rapid elimination of these forms thus occurs."

On the other hand, Langevin, Clay and Grace (1990) felt that natural crossing of cultivated and red rices could result in the "natural selection" of red rice types with many characteristics of cultivated rice that enhance their adaptability and competitiveness, and, thus, the difficulty of their control. This idea is in general agreement with that of Galli, Terres and Him (1982), who contended that weedy races of crops that are phenotypically similar but genetically dissimilar to the crop are most successful. Earlier, Jodon (1959) had observed that because red rice cross-pollinates "readily with ordinary rice" this hybridization would be expected to give rise to innumerable types of red rices but it had not (up to 1959). He then noted that there were only a few types of red rice and that they resembled each other more than they resembled cultivated varieties. In his opinion, the reason why red rice types are not more numerous is that: "…red rice hybrids (with cultivated rice) are later maturing than either parent. Consequently, a field is usually cut (harvested) before the hybrids can mature seed. In a sense, they are self-eliminating."

The fate of the segregating swarms from red × white hybrids and the reciprocal is an important issue in developing strategies for controlling red rices. It is addressed later in this chapter and in Chapter 6 because the most reasonable explanations of the fate of the segregates involve the three "weedy" traits discussed in subsequent sections and their interactions that appear to be critical for the success of a red rice types as weed.

Extent of natural crossing in rice

Rice is self-pollinating but, as is the case for other self-pollinating crop species, plant breeders have long known and acknowledged that the incidence of cross-pollination is significant and has to be considered in their work. The hybridization of weedy rices (including red rices) with cultivated rice has been reviewed comprehensively by Gealy (2005) and is discussed in the next section. Only a few of the classic studies of outcrossing in rice are introduced here along with findings that have generally been accepted. In 1938, five scientists undertook cooperative research to determine the extent of natural crossing in rice in the main rice areas in the United States of America (Beachell *et al.*, 1938). From the literature available to them, they learned that natural crossing in South Asia ranged from 1.1 percent in Burma (now Myanmar) to 4 percent in Bengal for cultivated varieties but up to 8 percent or higher for wild rices. The incidences of natural crossing in rice in other rice areas in Asia had been reported to be about 1 percent in Japan, 1.3–4 percent in Java, 2.4 percent for panicles bagged together in the Philippines and 0.07 percent in Ceylon (now Sri Lanka). Their experiments in the United States of America involved natural crossing of "normal" and glutinous rice varieties planted in adjacent rows in California, Texas, Louisiana and Arkansas. The results obtained indicated that the incidence of natural crossing varied among varieties, locality, distance, seasonal and environmental conditions, and was generally higher in the humid southern states than in California. Overall, the extent of natural crossing ranged from 0 to 3.39 percent, with an average of 0.45 percent for all locations. A later report from Malaya (now Malaysia) also indicated a 0.45-percent rate of crossing among varieties in that country (Brown, 1957). Jodon (1959), one of the authors of the multilocation experiments on natural crossing in rice, later discussed natural crossing in rice based on his experiences and observations in Louisiana. He stated that natural cross-pollination takes place between rice varieties or red rices growing close together and flowering at the same time at about a 1-percent rate for plants 30 cm apart. He speculated that about half of the panicles in a rice field bear one or more seed resulting from fertilization by pollen from another nearby plant. If the "nearby plants were a red rice and cultivated rice", the progeny would be a white × red intervarietal hybrid or the reciprocal.

The progress on development of herbicide-resistant varieties of rice for control of red rice and other weedy grass weeds that are developing resistance to various herbicides has stimulated much research on gene flow between cultivated varieties and weedy rices. The study by Langevin, Clay and Grace (1990) on the incidence and effects of crossing between cultivated rice and red rice in Louisiana was among the first in the new biotechnological perspective. They found that the percentage of natural crossing between red rice and selected rice varieties ranged from 1 percent for the Lemont variety, an incidence in line with the long-held view based on the studies and experiences of Beachell *et al.* (1938) and Jodon (1959), to an apparent 52 percent for the variety Nortai, which they attributed to the near synchronous flowering between the two lines. However, Gealy, Mitten and Rutger (2003) later suggested that this uncharacteristically high rate of outcrossing may have overestimated the actual crossing rate, at least in part, as a result of to the indirect assessment method used. Populations from the natural crosses were most frequently medium grain, taller and later in maturity than the cultivated parent. Studies on the hybridization of red rice with cultivated rices in the south of the United States of America accelerated in the late 1990s with the imminent release of the Clearfield rice varieties resistant to the herbicide imazethapyr. The NRRC has been at the forefront of much of these studies. Research there and at other institutions in the region are reviewed and discussed in the next section. Chapter 7 provides additional discussion on the incidence and risks of crossing between rice varieties and herbicide-resistant varieties.

HYBRIDIZATION OF RED AND CULTIVATED RICE IN THE UNITED STATES OF AMERICA

Red rice in the United States of America is genetically and morphologically diverse. While weedy rices were probably introduced into the United States of America as contaminants in imported seed, only limited kinds would have arrived via this channel. Natural genetic mutations also occur in plant populations, but the frequency of this is very low and could not possibly account for the extent of variability observed in red rice. The most plausible explanation for such variability among the weedy types is genetic introgression from cultivated plants, along with the original introductions of different weedy biotypes. The earliest surveys of rice fields in Louisiana yielded evidence that cross-fertilization between rice and red rice occurs, giving rise to plants with intermediate grain colours. The majority of red rice grains have a dark-red colour, but some have a lighter tint of shade between dark red and white (Dodson, 1898). Sometimes, only the seed coat is red and sometimes the red colour penetrates the endosperm. Historic red rice surveys indicate that the colour of red rice grains ranges from dark red to pink or light red (Kennedy, 1923, Williams, 1956). Many varieties of weedy rice in rice-growing countries worldwide exhibit a range of colour variation in seed. Indeed, data obtained over time on red rice in the United States of America support the hypothesis that rice and red rice hybridize naturally, albeit at low rates. In genetic studies with *O. sativa*, red pericarp colour has been established as a dominant trait controlled by two complementary genes (Adair and Jodon, 1973; Bres-Patry *et al.*, 2001). Other key dominant weedy traits are tall stature, high tillering capacity, grain shattering, pubescence, and dormancy (Cragmiles, 1978).

Some of the progeny from hybridization of red and cultivated rice are eliminated early from the hybrid swarm because of some undesirable trait, i.e. lateness or inability to mature before frost, reduced seed production, infertility, loss of the shattering trait, and reduced intensity of seed dormancy. Many fail to become established because of traits that reduce competitiveness, such as short stature, few and weak tillers, low leaf area, and tendency to lodge early. A few become established with most of the key traits of the dominant weedy parent and develop into relatively distinct types of weedy rice, usually with the red pericarp. Still fewer might evolve over time into a novel white-pericarp rice variety. As noted above, two of the stable SHR rices collected from seed rice fields in Mississippi had relatively few tillers, glabrous leaves, erect stems, and long grains – traits of cultivated rice (Do Lago, 1982). These two red rice mimics of cultivated rice have not become established as successful weeds, probably because they have few of the traits of the weedy rices. However, there is no doubt that many of the widespread and troublesome types of red rices in the south of the United States of America with dominant weedy traits also evolved from natural crossing of red and cultivated rice.

Genetic introgression into red rice

Oryza sativa is primarily self-pollinated. Anthers release their pollen just before the flowers open, but outcrossing can and does occur when the anthers remain exserted after the flowers close (Yoshida, 1981). Table 7 summarizes the main findings of the review of studies on the outcrossing of rice and red rice in the United States of America.

In Arkansas, Louisiana, Texas and California, outcrossing between synchronously flowering rice cultivars separated by 0.3–1 m averaged 0.45 percent overall with a maximum of 3.4 percent, and was detected at distances up to 9 m (Beachell *et al.*, 1938). Outcrossing was lower in California (0.16 percent) than in the south of the United States of America (0.52 percent). In recent studies, the maximum natural outcrossing between adjacent plants of herbicide-resistant rice and non-resistant rice in California, Louisiana and Texas ranged from 0.08 to 0.11 percent and was not detectable at separation distances of more than 1.8 m.

Floral synchronization is the key to *O. sativa* outcrossing because pollen can remain viable for only a few minutes once released into the environment (Yoshida, 1981). The greater the temporal separation between flowering of two rice plants the lower will be the probability of outcrossing. However, late flowers on an early-flowering plant could be available to outcross with early flowers on a late-flowering plant. Outcrossing between rice and red rice can proceed with either type as pollen donor or pollen acceptor, but red rice (usually taller) seems to be the dominant pollen donor (Estorninos *et al.*, 2003b; Zhang *et al.*, 2003). The height advantage for red rice seems the most logical explanation, but differential floral characteristics in rice and red rice could also be involved. The dominance of red rice as the pollen parent is not advantageous for the evolution of new red rice types. The survivability of the progeny would be diminished considerably as most of the hybrid seeds in the non-shattering panicle of the cultivated variety would be removed from the field with the harvested grain, and the few that shattered to the ground at harvest would have little dormancy and germinate and succumb to freezing temperature during the winter season. On the other hand, outcrossing with red rice as the pollen acceptor, i.e. female parent, would favour survival of the progeny and the evolution of new red rice types because many hybrid seeds formed in the early and easy shattering red rice panicle would shatter to the ground before harvest or as a result of harvesting, and many of these would survive the winter in the dormant condition. Maximum outcrossing rates between red rice and rice in the United States of America have ranged from undetectable (Estorninos *et al.*, 2003b; Zhang *et al*., 2003) to as high as 3.2 percent in an imidazolinone-resistant rice field in southwest Louisiana with poor red rice control (Zhang *et al*., 2004). With the exception of a single report of 3.2 percent crossing, the maximum outcrossing rates determined have been 0.7 percent or less. Flowering synchronization, plant height differentials, floral anatomy, red rice population, and environmental conditions probably all contribute to the variations in outcrossing rates reported and summarized in Table 7.

Outcrossing between Clearfield rice and red rice

(Note: Clearfield is the registered trademark of BASF for the crop production systems consisting of varieties that are resistant to imidazolinone [IMI] and of its IMI herbicide Newpath®. The Clearfield system varieties have the prefix CL before the variety number/name.)

In commercial fields of Arkansas, outcrossing between Clearfield rice and red rice was detected in 3 of 7 fields infested with BrHR rice, 5 of 8 fields infested with SHR rice, and 4 of 6 fields infested with BHR types (Table 8). This information was derived from a maximum of 100 escaped red rice plants sampled per field at maturity. Because outcrossing is strongly dependent on flowering synchronization, it can be deduced that the BrHR has the least overlap with Clearfield rices in flowering. The outcrossing rate differed among red rice biotypes. In general, BrHR rice showed the highest

TABLE 7

Outcrossing from rice to rice and from rice to red rice under conditions in the United States of America

Pollen acceptor / pollen donor	Location [1]	Outcrossing rates and separation distances	Reference
Rice – rice outcrossing			
O. sativa rice cultivar / *O. sativa* rice cultivar	Stuttgart, AR; Crowley, LA; Beaumont, TX; Biggs, CA	Distance: 0.3–1 m	Beachell *et al.*, 1938
		Outcrossing rate: 0.45% overall average; 3.4% maximum; 0.16% in CA	
		Distance: 9 m (TX only)	
		Outcrossing rate: 0.0–0.3%	
O. sativa non-resistant 'Cypress' / *O. sativa* gluphosinate-resistant rice cultivar (LLRICE62; variety, LL401)	Crowley, LA, and	Distance: 0–21 m from edge of gluphosinate-resistant rice	P. Shannon & S. Linscombe, personal communication, 2004 (as cited in Gealy, 2005)
	Beaumont, TX	Outcrossing rate: undetectable	
		Distance: adjacent plants (resistant and susceptible rice)	
		Outcrossing rate: 0.08%	
		Overall average: 0.0051%	
O. sativa susceptible rice cultivar (M202) / *O. sativa* gluphosinate-resistant M202.	Biggs, CA	Distance: < 0.5 m; alternate row design plus mechanical pollen dispersal	Fischer *et al.*, 2004
		Outcrossing rate: 0.010–0.216%	
		Distance: 0.3–15 m; circular design with concentric rings of susceptible rice from central herbicide-resistant rice pollen donor area	
		Outcrossing rate: 0.007–0.108%; undetectable > 1.8 m from transgenic rice source	
O. sativa susceptible rice cultivar / *O. sativa* gluphosinate-resistant rice cultivar	Robbins, CA (Davis, CA)	Adjacent plants: 0.1% outcrossing	Johnson, Roberts & Mitten, Bayer Crop Science, 2001 (as cited by Gealy, Mitten & Rutger, 2003)
		At 1.5 m: 0.01% outcrossing	
		At > 1.5 m: undetectable	
Red rice –- rice outcrossing			
O. sativa gluphosinate-resistant rice 'CPB6' and *O. sativa* susceptible cultivar 'Purple Haze'/ red rice (strawhull); also their reciprocal crosses	Baton Rouge, LA	Distance: 0.08–0.25 m	Zhang *et al.*, 2003
		Outcrossing rates: gluphosinate-resistant rice / red rice = 0.33%	
		purple rice / red rice = 0.7%	
		red rice / gluphosinate-resistant rice = undetectable	
		red rice / purple rice = undetectable	
O. sativa red rice ecotypes (8 different types) / *O. sativa* gluphosinate-resistant rice 'Bengal', 'Gulfmont' or 'Cypress'	Fayetteville, AR	Distance: < 0.25 m	Wheeler & TeBeest, 2001
		Outcrossing rate:	
		Overall average = 0.0146%	
		Maximum outcrossing = 0.37% (with blackhull red rice 10A / gluphosinate-resistant 'Bengal').	

Note: Significant overlapping of flowering periods was observed in the species pairs tested. In a hybrid produced from the cross 'a' / 'b', plant 'a' was the female and plant 'b' the male.

[1] AR = Arkansas; CA = California; LA = Louisiana; TX = Texas.

Source: Data modified from Gealy (2005).

TABLE 7

Outcrossing from rice to rice and from rice to red rice under conditions in the United States of America (continued)

Pollen acceptor / pollen donor	Location [1]	Outcrossing rates and separation distances	Reference
O. sativa red rice / *O. sativa* IMI-resistant rice cultivar	Stuttgart, AR	Distance: 0–6 m Outcrossing rate: Volunteer plants: CL121 = 0.003%; CL161 = 0.007% Hand-collected samples: CL121 = 0.01%; CL161 = 0.02%	Shivrain *et al*., 2006a
O. sativa red rice / *O. sativa* IMI-resistant rice cultivar	Stuttgart, AR	Distance: intermingled plants in natural infestation Outcrossing rate = 0.012%	Estorninos *et al*., 2002a
O. sativa red rice / *O. sativa* IMI-resistant rice (CL 121 and CL 141).	12 commercial imidazolinone-resistant rice field sites in southwest LA in 2002 and 2003	Distance: intermingled plants in natural infestation Outcrossing rate 2002: Average of all sites = 0.17% Maximum (site had poor red rice control) = 0.58% Outcrossing rate 2003: Average of all sites = 0.68% Maximum (site had poor red rice control) = 3.2%	Zhang *et al*., 2004; W. Zhang, personal communication, 2005
O. sativa red rice (Stuttgart Strawhull) / *O. sativa* IMI-resistant rice cultivar (CL121 and CL141 [same as CL3291]) Not possible to determine which plant type was the pollen donor and which was the pollen acceptor.	Stuttgart, AR	Distance: intermingled plants in natural infestation Crop grown in 2000. Area sprayed with imazethapyr in 2001. Outcrossing rate: CL121 (mostly coincident flowering) = 0.0013% CL141 (flowering mostly non-coincident) = 0.0016% Red rice seed production was estimated indirectly which may overestimate or underestimate outcrossing rates.	Estorninos *et al*., 2003a
O. sativa red rice (blackhulled and strawhulled, respectively) / *O. sativa* susceptible cultivars 'Kaybonnet' and 'Starbonnet', respectively; including reciprocal crosses.	Stuttgart, AR	Distance: In 2000, rice and red rice pairs with coincident flowering grown in adjacent rows Outcrossing rate: Kaybonnet / blackhulled red rice: 0.10% blackhulled red rice / Kaybonnet: 0.0% Starbonnet / strawhull red rice: strawhull red rice / Starbonnet: 0.14%	Estorninos *et al*., 2003b

Note: Significant overlapping of flowering periods was observed in the species pairs tested. In a hybrid produced from the cross 'a' / 'b', plant 'a' was the female and plant 'b' the male.
[1] AR = Arkansas; CA = California; LA = Louisiana; TX = Texas.
Source: Data modified from Gealy (2005).

TABLE 8
Estimated outcrossing rates between Clearfield rice (CL161) and different biotypes of red rice in commercial fields, Arkansas, USA

Red rice biotype	No. of fields sampled[1]	Fields with outcrossing	Range of outcrossing[2]	Average outcrossing
			(%)	
Blackhull	6	4	0.070–1.441	0.434
Brownhull	7	3	0.241–1.887	0.763
Strawhull	8	5	0.015–0.188	0.109
Overall average				0.435

[1] Panicles of up to 100 individual plants were collected in 2004 from 12 fields. Some fields were infested with more than one biotype of red rice. Seeds collected were planted in 2005, sprayed with 0.07 kg ai/ha imazethapyr post-emergence, three times at weekly intervals starting at V2, and tissues were collected from survivors for genetic assay.
[2] Percentage of outcrossing was estimated by dividing the number of confirmed hybrids by the number of red rice sprayed per sample.
Source: Data from an ongoing experiment by Burgos *et al*., unpublished.

outcrossing rate (0.763 percent), SHR rice the lowest rate (0.109 percent), and BHR types an intermediate rate (0.434 percent). Thus, although gene flow between BrHR rice and Clearfield rice occurred with the lowest frequency among fields, the degree of outcrossing in fields where it did occur was higher than with the other red rice biotypes. It may be of some consolation to both rice growers and weed scientists that SHR rices, which comprise about 80 percent of the red rice population, have the lowest outcrossing rate among the red rice biotypes. The degree of outcrossing detected in commercial fields was generally higher than that detected in small-plot research. This could be because of the higher pollen load in commercial fields than in mini-plots. A significant difference in outcrossing rate was also observed between Clearfield varieties: the outcrossing rate for CL161 with SHR rice was 0.008 percent compared with 0.003 percent between CL121 and SHR rice (Shivrain *et al.*, 2006a). Effective pollen flow from Clearfield rice was observed up to 6 m from the interface with SHR rice. The largest number of hybrids was found at the interface, which had an average outcrossing rate of 0.003 percent in experimental plots planted with CL161. The number of hybrids declined drastically at the 1-m distance to an average outcrossing rate of 0.001 percent. Beyond this distance, a very low, random number of hybrids (between 0 and 2) were detected at every metre beyond the interface.

Therefore, the recommended separation distance for rice seed production fields of 10 m is needed and justified (Khush, 1993). However, outcrossing has been documented up to 43 m between Minghui-63 and *O. rufipogon* in China (Song *et al*., 2003). Thus, several factors, some unidentified and some poorly understood, play a role in effective pollen flow and the resultant rate of outcrossing.

Characteristics of progeny from red and cultivated rice crosses

Distinctively different F_1 plant types are produced from crosses of cultivated rice with awnless red rice, e.g. late maturity, no awns, normal green lower stems or basal leaf sheaths, and medium-grain red seeds, than with awned BHR and or awned SHR rices, e.g. normal maturity, pink awns, purple lower stems, and medium-grain red seeds (Gealy, 2005). An understanding of the phenotypic traits expected in F_1 and F_2 hybrid populations can assist growers, agricultural professionals, and millers with red rice identification and management decisions. In studies of hybridization between Clearfield rice and SHR rice (Burgos *et al*., 2006b), the F_1 plants were distinctively taller than the rice or red rice parent and had leaves that were pubescent like red rice but erect like the cultivated rice parent (Plate 13). Hybrid vigour was also apparent in the crosses. The F_1 plants were 40–50 percent taller than the Clearfield parent regardless of the Clearfield variety used and the red rice parent, which averaged 110 cm in height,


N.R. BURGOS, 2005

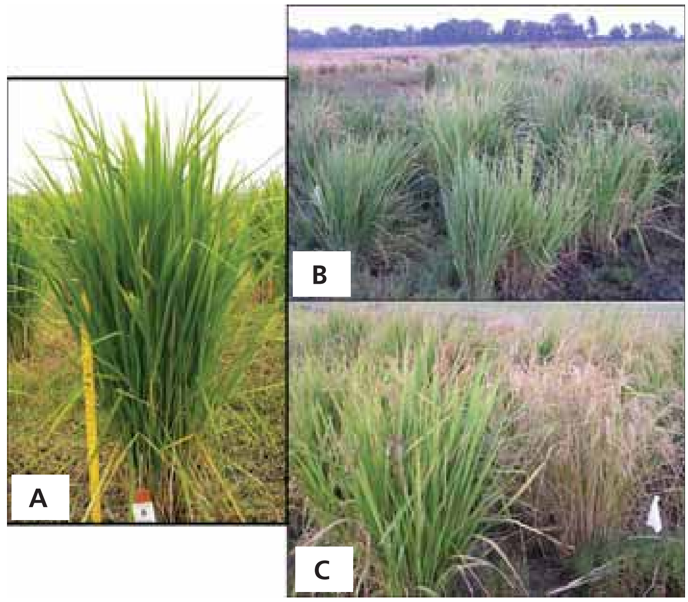
Plate 13
Typical F_1 phenotype of hybrids between Clearfield rice and red rice. Regardless of red rice parent, F_1 are generally taller, more vigorous, and more erect compared with the red rice parent.

and produced 45 percent more tillers than the Clearfield and red rice parents. Hybrids were confirmed each time an outcrossing experiment was conducted. All F_1 plants flowered later than their parents, which were 98 and 102 days after planting (DAP) for the SHR and CL161 variety, respectively. None of the hybrids with red rice as the female parent flowered within the normal growing season in the field. The phenology of the hybrids was maternally influenced because CL161 × red rice hybrids flowered 90 DAP, which was earlier than either parent. Spontaneous crosses between Clearfield rice varieties (CL121 or CL161) and SHR rice also produced essentially the same F_1 phenotypes as was observed with controlled crosses (Shivrain *et al*., 2006b). These results differ from those of another study (Gealy, Yan and Rutger, 2006) in which long-grain rice varieties pollinated by SHR rice produced F_1 plants that flowered later than either parent, and from the generally and long-accepted view of Jodon (1959) that "red rice hybrids (with cultivated rices) are later maturing than either parent." Regardless of this, in growers' fields, the crosses with red rice as the female parent are the most important because, as mentioned above, the hybrid seeds shatter and infest the field whereas the hybrid seeds produced with cultivated rice as the female parent are mostly harvested with the grain and removed from the field.

As noted above, the outcrossing rate between red rice and the Clearfield rices was affected strongly by variety, with CL161 having twice the outcrossing rate of CL121 (Shivrain *et al*., 2006a). As CL121 is earlier maturing and more closely synchronized in flowering with the SHR rice than the CL161 variety (Burgos *et al.*, 2004), the higher rate of outcrossing of the latter may have been related to its greater height and/or floral morphology. The hybrids between red rice and the Clearfield rices were all resistant to the imazethapyr herbicide and rather easy to spot in a rice field. They generally flowered very late, so that many of the seeds would not mature before the onset of cold weather. However, if the crop is planted and harvested early enough, or if warm days extend well into the autumn season, the late hybrid plants could head, flower and set seeds that are viable within about two weeks.

Resistance to the imazethapyr herbicide is inherited as a partially dominant gene (Shivrain *et al*., 2006b; Burgos *et al*., 2006b). About 50 percent of the F_2 plants will survive a herbicide application, while 25 percent of the population will exhibit an intermediate level of resistance. However, the F_2 plants will segregate into various plant types, some of which are shorter than the rice variety while others are much taller than the red rice parent (Plate 14). In continuing but unpublished work, about 5 percent of the F_2 plants were very short (80 cm or less), 25 percent were almost as tall as the CL161 parent, and the rest were much taller than commercial rice or the strawhull red rice parent. The phenology of F_2 plants also ranges from extremely early to extremely late, with the majority flowering 90–100 DAP, which is close to both parents. Some of the plant types with characteristics that are compatible with rice culture and critical weedy traits, e.g. shattering and dormancy, could in time evolve into stable populations, become established and contribute to the diversity of weedy rices. If such populations carried herbicide-resistant genes, the assemblage of red rice types in the south of the United States of America would be augmented by herbicide-resistant types.

In studies with F_2 plants derived from manual crosses between red rice and transgenic gluphosinate-resistant rice or non-transgenic, non-herbicide resistant rice, phenotypic characteristics such as seed germination and shattering varied widely, were often intermediate between the rice and red rice parents, and were not more weedy (e.g. dormant or shattering) than their original red rice parents (Oard *et al.*, 2000). Thus, only the herbicide-resistance trait was a major contributor to increased fitness in red rice populations derived from crosses with transgenic rice.



N.R. BURGOS, 2003 AND 2004

Plate 14
Expected phenotypes from crosses between herbicide resistant Clearfield rice and strawhull red rice. A: F_1 phenotype; B and C: segregation of F_2 plants into a wide range of plant heights and maturity periods. An extremely early plant and an extremely late plant are shown in C.

Summary

Summarizing studies on the natural crossing between cultivated and red rice in the south of the United States of America, Gealy and Estorninos (2004a, 2004b) noted that, while outcrossing rates between red rices and conventional or herbicide-resistant varieties have been variable, they have nearly always been less than 0.5 percent. The specific rate of outcrossing appeared to be influenced by many factors: the rice variety, the red rice ecotype, vertical and horizontal distances between panicles, synchronization of flowering, and aspects of the environment that are not well understood. This earlier work and the more recent studies reviewed in this chapter can be summarized as follows. Red rice in the United States of America is phenotypically and genetically diverse as a result of: multiple introductions of weedy red rices in contaminated imported seed during the nascent stage of rice culture in the United States of America; the natural hybridization among the imported red rice types and their progenies; and the natural hybridization between a succession of weedy red rice types and a succession of cultivated rice varieties. The herbicide-resistant rice technology already on-stream is a powerful tool for the management of red rice infestations in rice fields. However, it must be used in accordance with the protocols and recommendations that accompany the technology and with the other tools (cultural, chemical and regulatory) for managing weedy red rices in order to provide for and ensure sustainable control of red rice.