02

PERENNIAL RICE: CHALLENGES AND OPPORTUNITIES

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ABSTRACT

As the human population continues to grow, and governments increasingly incentivize the migration of people from rural areas to cities, there is pressure to produce more food with fewer resources, including water, fertilizer, and especially labour. The development of high-yielding, perennial cultivars of rice could help meet the need for more food while reducing the inputs required. Domesticated Asian rice (*Oryza sativa*) was derived from perennial ancestors. Moreover, the traditional practice of ratoon cropping demonstrates that domesticated Asian rice retains some of its original perennial character, though this varies greatly by cultivar. However, with currently available cultivars, the yields of first ratoon crops are typically 40 percent or less of main crop yields and subsequent decreases make further cycles of ratooning uneconomical. Thus, the key research and development challenges for perennial rice are to improve ratoon yields, increase longevity, and improve drought tolerance with the goal of facilitating perennial rice regrowth and production beyond irrigated systems and into seasonally dry upland and rainfed lowland environments. Opportunities (in order of increasing difficulty and potential gain) for developing high-yielding cultivars of perennial rice include: 1) breeding within domesticated Asian rice germplasm for improved ratooning ability and yield, 2) introgressing genes from the perennial, rhizomatous A-genome species *O. longistaminata*, 3) domesticating the rhizomatous species *O. longistaminata* and *O. australiensis*.

Keywords: perennial rice, *Oryza sativa*, *O. longistaminata*, ratoon, introgression

INTRODUCTION

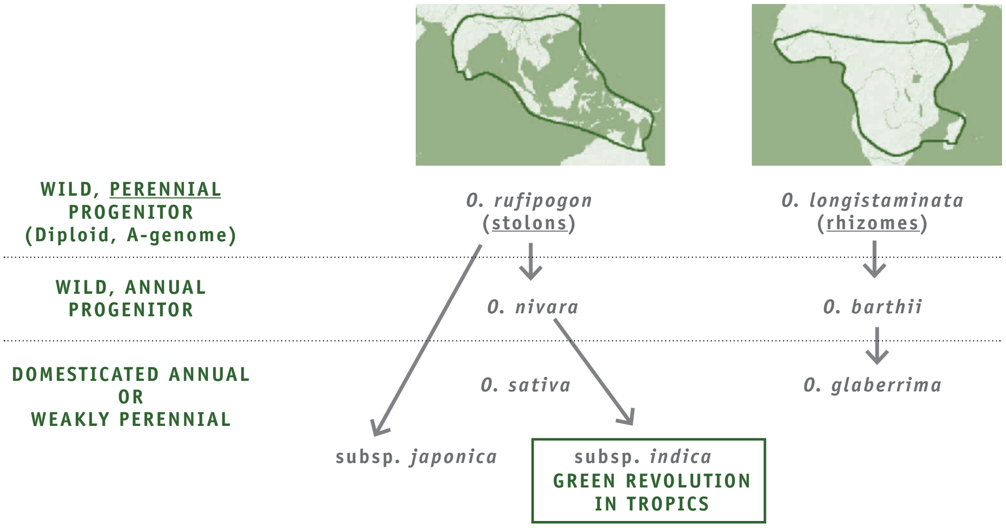
Many rice cultivars grown today are perennials that are cultivated as annuals (Figure 1). Genotypes of *Oryza sativa* vary greatly in their propensity to ratoon (regrow) after an initial harvest of grain (Chauhan *et al.* 1985; Krishnamurthy, 1988). Ratoon cropping of rice was a traditional practice, especially in East Asia (Hill, 2010), that became less common during the second half of the twentieth century. However, a notable modern exception has been an emphasis on ratoon crop production in the United States Gulf Coast to increase overall seasonal yields (Bollich and Turner, 1988), which is an economically viable strategy where warm weather persists long enough for a ratoon crop but is insufficient in duration for a new planting from seed to mature.

FIGURE 1. A RICE FIELD IN JAPAN DURING AUTUMN SHOWS VIGOROUS REGROWTH AFTER HARVEST OF THE FIRST CROP

Cool weather prevents development and harvest of a ratoon grain crop at this location.

Both species of domesticated rice, *O. sativa* from Asia and *O. glaberrima* from Africa, are derived from perennial ancestors, either directly or via an annual intermediary (Figure 2). Cheng *et al.* (2003) found that the progenitor species of *O. sativa*, *O. rufipogon*, consisted of four major clades, three of which were perennial and one of which was annual (the annual clade is sometimes referred to as *O. nivara*). Moreover, Cheng *et al.* (2003) found that the *indica* subspecies of *O. sativa* was derived from the annual *O. rufipogon* clade and that the *japonica* subspecies was derived from one of the perennial *O. rufipogon* clades. Though there is currently much debate about whether *O. sativa* was derived from a single or multiple domestications, the results of Cheng *et al.* (2003) are consistent with observations of some workers that *japonica* cultivars are typically better than *indica* cultivars for ratooning (Shahi and Raharinirian, 1988) and as parents for breeding strongly perennial rice (Sacks *et al.* 2007). In the Southern United States, which is the primary example of successful ratoon cropping of rice on a large commercial scale, production is based on tropical *japonica* cultivars (Lu *et al.* 2004). Recently, New Rice for Africa (NERICA) cultivars and their japonica parent were found to have higher ratoon yields under upland conditions than their *O. glaberrima* parent (Sanni *et al.* 2009). However, some of the green revolution *indica* cultivars, such as IR8 and IR64, have also been observed to ratoon well (Chauhan *et al.* 1985; Munda *et al.* 2009). In any case, it is clear that there is considerable genetic diversity within *O. sativa* for perennial growth, and additional diversity is present in its wild relatives, *O. rufipogon* and *O. longistaminata*. Perennation in *O. sativa* is by growth of axillary buds on older tillers (i.e. tillering), whereas *O. rufipogon* can additionally propagate from stolons, and *O. longistaminata* produces many long rhizomes that are the primary source of new shoots.

FIGURE 2. ORIGINS OF DOMESTICATED RICE IN RELATION TO PERENNIAL GROWTH



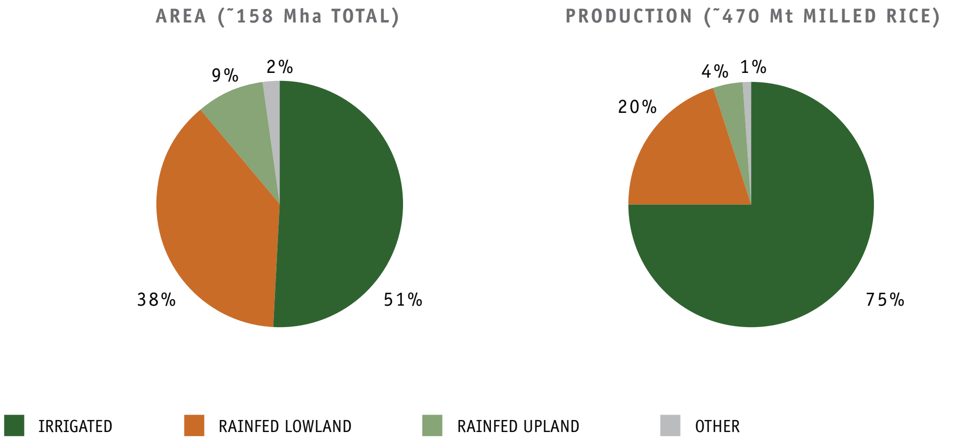
Source: http://www.knowledgebank.irri.org/extension/wild-rice-taxonomy.html

PROBLEMS THAT PERENNIAL RICE COULD HELP SOLVE

Rice is a critically important staple food and the demand for more production is expected to continue to increase, especially in developing countries. Deployment of perennial rice could meet important needs, such as increased production per growing season, reduced risks for farmers, lower labour requirements, less water needed, and protecting soil from erosion.

Irrigated rice accounts for 51 percent of the area planted to rice but 75 percent of rice production (Figure 3). In contrast, rainfed lowland rice accounts for 38 percent of the area but just 20 percent of production, and rainfed upland rice accounts for 9 percent of rice lands but only 4 percent of production (Figure 3). Thus, a major challenge for improving availability of rice is to increase production in rainfed systems. Where rainfed fields in tropical monsoonal environments cannot be converted to irrigated, a potentially valuable strategy for increasing production is to maximize use of rainfall via a ratoon crop. In contrast to annual rice cultivation, ratoon rice could take advantage of end-of-season moisture in a typical year, and also be positioned for even greater yields in wet years. Such a use of season-limiting moisture would be analogous to the use of ratooning in the Southern United States of America to take advantage of end-of-season warmth. Cultivars with tolerance to drought, in addition to high ratooning ability would be especially useful for rainfed production of a ratoon crop. By modifying crop duration from a single long-season crop to a medium duration main crop plus a short-medium duration ratoon crop, it may also be possible to reduce production risks associated with variable abiotic and biotic stress pressures. Adoption of early maturing rice cultivars was critical to the establishment of ratooning in the Southern United States of America (Bollich and Turner, 1988).

FIGURE 3. RICE AREA AND PRODUCTION BY CULTIVATION SYSTEM



Source: http://irri.org/index.php?option=com_k2&view=item&layout=item&id=9151&lang=en

Field preparation and planting of paddy rice, typically via initial establishment of seedbeds followed by transplanting of seedlings, is labour intensive. For upland rice, planting and especially weeding can require a major investment of labour. For example, in Central and West Africa, upland rice accounts for ~40 percent of the rice area, but employs ~70 percent of the region's rice farmers (http://irri.org/). As governments increasingly incentivize urbanization, the availability of labour for farm work will continue to be reduced. Thus, there is a great and increasing need to maximize production of rice per unit of labour. Perennial rice enables multiple harvests from a single planting, thereby improving labour efficiency. Though improvements in labour efficiency may be expected via mechanization, such gains come with capital costs that are often too great for many farmers in developing countries, whereas seed of improved perennial cultivars can be made available for little or no additional cost to farmers.

Hybrid rice has brought yield benefits to farmers who can afford to invest in this technology. However, hybrid rice seed is expensive to produce and thus is sold at a premium. If additional production in farmers' fields can be obtained from hybrid rice crops via ratooning, then the return on investment for a farmer would be greater (Bollich and Turner, 1988; de la Rosa, 2004) and this advantage could make it economically feasible for more farmers to adopt.

Water is a major input for rice production. Global climate change is expected to negatively impact availability of water for rice production by reducing winter snow-packs on mountains and by the melting of glaciers that feed rivers used to supply irrigation water for rice fields. It is well established that ratoon crops of rice require less water than main crops, thereby improving the overall efficiency of water use for rice production. Thus, increasing production of rice via cultivating more ratoon crops and increasing ratoon yields would further improve efficiency of water use.

Upland rice cultivation is source of soil erosion. This is especially true for hilly lands, such as those in Southeast Asia, where upland rice is grown in a traditional swidden system or under new plantings of tree crops such as rubber (Figure 4). Erosion of soil in the uplands fills downstream reservoirs with silt, thereby reducing the amount of water available for irrigated rice in the lowlands. Thus soil erosion has negative consequences on a regional level. The cultivation of perennial crops, such as perennial upland rice, would be expected to reduce soil erosion relative to current practices. This goal was the driving force behind the International Rice Research Institute (IRRI) Perennial Upland Rice Project during the 1990s. However, a successful cultivar of perennial upland rice would need exceptional drought tolerance to survive the long dry season that is typical in mainland SE Asia. Development of adapted perennial rice cultivars would be considerably less challenging for areas without a dry season or only a short dry season, than for long dry season environments. For example, in Mato Grosso, Brazil, some modern and high yielding cultivars of upland rice produce good ratoon crops under favourable environmental conditions (Santos *et al.* 2003).

FIGURE 4. UPLAND RICE PRODUCTION ON HILLY LANDS IN SOUTHEAST ASIA

Top: note upland rice on left side of photo among tree stumps from recently cleared land, and also note the large area of soil erosion on the steep area in the centre of the photo. Bottom left: upland rice growing under a new rubber plantation. Bottom right: a new rubber plantation with bare, eroding soil associated with a gap between the cycles of harvesting and planting of annual understory crops.

IMPROVING RATOONING ABILITY AND YIELD WITHIN *O. SATIVA*

Though ratoon cropping is practiced commercially in the southern United States of America and parts of southern China (Bollich and Turner, 1988; Xue-Bin *et al.* 1988), substantial improvements in regrowth ability and yield potential of ratoon crops would be needed for ratoon cropping to compete economically with new plantings from seed/seedlings in areas where conducive environmental conditions do not limit the time available for growing a subsequent rice crop. For those cultivars that can regrow well after harvest of an initial crop, first ratoon yields are typically 40 percent or less of main crop yields and subsequent decreases in yield make further cycles of ratooning currently uneconomical (Chauhan *et al.* 1985; Krishnamurthy, 1988). Thus, a key challenge is to breed cultivars that have high overall yield potential yet have high ratoon yields (at least on a per growing day basis) as well as high main crop yields. Though most ratoon crops have lower yields than main crops, there have been documented cases where both main crop and ratoon crop yields were both high and similar to each other, indicating that a possible path forward is to identify combinations of genotype and environment that result in multiple high yields. Another key challenge is to select genotypes that maintain high yields for more than one ratoon crop. Such a development would be a step-change for rice that would potentially make ratooning an economically attractive option for irrigated production environments that are not limited in duration by cold weather or other season-limiting conditions. High ratooning ability and low rates of missing hills are necessary but not sufficient for achieving high yields for one or more ratoon crops. Other desirable traits for improving ratoon cropping are drought tolerance, cold tolerance (especially at flowering stage for subtropical and temperate environments), duration adapted to the target environment, and highly resistant to pests and diseases.

Little information is available on the genetics of ratooning ability in rice. However, choice of parents can have a large effect, and heritabilities may be moderate to low (Shifen and Tingwen, 1988). Late stage selection is likely to result in slow and modest improvements. For greater and more rapid gains, early generation selection coupled with replication of genotypes would be desirable. Replicated early generation selection could be accomplished with doubled-haploid populations or by vegetatively propagating F_2 individuals.

INTROGRESSING GENES FOR PERENNIAL GROWTH FROM *O. RUFIPOGON* AND *O. LONGISTAMINATA*

Both *O. rufipogon* and *O. longistaminata* are sources of genes for improving perennation in *O. sativa*. Previous studies at IRRI indicated that choice of genotype within both the domesticated and undomesticated parent species has a large effect on the progenies' ability to grow perennially (Sacks *et al.* 2006, 2007). The main advantage of using *O. rufipogon* as a donor of genes for perennial growth to domesticated Asian rice is its high cross compatibility with *O. sativa*. However, stolons, which are the key perennating structure of *O. rufipogon*, are not well-suited to surviving drought because they may be exposed to sun and dry air on the surface of the soil if grown under upland conditions, or under rainfed production during the dry season. In contrast, the rhizomes of *O. longistaminata* are protected from desiccation by insulating soil. Additionally, *O. longistaminata*, which can form large monocultures in the wild, is more vigorous than *O. rufipogon*. Breeding barriers have typically limited the production of F_1 *O. sativa/O. longistaminata* progeny severely, and embryo rescue has usually been required to obtain early generation backcross progeny in large numbers (Chu and Oka, 1970; Hu *et al.* 2003; Ishikawa *et al.* 2011; Tao and Sripichitt, 2000). Moreover, associations between infertility and rhizomatous growth in early generations have required considerable breeding work to break (Chen *et al.* 2009). Recently however, Kanya *et al.* (2012) reported that crosses between *O. sativa* 'Basmati 370' and a Kenyan accession of *O. longistaminata* resulted in the production of over 500 hybrid seed (6 percent success) and that the F_1 hybrids, which germinated without embryo rescue, were remarkably fertile, producing more seed per plant than either parent. It is likely that *O. longistaminata* is the best species source of genes for improving regrowth potential of domesticated rice via introgression, given that it has vigorous perennial growth, great genetic diversity associated with broad geographic distribution and self-incompatibility, and the same A-genome as *O. sativa* (Kiambi *et al.* 2008; Melaku *et al.* 2013). The recent development of a whole genome fosmid library for *O. longistaminata* should facilitate identification and introgression of key genes from this species into domesticated rice (Li *et al.* 2012). Additionally, Shim (2012) has described several breeding strategies for introgressing genes from *O. longistaminata*. Though *O. longistaminata* is a promising source of genes for improving many traits in domesticated rice, few interspecific hybrids between *O. sativa* and *O. longistaminata* have yet been produced. A substantial public collection of *O. longistaminata* germplasm is available but it remains largely untapped.

In a hybrid population of *O. sativa* and *O. longistaminata*, rhizomatous growth was conferred by two dominant complementary genes for rhizome presence and many QTL of modest effect for degree of rhizome expression (Hu *et al.* 2003). Subsequently, candidate genes for rhizome expression were identified by gene expression analyses (Hu *et al.* 2011), which should further facilitate introgression efforts. Diligent breeding work over many years at the Yunnan Academy of Agricultural Sciences has resulted in the production of interspecifc progenies that have both long rhizomes and high fertility. Moreover, non-rhizomatous backcross progenies of *O. sativa/O. longistaminata* have been selected for their ability, under irrigated conditions, to produce three sequential harvests (one main crop and two ratoon crops) from a single planting, yet have high yields for all three harvests. Thus, introgression from *O. longistaminata* is also a useful strategy for improving ratooning in domesticated rice. Further use of *O. longistaminata* accessions and genes is expected to be valuable for rice improvement.

DOMESTICATING THE PERENNIAL RHIZOMATOUS SPECIES *O. LONGISTAMINATA* AND *O. AUSTRALIENSIS*

The main advantage of domestication as a breeding strategy over introgression is that breeding barriers associated with wide crosses are avoided. However, the main obstacle to domesticating a wild species is that desirable alleles for domestication and agronomic traits are in low frequency in the founder population. Thus, domestication can be expected to take considerable time and effort to produce acceptable cultivars for use by farmers. Nevertheless, domestication may be a viable option if breeding barriers will significantly limit introgression, and if many genes are needed from a wild species to achieve a particular breeding goal. For example, adaptation of rice to perennial growth while surviving seasonal drought may be a case in which domestication is the best option. Both *O. longistaminata* and *O. australiensis* have rhizomes which may enable the plants to survive in a dormant state during drought (Henry *et al.* 2010). Though this dormancy response has not been thoroughly explored, we expect that the trait is most strongly expressed in *O. australiensis* because its native habitat is more drought prone than that of *O. longistaminata*. Introgression may be a competitive option for developing drought-resistant perennial upland rice from *O. longistaminata*, but for the E-genome *O. australiensis*, severe breeding barriers to crossing with *O. sativa* would make domestication the only practical option. With their long, vigorous rhizomes and shattering seed, both *O. longistaminata* and *O. australiensis* are potentially invasive, which would be of particular concern outside of their native range. Thus, any domestication efforts would need to select for a moderate rhizome length, which balances the need for survival during drought with the need to minimize potential invasiveness. For initial breeding work to domesticate *O. longistaminata* or *O. australiensis*, a location where the species are native would be most desirable, so as to avoid introducing potentially invasive early generation plants to areas where they are non-native. In addition to reduced rhizome length, domesticated versions of these species would need to be non-shattering, semi-dwarf, and high-yielding. Fortunately, the sequence of many key genes for domestication of *O. sativa*, such as the non-shattering genes *sh4* and *qSH1*, and the semi-dwarf gene *sd1* are known (Konishi *et al.* 2006; Li *et al.* 2006; Monna *et al.* 2002), which should allow for relatively rapid domestication of wild rice species via targeted screening of germplasm and selection.

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