

8 Gene Flow in African Rice Farmers' Fields

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Introduction

West Africa is an important region for rice genetic resources. Here are found two species of wild rice (*Oryza barthii*, *O. longistaminata*) and an indigenous domesticated rice (*O. glaberrima*). In addition, the two subspecies of Asian cultivated rice (*O. sativa*) – *indica* and *japonica* – are extensively cultivated. Collection of wild rice in the Lake Chad basin has been dated to 3500 BP based on archaeological findings of wild rice remains (Klee *et al.*, 2004). It has been proposed that the domestication of African rice (*O. glaberrima*) began about this time, most likely in the upper Niger delta (Portères, 1962; Li *et al.*, 2011). Asian rice has been present in West Africa since at least the 15th century, introduced through cross-continental trading links with the Middle East during the Middle Ages (Carpenter, 1978) or coastal links with the Mediterranean from the arrival of the Portuguese on the West African coast (late 15th century). Since the colonial period or earlier, higher-yielding Asian rice has tended to predominate, especially in areas such as southern Nigeria, where rice is a recent crop. However, in older centres of cultivation – the major valleys of the West African savannah, the upper Guinean coastal region from Senegal to Sierra Leone, and some mountain outliers, such

as the Togo Hills – African rice continues to be present, and is locally important (Barry *et al.*, 2007; Nuijten *et al.*, 2009; Okry, 2011; Teeken *et al.* 2011; Temudo, 2011). In these older, established areas of rice cultivation, wild rice is sometimes still gathered locally (Richards, 1986; Nuijten, 2005).

It is often assumed that in traditional agriculture crops are enriched by gene exchange with wild and weedy relatives (De Wet and Harlan, 1975; Altieri and Merrick, 1987; Prain, 1993), although there seems little hard evidence for the movement of valuable traits from wild relatives into crops (Wood and Lenné, 1997). This, however, does not mean that no new potentially valuable traits arise from introgression (Jarvis and Hodgkin, 1999). Discovering actual gene flow between wild and cultivated species in the field is complicated by the fact that, because of pairing of homologous genes and other processes during meiosis and fertilization, fertile interspecific progenies resemble either the wild or the cultivated species. This is illustrated by research on gene exchange between *O. sativa* and *O. glaberrima* that indicates that as the interspecific hybrids are sterile, backcrosses are needed to restore fertility. Therefore, the fertile hybrid derivatives resembled the parental phenotypes (Sano, 1989). This explains why the

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interspecific rice types found by Nuijten *et al.* (2009) can be divided into two main forms, one morphologically similar to *O. glaberrima* and the other similar to *O. sativa*. This may also explain why, although it is often suggested that farmer crop management plays an important role in gene flow between wild and cultivated rice, the number of studies documenting recognition and selection by farmers of genetic variation arising from natural introgression is limited (Jarvis and Hodgkin, 1999). Maintaining gene flow between wild and cultivated species in farmers' fields may also meet concerns about the reduction of genetic diversity (see Chang, 2003; cf. Sang and Ge, 2007).

The significance of gene flow between cultivated and wild species is placed in a new light by work on a protracted model of crop domestication (Allaby *et al.*, 2008). This model emphasizes the need for more information on how populations of farmers influence gene flow between cultivated and wild species over long periods of time. It is wrong to assume that selection must be based on conscious management strategies by individual farmers. Even 'modern' management systems often depend on what is termed 'distributed cognition' (Hutchins, 1995). No single individual holds an overview of the direction in which collective action develops. Hutchins' (1995) example is the navigation of a modern warship. A model of this kind has been proposed for farmer crop selection, based on neural network engineering concepts of unsupervised learning. In unsupervised learning there is no master plan. The stable states of a network are a function of nodal weightings in a massively interconnected network. Rice farmers in a region such as West Africa, it has been proposed, approximate these network conditions (Richards *et al.*, 2009). From an empirical point of view, information is needed on the weights to be applied to the nodes. (Depending on the scale, nodes can be different actors, among others, farmers, varieties and plants.) Observation of gene flow rates and how farmers' actions influence the direction and amount of these flows is thus a crucial empirical step.

This chapter focuses on how farmers influence gene flow. Conscious management practices could be part of this influence, but not its sum total. We are equally interested in

the unintended consequences of farm management practices unconnected to variety choice, such as decisions over labour allocation that result in a particular field mosaic of planted varieties. This way we try to avoid the pitfall of imposing a breeder's rationale on farmer gene-flow management. Breeders seek to control gene flow according to genetic theory. Farmers weigh the nodes in a gene-flow network in a wide variety of ways, only some of which will be connected with their own (possibly imperfect) ideas about descent and inheritance in planting materials. Since gene flow is, at a biological level, the mechanism of 'extended domestication', detailed information on gene flow patterns in 'distributed' networks is important. The information also has practical consequences for food security in regions where adaptation (e.g. to climate change) depends to a significant extent on farmer seed choice. We need to know whether 'extended domestication' and 'unsupervised learning' remain robust, or whether they have begun to break down due to network fragmentation linked to the spread of market-based seed supply.

The relevance of our focus on documenting gene flow at field level is emphasized by work on the existence of local rice varieties in West Africa with an interspecific *O. sativa* × *O. glaberrima* background, resulting from gene flow between the two species in farmers' fields (Jusu, 1999; Semon *et al.*, 2005; Barry *et al.*, 2007; Nuijten and Van Treuren, 2007; Nuijten *et al.*, 2009). It has been shown that there is regional variation in the occurrence of these local interspecifics. Hybrid-derived farmer varieties do not occur everywhere the two species occur together. For instance, interspecific hybrid-derived rice varieties (so-called farmer hybrids) are much less common in the Togo Hills than in the upper West African coastal areas – especially Casamance, Guinea-Bissau and Sierra Leone (Nuijten *et al.*, 2009). Perhaps the relatively earlier arrival of Asian rice on the upper Guinea coast (Angladette, 1966) has played a part in the development of interspecific varieties as it has increased the window of opportunity for interspecific hybridization. Topography has also played a part in keeping *O. sativa* and *O. glaberrima* physically apart on the Togo side of the Togo Hills (*O. sativa* is confined

to lower elevations with more fertile soils and *O. glaberrima* is cultivated in poor upland soils at higher elevations). On the Ghanaian side of the Togo Hills, local cultural practices have also contributed to the physical separation of the two species. In general, local communities on the Ghanaian side of the Togo Hills favour Asian rice for commerce, and reserve African rice for ceremonies and ritual usage (Teeken *et al.*, 2011). This suggests that farmers' practices influencing gene flow need to be explained with reference to a range of cultural and environmental factors (Nuijten 2005, 2010; Teeken *et al.*, 2010, 2011; Nuijten and Richards, 2011). But only a handful of studies exist on how farmers 'manage' gene flow in these diverse circumstances (Dyer *et al.*, 2011). In particular, rice has been little studied in this regard (Jarvis and Hodgkin, 1999).

Variation in farmer strategies is known. The reasons why are not fully established, and ought to be given growing interest in endogenous processes of crop development (Semon *et al.*, 2005; Barry *et al.*, 2007; Nuijten *et al.*, 2009). For instance, in some cultures it is considered good practice to cultivate the two rice species mixed (among other reasons, to spread risk and ensure a good harvest), whereas in other cultures seed purity is emphasized. In cultures where seed purity is emphasized (and it may be for aesthetic as well as practical reasons), selection of seeds from the middle part of the field is often thought desirable (Longley and Richards, 1993), though there are few if any records on how often this ideal is met in practice. In other settings maintaining low levels of mixture is considered virtuous, since this is connected with the probability of finding new plants in the field and in-field diversity makes farming impractical (Richards, 1986). A local idea that mixture serves as a kind of gene bank has been reported (Nuijten, 2005). Temudo (2011) reports that mixture can help identify theft. The role of men and women in seed selection and seed exchange may also be very different across different ethnic groups. For example, in The Gambia both male and female farmers think that women have the skills and patience to develop new rice varieties by selecting off-types in the field and then testing them for several years (Nuijten, 2010). In Sierra Leone, by contrast, men and women are

thought to be equally capable of developing new rice varieties (Richards, 1986).

Thus, we argue that knowing more about gene flow in farmers' fields is important for two reasons: (i) it supports management approaches that help to preserve processes underlying endogenous crop development, including *in situ* gene flow between wild and cultivated rice species, and the associated emergence of inter-specific progenies; and (ii) to understand how to link these 'unsupervised' processes with formal variety development. The need for a decentralized varietal development approach in which farmers have an essential role has become clearer, not only in Africa (Gridley *et al.*, 2002; Dorward *et al.*, 2007; Eñisue *et al.*, 2008; Nuijten *et al.*, 2009; Mokuwa *et al.*, 2013), but worldwide (Almekinders and Elings, 2001; Ceccarelli *et al.*, 2001, 2010; Sperling *et al.*, 2001; Witcombe, 2002; Gyawali *et al.*, 2007; Desclaux, 2008; Østergård *et al.*, 2009; Joshi *et al.*, 2012). Conserving the 'unsupervised' system may offer a cost-efficient way of supporting a continued output of robust, adapted varieties for farmers not yet within reach of the formal system.

Methodology

The information provided in this chapter is based on a review of the literature and extensive fieldwork in The Gambia (2000–2003, 2007 and 2008), Senegal and Guinea-Bissau (2007 and 2008), and Sierra Leone (various times from 1981 to 2008). The research focused on upland rice farming systems and used interdisciplinary approaches integrating social science and biological science research methods (Nuijten, 2011). This approach is based on critical realism (Sayer, 2000), of which the Context Mechanism Outcome configuration is a central element (see Pawson and Tilley, 1997). Depending on the research question, candidate mechanisms are postulated, after which various research methods are used to test the candidate mechanisms. Critical realism does not exclude positivistic or post-modern research approaches and can be considered a framework for integrating methods from the social and biological sciences. For this research it implies describing the socio-economic and biological aspects of the farming context,

and testing socio-economic, biological and complex socio-biological candidate mechanisms for explaining the dynamics of gene flow in rice-farming systems. The research methods used consisted of various qualitative and quantitative surveys with farmers (Richards, 1986; Nuijten, 2005), field mapping (for methods see Nuijten and Richards, 2011), field observations, field trials and molecular analysis for comparisons of seed materials collected from farmers at the phenotypic (Nuijten and Van Treuren, 2007) and molecular levels (Nuijten and Van Treuren, 2007; Nuijten *et al.*, 2009).

Gene Flow as a Mechanism

Although much research has been done on the genetics of the isolation barriers between various rice species found in West Africa (Sano, 1989; Heuer and Miézan, 2003; Garavito *et al.*, 2010), the literature is not conclusive on the possibility and level of introgression between species of the *O. sativa* complex. According to Second (1991), *O. barthii* and *O. longistaminata* are the only rice species of the *O. sativa* genome group between which no introgression is possible, although Chu and Oka (1969) suggest introgression is possible between these two species. No sterility barriers exist between *O. barthii* and *O. glaberrima*, which are closely related (Chu and Oka, 1969; Second, 1982; Wang *et al.*, 1992). There has also been some lack of clarity about the levels of introgression among *O. sativa*, *O. barthii* and *O. glaberrima*. Some have reported that *O. sativa* is completely isolated from *O. glaberrima* and *O. barthii* (Chu and Oka, 1969; Spillane and Gepts, 2001), but artificial hybridization has been successful in the laboratory (Sano, 1989; Pham and Bougerol, 1993; Jones *et al.*, 1997; Heuer and Miézan, 2003) and some level of introgression does seem to occur in the field (Semon *et al.*, 2005; Barry *et al.*, 2007; Nuijten *et al.*, 2009). Information about the direction of gene flow between the different species is contradictory, most likely because the levels of interspecific gene flow are low and, hence, difficult to measure. We assume that some gene flow is possible between all species in all directions, although the actual levels of gene flow are not known.

The only allogamous rice species known in West Africa is *O. longistaminata*. All other rice species in West Africa are strongly autogamous. The level of cross-pollination of *O. sativa* is well studied, in particular in relation to genetically modified (GMO) rice (for a historical overview see Gealy *et al.*, 2003), but reports on the level of cross-pollination in *O. barthii* and *O. glaberrima* are difficult to find (Grist, 1986; Oka, 1988). One interesting question is whether there may be more gene flow from the other rice species to *O. longistaminata* than vice versa. The low levels of cross-pollination together with the strong F_1 sterility barriers make introgression between the various rice species rather rare, and consequently difficult to quantify.

Chances of Co-flowering

Between cultivated and wild species

Oryza barthii × *O. glaberrima* and
O. longistaminata × *O. glaberrima*

The extent of sympatry¹ of *O. glaberrima* with *O. longistaminata* and *O. barthii* varies widely over time and space across West Africa and is shaped by a complex interplay of agroecological, socio-economic and cultural factors. As a result the overlap in co-flowering varies accordingly. Both *O. barthii* and *O. longistaminata* are found throughout West Africa. *Oryza longistaminata* grows only in lowlands that are seasonally submerged. *Oryza barthii* is found over a wide range of lowlands, including the hydromorphic zone, while *O. glaberrima* is grown in uplands and lowlands. In Sierra Leone and Guinea, some plants resembling *O. barthii* grow as weeds in upland fields, and these are on occasion collected for seed and planted (Richards, 1986). Aside from being deliberately planted from time to time, the (semi) wild material persists when panicles are harvested along with the main cultivar and the seed is only incompletely rogued (Richards, 1986).

Oryza barthii × *O. sativa* and
O. longistaminata × *O. sativa*

Almost all lowlands are today cultivated with *O. sativa* varieties. This suggests that, compared to *O. glaberrima*, there are more opportunities for

co-flowering of *O. sativa* with *O. barthii* and *O. longistaminata*. In areas where farmers transplant rice, they weed out the wild species through ploughing (Nuijten, 2005). In lowland areas where rice is broadcast, some farmers are able to differentiate wild from cultivated rice at the vegetative stage whereas others cannot, resulting in diverse levels of wild rice in adjacent fields. In The Gambia, the wild rices tend to flower earlier than the cultivated rice (Nuijten, 2005). The overlap in co-flowering depends on the duration and the level of photoperiod sensitivity of the cultivated rice varieties. In lowland areas adjacent to the cultivated rice, farmers generally leave *O. barthii* to grow as it can be harvested for food (Richards, 1986; Nuijten 2005). Thus, some farmer practices (ploughing, weeding) reduce the chances of co-flowering, while other practices (cultural value of wild rice as a food) allow co-flowering (Nuijten, 2005). The genetic background of some semi-wild varieties resembling *O. barthii* collected in Guinea and Sierra Leone (Nuijten *et al.*, 2009) suggests that gene flow occurs between *O. sativa* and *O. barthii*. The exact implications and potential benefits of these findings need to be studied further.

Among cultivated species

Oryza sativa × *O. glaberrima*

Oryza sativa and *O. glaberrima* are often found in the same field across the upper Guinea coastal region, whereas this is not common in the Togo Hills (Teeken *et al.*, 2011). The reasons why farmers purposively plant the species in mixtures are agronomic (e.g. increase in yield, prevention of lodging, more simultaneous flowering, or a second harvest on the same land due to different flowering periods) and related to local beliefs (to encourage a good harvest or to prevent witchcraft). Often *O. glaberrima* is considered as the first (i.e. ancestral) rice (in historical terms) and hence good to have in a field with *O. sativa*, to guide it, much as an indigene guides a settler to understand the local terrain (Richards, 1986; Nuijten, 2005). But the importance of having pure *O. glaberrima* seed (with its distinctive grain shape in addition to its red seed coat) for rituals is the main reason why farmers in the Hohoe area (Ghana) do not mix *O. sativa* and *O. glaberrima*

(Nuijten *et al.*, 2009; Teeken *et al.*, 2011). In countries like The Gambia and Senegal farmers have largely abandoned the cultivation of *O. glaberrima*, but it is still a frequent weed in farmers' fields, particularly in the transitional zones (Nuijten, 2005). Despite the fact that Gambian and Senegalese farmers do not like to have *O. glaberrima* in their fields, they do not bother to rogue it carefully from their seed (Teeken *et al.*, 2011). Elsewhere, for example in southern Guinea-Bissau, Guinea and Sierra Leone, *O. glaberrima* is liked and reputed to have better nutritional or therapeutic properties than *O. sativa* (Richards, 1996; Teeken *et al.*, 2010). The implication is that various cultural factors, together with agroecological factors, influence the level of gene flow between the two species in different ways.

Oryza sativa subsp. *indica* × *O. sativa* subsp. *japonica*

In general, in West Africa, varieties of *O. sativa* subsp. *indica* are grown in the lowlands and varieties of *O. sativa* subsp. *japonica* are grown in the uplands (De Kochko, 1987a; Barry *et al.*, 2007). However, some *indica* varieties can be found in upland fields, as a plot or mixed in plots with *japonica* (Nuijten and Van Treuren, 2007; Nuijten and Richards, 2011). For example, improved varieties developed for irrigated lowland cultivation, known locally as 'Peking' and 'CCA', were adopted by farmers for upland cultivation in The Gambia during the 1970s and 1980s (Nuijten, 2005). In various regions of Guinea-Bissau, varieties of both subspecies were found growing adjacently or mixed in upland areas and transitional zones (Nuijten, unpublished). Mixed stands of both subspecies may also be found in other regions in West Africa, such as in Guinea and Sierra Leone, as both subspecies are cultivated in lowland and upland areas (Okry, 2011; Teeken *et al.*, 2011; Mokuwa *et al.*, 2013). Whether *japonica* varieties are grown in lowland areas has not been studied. An F₁-hybrid sterility barrier exists between the two subspecies of *O. sativa*, although not as strong as the one between *O. sativa* and *O. glaberrima* (Oka, 1988). The presence in the field of varieties with an inter-subspecific background in West Africa has been reported (De Kochko, 1987b).

Field Settings

Adjacent plots may experience gene flow. Often farmers within a village will plant their rice in a single area. In the case of upland rice this is commonly done for sharing labour to clear vegetation, to make the burning process more effective and to reduce pest damage (Richards, 1986; Nuijten and Richards, 2011). In lowland areas fields are also situated in single areas, often because of limitations in land. Whether two adjacent rice varieties belonging to different species or subspecies then co-flower along a field boundary depends on various factors (Nuijten and Richards, 2011). The planting dates on adjacent plots may differ, especially if farmers share labour for planting. The duration of the rice varieties may differ, with no gene flow between varieties with different flowering periods if they are planted at the same time. Conversely, types with longer and shorter flowering periods may coincide in flowering if planted at different times. For that, topography is an important factor, since farmers often plant slopes (in inland valleys and hilly areas) with varieties with different durations to avoid labour bottlenecks and food scarcity (Richards, 1986). Rice varieties with the same flowering intervals may not exchange pollen if they have been planted at different levels on a slope. Those with different flowering intervals might overlap in flowering at a field boundary if the longer-duration variety is planted first on a lower slope. Thus, precise information is needed for assessing cross-boundary gene flow – on the number of rice varieties planted, their flowering period, planting dates, and location in the field, and the topography (Nuijten and Richards, 2011).

An important finding from rice farms in The Gambia, however, is that the chance of gene flow is much greater among co-flowering plants within a single field than across field boundaries. It was estimated that the average rate of cross-pollination between different varieties within the same field was 0.125%, some 25 times higher than the estimated average rate of cross-pollination between different varieties in neighbouring fields (0.005%) (Nuijten and Richards, 2011). Data collected by Okry (unpublished) suggest similar rates for upland rice farms in

south-west maritime Guinea. If these findings are replicated for other rice-farming systems in West Africa then it seems that mixing of seed – whether deliberate planting of *O. sativa* and *O. glaberrima* within one field (Longley and Richards, 1993; Jusu, 1999; Teeken *et al.*, 2011), or due to a relaxed attitude to roguing off-types – is the more likely origin of varieties with an interspecific background than planting of *O. sativa* and *O. glaberrima* in adjacent plots. The findings of Nuijten and Richards (2011) also imply that the chances of cross-pollination between wild and cultivated species are higher when the wild rice plants are found within rice fields (i.e. when wild varieties remain unweeded), rather than as populations occurring on a field margin.

From F₁ Hybrid to a New Variety, Taking *O. sativa* × *O. glaberrima* F₁ Hybrids as Starting Point

A crucial factor in the development of interspecific varieties – after the emergence of rice plants with an interspecific background – is the natural backcrossing process in the field. *Oryza sativa* × *O. glaberrima* F₁ hybrids with the cytoplasmic DNA from *O. sativa* do not produce pollen (Sano, 1989), although there may be exceptions (Pham and Bougerol, 1993). F₁ hybrids can backcross to either species, provided co-flowering occurs. Various scenarios for backcrossing are illustrated in Fig. 8.1. Two main scenarios for backcrossing can be identified and are described in detail below.

First scenario: backcrossing to the F₁ hybrid

F₁ hybrids are known to farmers – as ‘useless’ plants that flower but set no seeds. In very rare cases, F₁ hybrids do produce a few seeds (one or two per plant), as the result of pollination from surrounding ‘normal’ plants (Nuijten, 2005). These seeds will not be harvested (as the farmer will consider the mother plant useless) and, if not eaten by birds or other animals, may co-flower the next season if rice is planted in the same field. In the case where fertility is restored

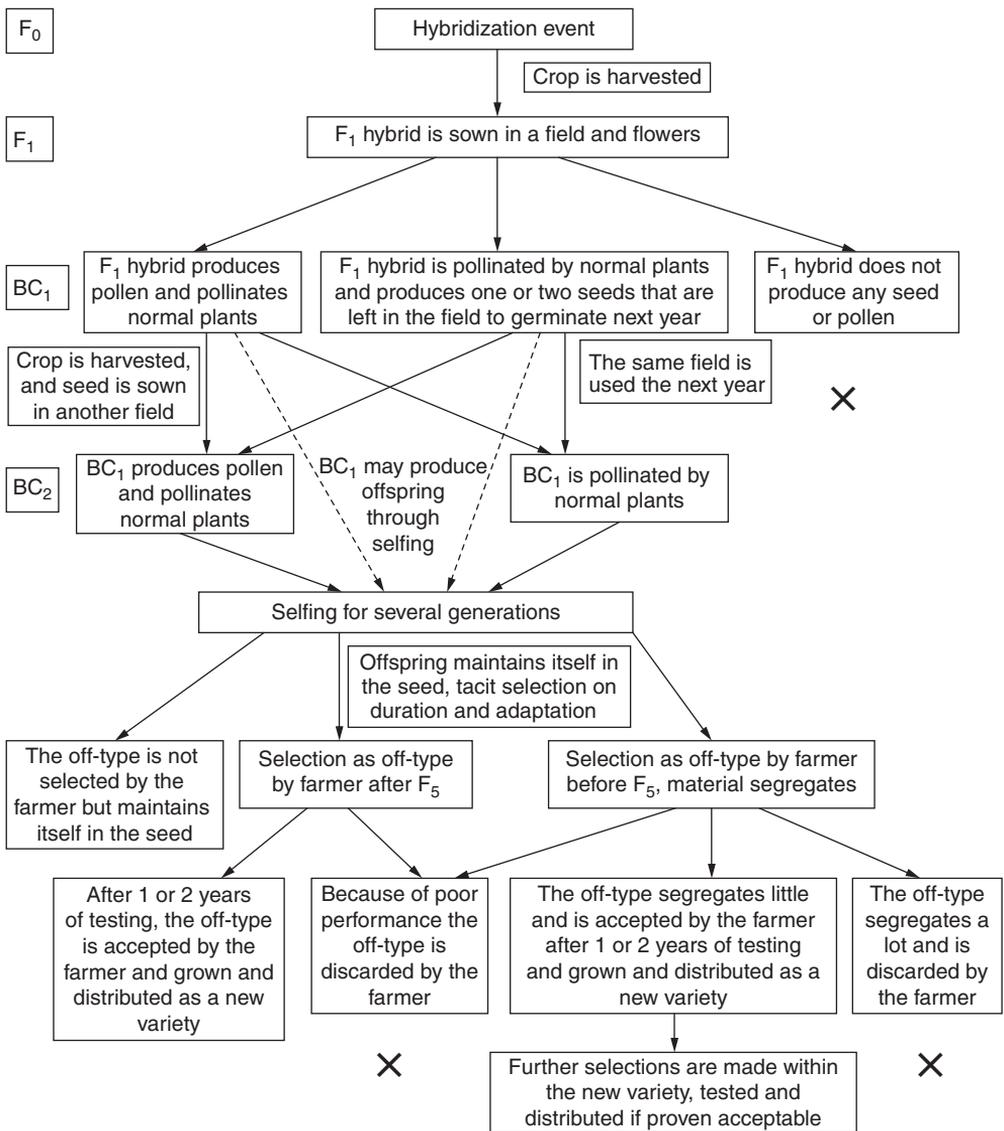


Fig. 8.1. Scenarios for the development of rice varieties with interspecific background.

with the first backcross, the progeny of the backcross may produce fully filled panicles which can then be included in the harvest by a farmer. Whether or not partly fertile panicles are included in the seed depends on the harvesting method used. If farmers use a sickle, a partly filled panicle is likely included in the harvest (Fig. 8.2), but this is less likely if farmers use a

knife. Another possibility is that the fertility of the backcross is not fully restored, and that the pollen produced by the backcross pollinates a few flowers of surrounding normal plants. In both sub-scenarios the same field needs to be cultivated for at least two seasons. For upland rice a general rule is not to sow rice for a second season in the same field.

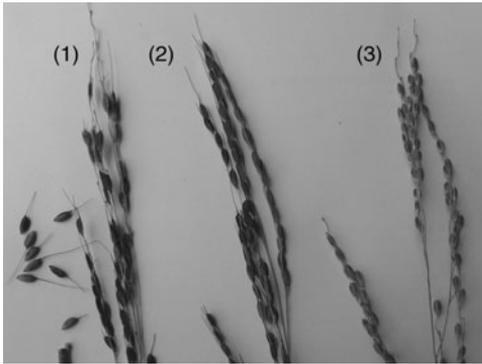


Fig. 8.2. Two off-types found in a field with the variety Pa Three Month (farmer hybrid with semi-droopy panicle, e.g. variety with interspecific background) in Kamba, Sierra Leone, 2009. Most of the flowers on panicle (1) are unfertilized and have awns similar in colour to those of *O. barthii* and interspecific F_1 hybrids. The seeds of panicle (1) dropped off very easily. The features of the (fertile) off-type (2) are intermediate between the off-type (1) and the variety Pa Three Month (3). Molecular analysis may clarify the genetic status of the two off-types.

Second scenario: backcrossing to the parent

The other scenario is that F_1 hybrids do produce some pollen that pollinates surrounding plants. So far, research on the fertility of crosses between *O. sativa* and *O. glaberrima* has not found an F_1 progeny that produces pollen, but it is suggested that wide compatibility varieties may be able to produce F_1 hybrids with fertile pollen (Pham and Bougerol, 1993). In this scenario, the backcrossed seed will not be recognized by a farmer (as it sits on a panicle of a normal plant), and will be included in the seed for the next season. Assuming two backcrosses are needed to restore full fertility, this in-field backcrossing needs to be repeated in the next two seasons, in which the backcross pollinates surrounding normal plants, of which some will be included in the seed for the following year. This scenario is not limited to rice-growing areas where the same fields are used for several years, or where rice ratoons, but is also possible in upland areas where farmers only grow rice for one year and then move to a new area to clear fields for the next season's rice farms.

More research is needed to decide which of the scenarios in Fig. 8.1 are more likely, and under what conditions. Among other observational requirements, it is necessary to observe – in detail over a season – a sample of different locations to work out the co-flowering intervals of the different rice types, including ratoons of the main cultivars.

After the backcrossing

When fertility is fully restored after two or three backcrosses, the offspring of the interspecific cross may maintain itself in the farmer's seed through self-pollination, if it is adapted to the local agroecological conditions, and if the farmer does not consider the offspring as clearly inferior.

When the level of mixture in the field is low, farmers apply negative selection, only roguing those plants with an inferior morphotype (Nuijten, 2005). The roguing is done either at harvest or when seed is being prepared for saving (Richards, 1986; Nuijten, 2005). The rigour of roguing also depends on the availability of time and labour. Only when the level of mixture is high do most farmers decide to remove all off-types. Women may object to pounding mixtures of varieties that have different threshabilities, cooking times, pericarp colours, etc. Conversely, when the level of mixture in the field is low, an off-type (being the progeny of a backcross) may readily remain in the seed. So long as it is not considered to be clearly inferior farmers will not bother to remove it (Nuijten, 2005).

Some farmers even prefer mixed material, since (with small plots) they may have time to sort and try out off-types (Richards, 1986), or be able to rediscover lost varieties (Nuijten and Richards, 2011). Depending on their socio-economic position, some farmers may have sufficient time – in their own words 'patience' – to look for off-types (Nuijten, 2010). Such farmers exercise positive selection for off-types, having learned the value of experimenting with 'new' types (often on difficult land). Eventually, off-types that seem valuable to the farmer (in terms of duration, panicle size, grain size, tillering, etc.), may be selected by farmers for testing to see whether the off-type may make a useful new variety. If after 1 or 2 years of testing the

farmer finds the new variety useful, he or she gives some seed to friends and relatives for testing (Nuijten and Richards, 2011). If the new variety endures this cycle of testing successfully a new variety has been developed. A valuable off-type, once separated out and carefully tested, may bring prestige or gratitude to the farmer who selected it in the field, if it has some useful trait (e.g. taste, yield, duration, ability to grow on low-fertility soils, tillering ability). This prestige and gratitude is reflected in the newly developed variety being named after the farmer who selected it as an off-type (Nuijten and Almekinders, 2008).

Participatory research with farmers in The Gambia suggests that off-types that segregate a lot are abandoned very quickly. These farmers were given F_3 progenies, but they complained that the level of mixture was too high (Nuijten, 2005). In fact, various farmers who had developed new varieties from selected off-types said they never observed segregation in the progeny. Morphological observation of the farmer hybrids (rice varieties with an interspecific background as described by Nuijten *et al.*, 2009) suggests that some of these farmer hybrids look completely uniform, whereas others show some segregation for one or two traits (e.g. husk colour, awning, basal sheath colour).

The spread of new varieties depends on various factors. Important factors are climatic variability and climate change. Some farmer hybrids identified by Nuijten *et al.* (2009) are very short in duration and were quickly adopted in The Gambia and southern Senegal in the 1970s and 1980s when rainfall was reduced. War, such as the conflict in Sierra Leone, may force farmers to crop their lands more frequently (due to security concerns), and in these cases there is a greater need for varieties adapted to poor soils and low management. Cultural factors may determine patterns of out-migration (in times of peace and war) and hence influence the dispersion of new varieties over wider regions.

Macro, Regional Settings

It is not only the micro setting at field and village levels that shapes farmer activities in relation to crop development, but also the macro (regional) setting. The above illustrates that distances

between the nodes of the networks farmers are working in vary from short to very long. How exactly the macro/regional setting influences farmer activities is not yet well understood. Portères (1962) thought that the domestication of *O. glaberrima* took place in the Inner Niger Delta in Mali because of the large diversity found there. Archaeological findings show that gathering of wild rice also took place in the Lake Chad basin (Klee *et al.*, 2004), and this therefore is a second possible site for initiation of the long-term domestication cycle as described by Alleby *et al.* (2008). Domestication of rice in West Africa began in a wetter phase, about 3500 BP (see McIntosh and McIntosh, 1981), so it is likely that early varieties were taken south by populations of gatherers following the gradual shift of the savannah and forest zones towards their present position (see Brooks, 1989). Earlier arid phases (enlargement of Dahomey Gap) served to split a number of West African animal and plant species into 'upper' and 'lower' West African populations. It is known that this happened with oil palm (Cochard *et al.*, 2009). But it is not known if there are similar differences among wild rice populations in the region. If so, the domestication of African rice based on a western and eastern focus (Inner Niger Delta and Lake Chad) might preserve, in a similar way to oil palm, some degree of ancient geographical and evolutionary differentiation in the genetic make-up of African rice.

Semon *et al.* (2005) suggest that *O. glaberrima* from northern Nigeria is genetically different from *O. glaberrima* from western West Africa. Our own data point to an upper Guinean coast gene pool being somewhat different from *O. glaberrima* collected in the Togo Hills (Nuijten *et al.*, 2009). There was once a debate among anthropologists and linguists about whether the people of the Togo Hills belonged to some kind of a remnant West African palaeolithic population (Westermann, 1954). Notwithstanding a strong argument based on anthropological and historical studies (Nugent, 1997), the idea that there may be some connections in language and material culture (e.g. African rice) across the chain of West African uplands north-eastwards from the Togo Hills, through the Atacora Mountains and Jos Plateau (central Nigeria), to the Adamawa Plateau, adjacent to the Lake Chad basin (Blench, 1989) is not entirely dead. To shed

more light on this, further investigation, with (e.g.) molecular markers, with more extensive sampling, in particular from the western and eastern halves of West Africa, is needed (see Li *et al.*, 2011).

Linking the Macro Level with the Micro Level

In addition to biological data, better archaeological, historical and anthropological data will improve our understanding of the level of differentiation in genetic material on the upper and lower Guinea coast compared to Mali, central Nigeria and regions adjacent to the Lake Chad basin and, most importantly, the development of the wide range of rice-farming systems across West Africa, at micro and macro levels. The interspecific rice types in the upper Guinea coast region (from Senegal to Sierra Leone) identified by Nuijten *et al.* (2009) can be sub-divided into two types resulting from a combination of natural and cultural selection pressures. The earliest cultivation of the interspecific rice types appears to have been in Sierra Leone and Guinea-Bissau, which were connected through trade overseas (Mouser *et al.*, forthcoming). Both sub-types seem to have advantages under adverse conditions such as drought and war (Nuijten *et al.*, 2009). They are found cultivated adjacent to fields with *O. sativa* and *O. glaberrima* varieties, and within fields, mixed to various degrees, with varieties of *O. sativa* and *O. glaberrima* (Nuijten and Richards, 2011). Although it is not clear whether an F_1 -hybrid sterility barrier exists between these farmer hybrids (varieties with an interspecific background) and *O. glaberrima* and *O. sativa*, it is likely that some hybridization, leading to the development of new varieties, takes place. As such, the farmer hybrids contribute in various ways to the portfolio of rice varieties managed by farmers working under sub-optimal farming conditions, indirectly increasing the coping strategies of farmers. They may also have

potential relevance for exploitation by plant breeders (Nuijten *et al.*, 2009). Future advances in crop development could be achieved through better co-operation between scientists and rice farmers working under sub-optimal conditions in order to provide solutions in a world of increasing socio-political and climatic uncertainty.

Conclusion

Without an integrated approach for crop development it will not be possible to: (i) set up a management approach to maintain farmers' activities resulting in the development of new germplasm; or (ii) better understand how to link farmer crop development with scientific crop development (through participatory plant breeding). In this chapter we have described several scenarios for the development of interspecific rice varieties. Much information on how farmers influence gene flow is not yet known, both at micro and macro levels. From an empirical point of view, more information is needed on the weights applied by farmers to the nodes and the ways farmers weigh the nodes in a so-called gene-flow network. In order to do that, biological data on gene flow and the level of interspecific mixtures within farmers' fields need to be integrated with, among other things: (i) anthropological data on farmer practices in relation to field use and co-flowering of different rice species, and what type of farmers experiment with off-types and under what sorts of conditions; and (ii) with historical data on trade routes, cultural linkages between ethnic groups and time and place of introduction of various types of *O. sativa* in West Africa. Although such data sets seem very diverse, they can be analysed in an integrated way using an interdisciplinary approach, combining natural-science modelling approaches with social-science descriptive approaches (Nuijten, 2011; Nuijten *et al.*, Chapter 29, this volume).

Note

¹ 'Sympatry' is defined as 'species occupying the same geographical range without loss of identity from inter-breeding' (modified from www.merriam-webster.com/dictionary/sympatry, accessed 14 February 2013).

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