ISSN 1479-2621
Plant Genetic Resources: Characterization and Utilization (2011) 9(3); 361–374
doi:10.1017/S1479262110000481

Pollen flows within and between rice and millet fields in relation to farmer variety development in The Gambia

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Received 10 August 2010; Accepted 17 December 2010 – First published online 17 January 2011

Abstract

In areas with less favourable conditions for agriculture, informal seed systems permit gene flow through pollen to play a crucial role in the development of new varieties. An important factor with great impact on cross-pollination is the plant breeding system, but so far this is little studied within the context of low-input farming systems. This research studied the chances of cross-pollination within and between rice fields in The Gambia. Size and time of flowering were measured for 28 rice fields in one village. The level of mixture was measured in 90 seed lots of rice collected from four villages. Based on the results, we suggest that in general cross-pollination between different rice genotypes occurs more often within fields than between fields. No clear relationship was found between the level of within-field mixture and socio-economic status of farmers. Some comparison was made with millet, which allowed the identification of various factors influencing pollen flow between different genotypes. Effective pollen flow (between genotypes) is a function of a number of factors, such as the rate of cross-pollination of a crop, number of off-types within fields, variety distinctiveness, farmer expert knowledge, length and reliability of the rainy season, growth duration of different varieties, availability of fields, pest pressure and number of varieties grown per field or per farmer. We hypothesize that a low cross-pollination rate is more favourable for the development of new varieties in farmer fields than a high cross-pollination rate.

Keywords: crop breeding system; millet; pollen flow; rice; The Gambia; variety development

Introduction

In areas with less favourable conditions for agriculture, such as in dryland West Africa, informal seed systems are the most important seed source for farmers (Richards, 1985; Amanor *et al.*, 1993; Ndjeunga, 2002). These systems permit gene flow through pollen to play a crucial role in the development and maintenance of landraces. Through their farming practices, and the impact of external factors such as land availability and rainfall patterns, African farmers both promote and prevent cross-pollination between genotypes, and presumably largely without conscious intent. Because of the clustering of fields of rice (*Oryza sativa* L. and *Oryza glaberrima* Steud.) and the cultivation of many different varieties, farmers enhance the chances of cross-pollination between rice varieties in Sierra Leone (Richards, 1996). In Ethiopia, farmers minimize the chances of cross-pollination by planting different sorghum (*Sorghum vulgare* L.) landraces at different times and in separate fields (Teshome *et al.*, 1999). Elsewhere, intensive cultivation does not permit all farmers to isolate their fields to prevent cross-pollination in maize (*Zea mays* L.) in certain areas of Mexico (Bellon and Brush, 1994).

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An important factor having significant impact on cross-pollination, but hitherto little studied within the context of low-input farming systems, is the plant breeding system. One might expect that cross-pollination is a more important source of diversity for cross-pollinating crops than for self-pollinating crops. However, in addition to being a creative force, pollen flow can also be a constraining force in evolution (Slatkin, 1987), and this applies to crop varieties in farmer fields. If there is a lot of cross-pollination, new 'better' genotypes segregate and hybridize continuously and cannot maintain themselves in a population. Hence, farmers may select interesting looking plants in cross-pollinating crops like maize or pearl millet (*Pennisetum glaucum* [L.] R.Br.), but subsequently notice that the progeny is different from the parent and has, partially, lost its interesting characteristics. In the case of rice (a self-pollinating crop), not many hybrids will develop in farmer fields, but those superior genotypes that develop after several years of segregation and selfing are stable and endure for several years, awaiting notice and selection by farmers. The cross-pollination rate for rice is assumed to be about 0.5% (Purseglove, 1985; Grist, 1986), somewhat higher for the *japonica* subspecies than for the *indica* subspecies (Oka, 1988), and recent findings suggesting lower rates (Messeguer *et al.*, 2004; Rong *et al.*, 2004), while for millet, it ranges between 70 and 80% (Rao *et al.*, 1949; Burton, 1974). Seemingly, this difference explains why there are frequent accounts of farmers developing new varieties of rice (Lambert, 1985; Richards, 1986, 1996; Bertuso *et al.*, 2005; Nuijten, 2005), but no such reports for millet.

However, little measured evidence has been offered of actual gene flow processes at work in farmer rice fields. Now that there is clear evidence that interspecific farmer varieties of rice have developed in farmer fields in West Africa (Nuijten *et al.*, 2009), it is important to understand these underlying processes better. This article aims to provide information on actual gene flow during a growing season within and between farmer rice fields, with some comparison with pearl millet.

The Gambia is a small West African country with extensive rice and millet cultivation. Here, it is common that rice is cultivated by women and millet by men. Rice is cultivated in both lowland and upland areas, whereas millet is only cultivated in upland areas. Of rice, many varieties are cultivated. The average rice farmer cultivates two or three varieties, and within a village, it is typical for more than ten varieties to be grown, primarily depending on ecological variation. Men usually grow one variety of millet, and within a single village, it is normally the case that only one, or sometimes two varieties of millet will be planted (Nuijten, 2010).

Materials and methods

The flowering periods of different rice plots were observed in detail in three upland areas in the village of Tujereng in 2000. In each area, nine or ten adjacent rice fields, each consisting of several plots (farmers divide their fields into plots), were mapped to estimate the possibility of cross-pollination (two areas were partially mapped, while one was mapped completely). A compass and a tape were used to map and calculate the size of the fields. The level of flowering was measured for each separate plot twice a week. Also some basic agronomic features were recorded, such as stand of the field, visual uniformity, date of weeding and date of harvesting.

To compare rice genetic diversity between villages (Nuijten and Van Treuren, 2007), 100 samples of 300–400 panicles each were collected from farmers in the villages Faraba, Janack, Kitti and Tujereng (Supplementary Fig. S1, available online only at http://journals.cambridge.org). The selection criteria for the case study villages were that the similar types of rice millet were cultivated, i.e. short duration upland rice and late varieties of pearl millet. The upland rice was cultivated in typical upland areas (prepared for cultivation through slash and burn) or in the upper stretched of the lowlands were usually no water stands. The four villages were selected, so that they formed a line from west to east at intervals of 20–30 km. In terms of farming practices, there are no clear differences between the case study villages. The reason to work in the western part of the country was the limited number of interventions in agriculture, which allowed for an approximation as close as possible of the traditional farming system.

The rice samples were collected in a stratified manner such to obtain a range of materials representative of all upland rice varieties grown locally. Of the 100 samples, 90 samples were considered representative of the variation in farmers' fields because farmers had not applied any selection on those samples. The mixed-in panicles (indicated as other varieties by women farmers) were removed and analyzed to assess possible differences in quantity, number and type of mix-ins between seed lots, farmers' fields and villages.

For millet, this was more difficult because many men said that there are no mixtures in their variety of millet. And even though some men did give a description of millet varieties, it was not possible to get a consistent account of what the actual variety grown and mixtures in the field looked like. The main descriptor of millet varieties was seed colour (black and white), but during a grouping exercise conducted in Tujereng and Faraba (two villages where farmers grew black millet), some men grouped big impressive white-seeded spikes with samples having black spikes (Nuijten, 2010). For rice, there was lack of clarity about only one (named) variety, which (in fact) comprised different types.

In contrast to rice, millet fields are scattered all over the village. In total, 11 fields were mapped, selected at random from the compounds within which interviews were conducted. Although in all fields, except one, the same variety was grown, the question remained whether these fields were isolated in time and/or space. The millet fields were monitored on a weekly basis.

Much of the qualitative information obtained from farmers in this article is based on informal interviews and field walks in the villages of Tujereng, Faraba, Kitti and Janack. Some data derive from a country-wide questionnaire survey on farming practices and farmer crop and variety management conducted with 135 compounds in 11 villages in 2002.

Results

Influences of cultivation practices on pollen flow

In The Gambia, rice fields can be found in clusters. In the lowlands, space is often limited, 'forcing' farmers to situate their fields adjacent to each other. In the uplands, clustering of rice fields has the advantages of easier clearing and burning, and reduction of pest damage. Figure 1 shows the flowering patterns of three upland rice areas in Tujereng, as observed in 2000. In each area, two varieties were commonly cultivated: *Kari Saba* and *Binta Sambou* (Table 1). Each of the three areas was cultivated by groups of women with different socio-economic backgrounds (Supplementary Table S1, available online only at http://journals.cambridge.org). The differences between the three areas and their cultivators are summarized as follows:

(1) The fields in Area 1 were mostly cultivated by women who belonged to founding families in the village. Half of them did not have a husband able to clear the land (either the husband died, or was ill or old), and all of them worked on 'second year' *tandako* (an upland rice field used for a second year), which had the disadvantage that it was very weedy. Fields in Area 1 were small and many different varieties were grown. The relatively high number of plots per field is due to the large number of varieties cultivated in these fields.

(2) The fields in Area 2 were mostly cultivated by women who did not belong to founding families. Many of these women also did not have a husband to clear land for them. Before rainfall declined in the 1970s, this area was shallow wetland and cultivated every year. Because of continuous cultivation, the area was relatively easy to clear by the women themselves. However, weeds were abundant and soil fertility was lower than in Areas 1 and 3, because of continuous cultivation. Fields were quite small, and fewer varieties were grown, compared to Area 1. The relatively high number of plots per field is due to the somewhat undulating nature of the ground within some of the fields in Area 2.

(3) The fields in Area 3 were cultivated by women who did not belong to founding families and who did have a husband (or other male relatives) to clear the land for them. The households these women belonged to were bigger than the households of the women working in Areas 1 and 2. Fields were relatively big, and only common varieties were grown in this area. The average number of varieties cultivated by the women in this area was the lowest. In Area 3, the size of the plots was mostly defined by the sowing dates. Because of access to a larger labour force, the farmers in this area were able to sow larger plots in one day than in Areas 1 and 2.

Flowering was most uniform in Area 3 and least uniform in Area 2. A potential reason for the highest uniformity in flowering occurring in Area 3 is that all varieties had a similar time of flowering (number of days between sowing and flowering) and were planted at the same time. Area 2, where fewer varieties were sown than in Area 1, showed the greatest variation in flowering, probably as the result of differences in sowing dates and differences in weeding. Except for the variety *Bonti*, none of the varieties grown in these three areas (listed in Table 1, and illustrated photographically in Fig. S2) were photoperiod sensitive (data not shown).

In Tujereng, women try to sow rice as early as possible (particularly in the uplands), but the actual planting date is determined by various practical factors. One factor is the time of clearing of the fields. (For which they depend on men in the upland fields). Another factor is labour availability. Some plots and/or fields are sown or planted piece by piece by one person, while other plots and/or fields are sown or planted in one day by a *kafo* (a work group), resulting in mosaics with plots of different sizes and sowing dates. Between-plot alleys are not sown (in the uplands this is to enable bird scaring) but sometimes these paths are very narrow, even to the extent that sometimes it is difficult to see where one plot ends and the other starts.

In the lowlands, the same woman usually works in the same plot every year, although it also happens that a woman might lend her field, or part of her field, to

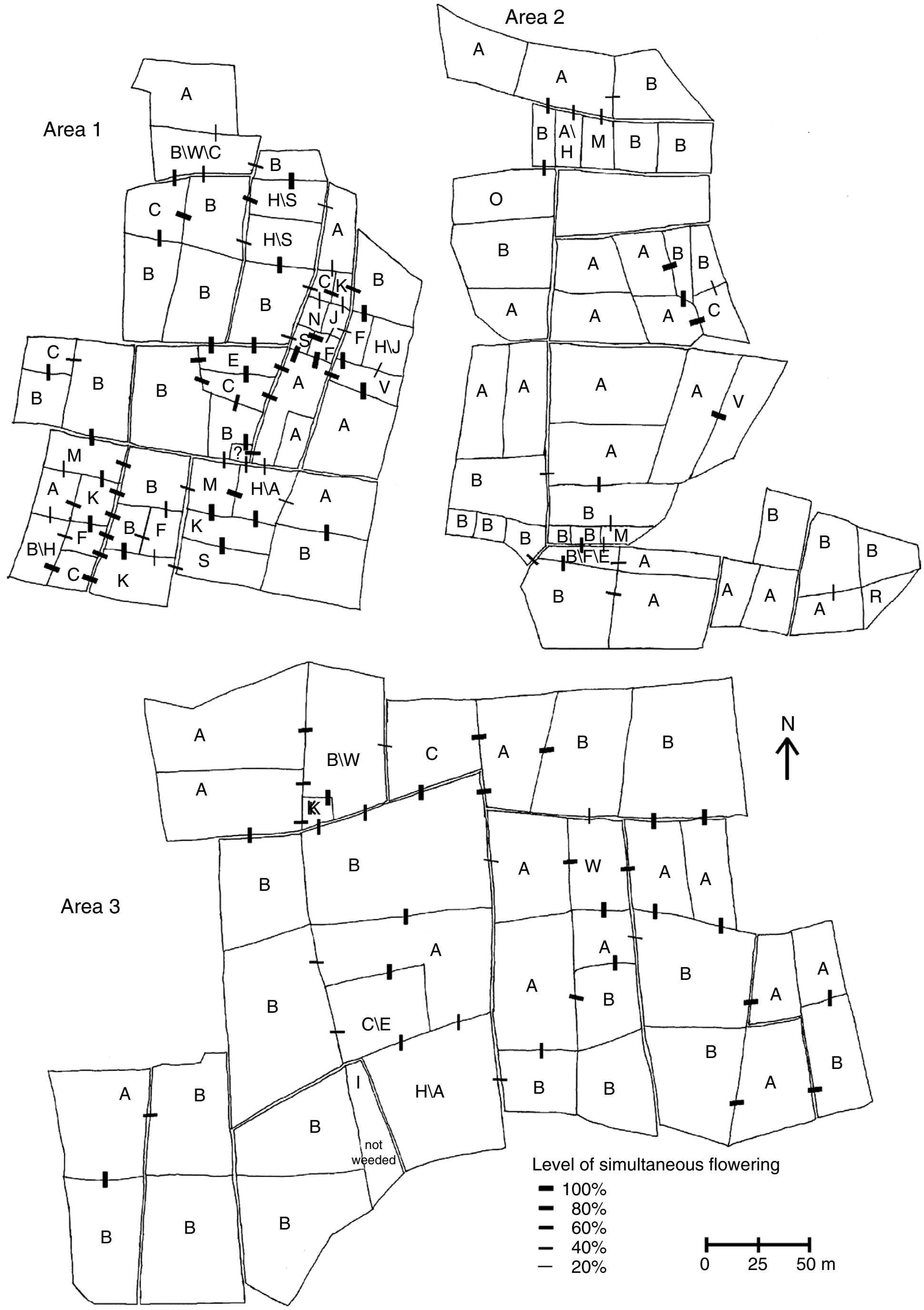

Fig. 1. Flowering periods of rice varieties in Areas 1, 2 and 3 in 2000. The letters indicate the varieties grown (for full names, see Table 1). The short lines across plot boundaries indicate the coincidence of flowering between plots. Boundaries between fields are indicated with double lines, and boundaries between plots are indicated with single lines.

another woman. In the uplands, rice field locations are moved around from year to year: each year, before the season starts, women intending to plant rice will find out from each other who wants to grow rice where, and each year it happens that groups change and women find themselves working together in different groups. Some women, however, prefer to work together in the same group every year. Groupings are usually based on friendship and/or kinship within the village.

A few farmers in Area 1 were known for their skills in distinguishing between different varieties. Farmers in Area 3 seemed to be less good at distinguishing varieties

Table 1. Distribution of varieties per study area shown in Fig. 1

Letter in Fig. 1	Variety name	Subspecies	Area 1	Area 2	Area 3
A	Kari Saba	Farmer hybrid[a]	8	18	14
B	Binta Sambou	Farmer hybrid	15	19	16
C	Sefa Koyo	*Oryza sativa* ssp. *japonica*	6	1	2
E	Bendou	*O. sativa* ssp. *indica*	1	1	1
F	Sefa Fingo	*O. sativa* ssp. *japonica*	4	1	0
H	Hombo Wulengo	*O. sativa* ssp. *japonica*	5	1	1
I	Test plot off-type	?	0	0	1
J	Jokadu Mano	*O. sativa* ssp. *indica*	2	0	0
K	Kukur	*O. sativa* ssp. *japonica*	2	0	1
M	Mani Mesengo	Farmer hybrid	2	2	0
N	Sefa Nunfingo	*O. sativa* ssp. *japonica*	1	0	0
O	Bonti	*O. sativa* ssp. *indica*	0	1	0
R	Sainy Kolly	*O. sativa* ssp. *indica*	0	1	0
S	Sonna Mano	*O. sativa* ssp. *japonica*	4	0	0
V	Foni Mano	*O. sativa* ssp. *indica*	1	1	0
W	Mani Wulendingo	Farmer hybrid	1	0	2
?	New variety (no name)	?	1	0	0

[a] Varieties with a genetic background intermediate between *Oryza glaberrima* and *O. sativa* (Nuijten *et al.*, 2009).

but even so included one farmer who developed a new variety called *Binta Sambou* (Nuijten, 2005). A few off-type panicles were harvested separately, of which the seeds were planted separately the next year under the supervision of Binta Sambou. After 2 years of testing, the variety was given to other farmers, and later spread into southern Senegal. The variety was identified as intermediate between Asian and African rice (Nuijten *et al.*, 2009). In Area 2, some experimentation was going on with newly introduced varieties. The women who were most expert at identifying rices tended to be older, but some younger women also introduced and experimented with new varieties. There are some apparent patterns linking experimentation with social status, age and other socio-economic variables, but these patterns are far from clear-cut, and deviations from the general trend occur.

In the uplands, women sometimes plant varieties of different durations, often by sowing the long duration varieties first and the short duration varieties second. The long duration varieties are 'old' farmer varieties preferred because of their good taste, which do not really fit a rainy season that has shown signs of shortening in recent decades. For this reason, the long duration varieties are often planted first to catch whatever rain they can. Usually, these varieties are sown in small plots, while the better-adapted 'common' varieties are sown in much bigger plots. Unlike the long duration varieties, the common varieties are sometimes sown piece by piece, and as a result may flower at different periods. Whether this is the case mainly depends on labour availability. Depending on the time of sowing of the common variety planted adjacent to the 'old' farmer variety sown first, the common and 'old' farmer varieties at times flower simultaneously. In Fig. 1, the common varieties are indicated with A and B, and the 'old' varieties with C, E, F, H, K and N.

Proximity of plots and coincidence of flowering create possibilities for cross-pollination between plots with different varieties. However, because rice is a selfing crop, chances of cross-pollination are low. Moreover, the furthest distance over which cross-pollination in rice can take place is about 2–3 m (Srinivasan and Subramanian, 1961; Messeguer *et al.*, 2001). The harvesting of seed by farmers allows some products of cross-pollination to germinate and flower in the next season. When farmers select seed, they tend to harvest it from a good part of the field, irrespective of whether it is close to the border or not (Nuijten, 2005). This finding differs from a report by a colonial agriculturalist (Squire) claiming that farmers in Sierra Leone avoided edge-reaped seed when making up batches of seed rice for replanting (Richards, 1985).

Mixtures and off-types

Through careful observation of rice fields, one can see differences in the level of mixtures and off-types between fields. First, the nature and causes of off-types will be discussed. After that, the chances of cross-pollination within and between fields will be discussed. Of 90 samples of varieties collected from farmers (300–400 panicles per sample), all 'off-type' panicles were removed, based on farmers' directions. The 'off-type' panicles were analyzed to assess possible origin and differences in quantity between varieties, farmers' fields and villages. The term 'off-types' refers to panicles that were either (1) currently grown varieties in the same or other villages ('mix-ins'), (2) old disappeared varieties, (3) unidentifiable genotypes of *O. sativa* or (4) unidentifiable genotypes of *O. glaberrima*. A majority of the mix-ins were other varieties grown in the same village. A few 'off-types' were *O. glaberrima* materials (6%), and a few (±2%) were old, disappeared *O. sativa* varieties. A number of panicles (±3%) could not be identified by farmers, of which a part (±0.04% of all off-types) segregated when sown and thus are products of cross-pollination.

The quantities of off-types varied between villages. Samples from Tujereng and Kitti contained more off-types than samples from the other two villages (Table 2). The average number of off-types found in the samples from Kitti is higher than those from the other villages (Table 2). It is difficult to give a good explanation for these differences. A partial explanation may be that the geography of the lowlands of Kitti is distributed such that the village farmland forms a mosaic of higher and lower areas, and varieties of different duration are (for this reason) planted in neighbouring fields. An explanation for the relatively low number of off-types in Janack is the reintroduction of rice farming by an non-governmental organisation (Sint Joseph Family Farm), around 1990, which emphasized seed purification during its trainings (Nuijten, 2005).

The number and quantity of off-types varied between fields, mainly related to differences in distinctiveness of the varieties planted (Supplementary Fig. S2, available online only at http://journals.cambridge.org), farmer seed selection practices, seed storage practices and agronomic practices for specific varieties. An example of the latter is that farmers think the variety *Hombo Wulengo* should be planted as a mixture to perform well. As long as the number of off-types are not too many, and they do not differ too much agronomically (e.g. plant height or duration) and in terms of processing (e.g. dehulling) or cooking (e.g. ability for cooked rice to be edible the whole day) from the planted variety, farmers do not bother too much about the presence of off-types in their fields. Farmer seed selection is primarily aimed at the removal of unwanted off-types and diseased panicles. Some women are quite happy with mixtures, as this offers them opportunities to retrieve seed of varieties lost because of drought or accidents during storage. In effect, such a field can function as a local genebank. Some women have a greater interest in seed selection and variety management than others. Older women have more experience than younger women, and often the first wife (normally the oldest) takes the lead in rice farming and knows more than the others about seeds (if the wives of one husband work together).

The number and quantity of off-types also vary between plots within fields (each field is divided into plots, separated by walkways to enable bird scaring) because the morphological distinctiveness varies between varieties. Varieties like *Sefa Fingo* or *Mani Wulendingo* (Supplementary Fig. S2, available online only at http://journals.cambridge.org) have a much more distinctive grain, and plots planted with these varieties contain only few off-types. A variety with a

Table 2. Differences in quantity, number and frequency of sorts of off-types found in rice samples collected in four villages in 2000

	Tujereng	Kitti	Faraba	Janack	Total
Total number of samples	44	12	16	18	90
Quantity of off-types (% of sample)					
< 3	9	5	7	10	31
3.1–7.5	11	2	7	4	24
7.6–15	3	1	0	4	8
15.1–30	14	3	1	0	18
> 30	7	1	1	0	9
Average	14.9	10.8	6.4	4.4	10.7
Number of off-types					
Average number per sample	4.1	5.6	3.2	2.7	3.9
Std. deviation	2.26	2.23	1.60	1.71	2.18
Total number per village	29	29	20	18	38
Sorts of off-types (%)					
Oryza sativa ssp. *indica*	70	92	94	95	83
O. sativa ssp. *japonica*	64	46	12	32	45
Oryza glaberrima	11	46	29	0	17
Farmer hybrid[a]	91	77	59	58	76

[a] Varieties with a genetic background intermediate between *O. glaberrima* and *O. sativa* (Nuijten *et al.*, 2009).

light red husk colour, *Hombo Wulengo*, contained the highest number of off-types, ranging from off-types with a red husk colour to off-types with a straw husk colour (data not shown). Hence, it is easier to keep certain varieties pure than others. In relation to the varietal morphotype, not only the number and quantity of off-types differ per variety, but also each variety harbours a different set of off-types, potentially influencing the direction of within-plot gene flow.

Estimates of cross-pollination for rice

Level of cross-pollination within rice plots

The average cross-pollination rate in rice is generally assumed to be about 0.5% (Purseglove, 1985; Grist, 1986). Many average rates from various experiments, summarized in Table S2 (Supplementary Table S2, available online only at http://journals.cambridge.org), are in line with this figure. Except for the study by Brown (1957), the percentages shown in Table S2 (Supplementary Table S2, available online only at http://journals.cambridge.org) are based on experiments in which the varieties were planted in an equal ratio, and the plants were spaced at an equal distance from each other. The experiment conducted by Brown (1957), yielding a rate of 0.41%, consisted of 3/4 of male plants and 1/4 of female plants. When adjusted to an equal plant ratio, using the formula in Table 3, the cross-pollination rate found by Brown is about 0.55%. More recent studies on the level of pollen flow tend to give lower percentages (Supplementary Table S2, available online only at http://journals.cambridge.org). An explanation for these lower percentages may be that these experiments were conducted under lowland conditions, and that cross-pollination may have been reduced due to the extensive tillering of the plants reducing the pollen flow between plants. An additional explanation for the much lower rate found by Messeguer *et al.* (2001) is that they conducted the experiment with only one variety that happened to have a low cross-pollination rate. It seems that the experiments conducted up to 1961, mentioned here, resemble current upland conditions in West Africa more than the experiments conducted more recently. Hence, in the following calculations, we use an average rate of 0.5%.

Table 3 shows estimations of the level of cross-pollination within plots between a variety and the off-types in relation to the quantity of off-types found in the rice samples. For the estimation of the rate of cross-pollination within a plot between plants of a variety and off-types, the following formula is used: $x/0.5 \times y/0.5 \times z$, in which x stands for the flow of pollen from the variety to the off-type plants relative to an equal distribution of pollen of the variety and the off-type, y stands for the percentage of off-type plants relative to an equal distribution of plants of the off-type and the variety, and z stands for the rate of cross-pollination (0.5%) with an equal ratio of pollen from the variety and the off-type plants and equal ratio of plants of the variety and the off-type plants (as was the case in the experiments of Beachell *et al.* (1938) and Roberts *et al.* (1961)).

Applying the above formula on the samples shown in Table 2 yields the cross-pollination rates shown in Table 3. The average percentage of off-types over all samples is 10.7% (Table 2). The average over the village means is only 9.1%. The second percentage is lower than the first because the sample number from Tujereng is much higher than from the other three villages. The average cross-pollination rate between a variety and off-types growing in the same field across the villages is 0.14%, based on the average village percentages of off-types. The rate ranges from 0 to 0.46%, the latter being close to the average cross-pollination rate in rice.

This implies that sowing seed will contain on average 0.14% of seed produced through cross-pollination (ranging from 0 up to 0.46%). Of every 10,000 seeds, we can expect 14 seeds to be hybrids. These numbers are small, but not insignificant. The average farmer in the study area sows ±0.9 ha, for which she needs 40 kg of sowing seed. Given that 100 seeds on average weigh

Table 3. Average cross-pollination rate between a variety and off-types in rice fields, estimated for samples collected in four villages

	Tujereng	Kitti	Faraba	Janack	Total
Total number of samples	44	12	16	18	90
Average percentage of off-types in samples	14.9	10.8	6.4	4.4	9.1
Average cross-pollination rate between variety and off-types[a]	0.22	0.17	0.10	0.08	0.14

[a] Using the formula $x/0.5 \times y/0.5 \times z$, where x is the percentage of pollen of the variety of the total of pollen from the off-types and of the variety reaching the stamens of the off-type plants, divided by the percentage of pollen in an experiment with equal distribution of two genotypes (like in Roberts *et al.*, 1961); y is the percentage of plants of the off-types of the total of plants of the off-types and of the variety in a field, divided by the percentage of plants with an equal distribution of two genotypes, and z is the average crossing rate in rice of 0.5%.

2.5 g, 40 kg contains 1.6 million seeds, of which about 2200 will be hybrids. To obtain that quantity, she needs to harvest an area of about 400 m^2, which contains ± 12.000 plants, of which up to 55 plants will be the product of hybridization. Depending on the skill of the farmer at recognizing rice types, time available for sorting panicles and distinctiveness of the progeny of the hybrid plants, there is a chance they will be (1) missed at harvest and included in the seed for next year, (2) harvested separately to be sown in a separate plot in the next year, or (3) rogued and eaten.

Usually, varieties with a distinct husk colour and shape contain fewer mixtures, and chances of cross-pollination are smaller, whereas varieties with a non-distinct husk colour and shape contain more off-types (also with non-distinct husk colour), and chances for cross-pollination are higher. However, in the latter case, products of cross-pollination can often go unnoticed because they also inherit the non-distinct husk colour and shape of their parents.

Level of cross-pollination between rice plots

Research on the rate of cross-pollination in relation to distance suggests that the cross-pollination rate for rice decreases over distance in an exponential way (Beachell *et al.*, 1938; Messeguer *et al.*, 2001; Messeguer *et al.*, 2004). For comparison of the rate of cross-pollination within plots and rate of cross-pollination between plots, the study by Srinivasan and Subramanian (1961) is very useful. In their experiment, in which they planted two varieties side by side, they found no cross-pollination further than 2.1 m. Using a similar set-up, Messeguer *et al.* (2001) found no cross-pollination at 2.4 m. Studies with an open space of 9–10 m between two varieties showed very low levels of cross-pollination (Beachell *et al.*, 1938; Messeguer *et al.*, 2004). Findings from Srinivasan and Subramanian (1961) and Messeguer *et al.* (2001) resemble actual field settings.

For those fields and plots for which flowering period was recorded, the chances of cross-pollination between different varieties in neighbouring fields were calculated for each of the three areas in Tujereng described earlier (Fig. 1). The average cross-pollination rate between plots over a distance of 3 m found by Srinivasan and Subramanian (1961) of 0.035% is used in the formula below. The path between plots is about 0.5 m wide. Hence, a distance of 2.5 m instead of 3 m is used for the calculation of the area where cross-pollination is possible. A problem is that the rate of cross-pollination decreases exponentially over distance, which means that the chances of cross-pollination in the area subtracted for the path (0.5 m) are much higher than 1 m away from the border. The calculations below are thus a slight overestimation of the chances of cross-pollination between plots. Per plot, the rate of cross-pollination with neighbouring plots was calculated as follows:

Total area of a plot where cross-pollination with

different varieties in neighbouring plots is possible

× level of overlap in flowering between fields

× average cross-pollination rate of rice/total plot area

The cross-pollination rates are only calculated for those plots of which the flowering in neighbouring plots was recorded. The cross-pollination rate ranges between 0.000% in Area 2 and 3 to 0.023% in Area 1. Per area, the average cross-pollination rate is calculated over all plots. The overall average cross-pollination rate between different varieties in neighbouring fields is 0.005% (Table 4). The average in Area 1 is much higher than in Areas 2 and 3. The higher pollination rate in Area 1 is caused by the high number of varieties sown and the relatively small plot sizes in that area. In Area 2, the rate is lowest, because in many neighbouring fields, the same varieties are sown and different varieties grown in neighbouring plots differ in flowering period, either caused by differences in growth period or through differences in sowing dates. The low rate in Area 3 is caused by the relatively low number of varieties sown and by the large plot sizes.

The average cross-pollination rate between different varieties in neighbouring fields is about 25 times lower than the average cross-pollination rate between varieties within fields, being 0.14%. Both values represent cross-pollination rates at field level. This means that new genotypes are more likely to develop through cross-pollination between varieties within fields than between varieties in different (but adjacent) fields.

This comparison is partly based on data from Tujereng. The average area per variety is larger in most other villages, similar to Area 3 (Nuijten, 2005). This means

Table 4. Average percentages of cross-pollination in rice at plot level between neighbouring plots with different varieties if 0.035% is assumed as the average cross-pollination rate over a distance of 3 m, calculated for three upland rice areas in Tujereng

	Number of plots[a]	Number of varieties	Pollination rate	Range
Area 1	24	14	0.009	0.001–0.023
Area 2	19	10	0.002	0.000–0.006
Area 3	26	8	0.003	0.000–0.009
Total	69		0.005	

[a] For these calculations, only those plots were included, which were surrounded by rice plots or forest edges.

that the difference in cross-pollination between plots and within plots is likely to be larger in other villages. From this information, it can also be understood that in villages where two or three varieties are commonly used, the level of cross-pollination between fields will be lower than in villages where no common varieties can be identified and where, at village level, farmers grow a larger number of varieties.

A comparison with millet

Here the factors influencing pollen flow in millet fields are briefly described, to help bring out what is distinctive about the situation with rice. We are aware that in addition to crop breeding systems, rice and millet differ in other traits, such as plant architecture, and size and shape of the inflorescence, and that not all differences in variety development by farmers can be directly related to crop breeding system.

Influences of cultivation practices on pollen flow

The sowing dates of millet fields differ. When the millet is directly seeded, the millet may be sown before the first rains, between late June and early July. When oxen are used to plough the field first, sowing is after the first rains, between mid and late July, depending on the availability of oxen. Some farmers who use the fulcrum shovel (typically used by Jola and Balanta lowland rice farmers) for ploughing may plant up to late July. Furthermore, soil fertility, and time and frequency of weeding also influence plant development, and thus time of flowering. A certain degree of photoperiodic sensitivity of late millet (contrary to early millet) means that differences in farming practices cause small differences in flowering between late millet fields. Because of extended within-field flowering periods, in general, there is a considerable overlap in flowering, with the main flowering occurring between mid and late October.

Some fields are next to each other, while other fields are rather isolated. The locations of the fields change every few years (particularly those worked by migrant strangers who do not own land they farm), and in that way the different fields, and the millet gene pools, of different farmers can become connected to each other at various points in time, e.g. because farmers carry their seeds to new sites. Since millet fields are planted in upland areas where land is relatively abundant, they can be situated anywhere in the village, and at times, this will bring them close to millet fields farmed by men from other villages. Hence, the millet gene pools of various villages could, in principle, be connected through pollen flow between their fields. The more densely populated an area is and the smaller the distances between villages, the more likely that millet fields of neighbouring villages are situated next to each other.

The guidelines for millet seed production indicate that to prevent cross-pollination between fields, the isolation distance should be at minimum 400 m (Gupta, 1999). This suggests that gene flow is possible between distant fields. However, under experimental conditions, the rate of cross-pollination was 3.7% at a distance of 1 m and only 0.02% at a distance of 55 m (Burton, 1974). It is possible that because of the set-up of the experiments, these rates of cross-pollination are somewhat underestimated, but they do indicate that effective cross-pollination over longer distances is very limited. Insects are another common vector of cross-pollination in millet, but it is unclear over what distances cross-pollination by insects is effective (Leuck and Burton, 1966). So although, theoretically, gene flow through pollen is possible between villages, the rate of this gene flow is likely to be negligible.

Mixtures and off-types

For millet, many farmers at first said they did not have off-types in their field. Further on in the research, cycle responses were clarified. Now, millet farmers said they had some off-types, but could not clearly describe which plants belonged to the variety and which to the off-types (Nuijten, 2005). Hence, it was not possible for them to separate off-types from varieties, as was done by farmers for rice. The remark ‘millet is millet’ was often used by farmers during interviews. This may explain why farmers only grow one variety of millet. Many farmers perform some kind of selection to obtain good quality sowing seed, but also to keep the right characteristics in their variety. Although the sample sizes are not large enough to permit statistical testing, it is indicative that in Foni region, where all farmers grow *white sanyo*, sowing seed contained fewer black grains (16.4%, nine samples) than the *white sanyo* grown in Kombo region (22.4% black grains, six samples), where many farmers grow *black sanyo* instead of *white sanyo*. Most *black sanyo* grown in Kombo also often contained a small percentage of white grains (11.8%, 18 samples). One farmer in Kitti (part of Kombo region) had purposefully mixed the two varieties in a close to equal ratio.

Level of cross-pollination within and between millet fields

Because it is not possible to define objectively what makes an off-type in millet, the exact percentages of off-types are not known. Hence, it is not possible to give estimations for cross-pollination between a variety and off-types within a field, as has been done for rice. As the seed samples of *white sanyo* collected in Kombo region contained more off-types than the *white sanyo* samples from Foni region, it is suggested that cross-pollination between *white sanyo* and black-seeded off-types is more likely to occur in Kombo region than in Foni region. It seems likely that the cultivation of several varieties within a villages leads to higher levels of seed mixture with the result of more cross-pollination within fields. Furthermore, it is likely, given the exponential decrease in pollination rates over distance (Burton, 1974), that cross-pollination occurs more readily within fields than between fields, similar to the situation for rice.

Discussion

The data presented in this article show how cultivation practices affect mixtures of varieties in the field and the chances of gene flow within and between fields. It has been shown that the chances for genetic recombination in rice are much higher within fields than between fields. In all, it can be seen that effective pollen flow is a function of a number of factors:

(1) Cross-pollination rate of a crop: the higher the rate, the more likely cross-pollination occurs between different genotypes.
(2) Number of off-types within fields: this is the result of variety distinctiveness, farmer expert knowledge, amount of time a farmer spends on seed selection and farmer preference for maintaining off-types in a field.
(3) Distinctiveness of varieties: the less distinctive a variety, the higher the number of off-types in a field.
(4) Expert knowledge of farmers: older women tend to have more expert knowledge, but certain young women brought new varieties into the village, possibly creating new opportunities for cross-pollination between different genotypes.
(5) Length and reliability of the rainy season and growth duration of different varieties: if women grow several rice varieties of different duration, they often sow the late maturing varieties first and the early maturing varieties later, resulting in simultaneous flowering, and thus enhanced possibilities for cross-pollination between these varieties.
(6) Availability of fields: rice lowlands are often scarce in The Gambia, so women are forced together in the same area. Whereas upland fields suitable for millet cultivation are often abundant, upland rice fields are often found in clusters to make labour for clearing easier.
(7) Pest pressure and field location: upland rice is often grown in or near forested land, where, apart from birds, other pests like monkeys, grasscutters and rabbits are common. To reduce the border area with the forest, women prefer to cluster their fields as much as possible.
(8) Number of varieties grown per field: for rice, several varieties are grown per field, not only allowing more cross-pollination, but also increasing the chances of (physical) mixing of seeds.

Although chances for cross-pollination in rice are low, field layout and farming practices tend to enhance whatever chances are present. It so happens that for millet in The Gambia several of these factors tend to be limited, and the chances for the development of new varieties of millet are very small. In the case of millet, farmers predominantly grow the same variety within a village. The consequence is that pollen flow between neighbouring fields will result in the exchange of the same genetic information. This is unlike Nigeria, Burkina Faso and Niger, where farmers grow several varieties of millet, usually three (Busso *et al.*, 2000; Berthaud *et al.*, 2001), or maize in Mexico, where each farmer grows several varieties (Bellon and Brush, 1994; Louette, 1997). Compared to Gambian farmers, maize farmers in Chiapas in Mexico have a much wider sowing window (of up to 6 weeks), which can both increase and decrease chances of cross-pollination between different varieties (Bellon and Brush, 1994). Mexican maize farmers, however, do not seek to isolate different varieties (Louette, 1997). The wider sowing window enables farmers to choose to vary the sowing dates of early and late maturing varieties, with the effect that the flowering of varieties with the same duration may not coincide and that the flowering of varieties with different durations may coincide.

The effect of breeding system

Even though cross-pollination in rice is very low, there are possibilities for the emergence of new varieties and genetic variation in rice, whereas this is less likely to happen in millet (Nuijten and Almekinders, 2008). Because millet is an outbreeder and varieties show a wide intra-varietal diversity, new genotypes are not discovered so easily by farmers, and of the few that are discovered it is often their fate to segregate and disappear again in the gene pool. If two rice varieties cross-pollinate, however, a new genotype can develop which does not lose its characteristics through continuous cross-pollination since rates of outcrossing in rice are so low.

Irrespective of the breeding system of a crop, cross-pollination within fields is generally larger than between fields. One might expect that given the large isolation distances (400 m) used for a crop like millet in seed multiplication programmes (Gupta, 1999), pollen of millet travels much further than that of rice. However, because cross-pollination rates at distances greater than 20 m are negligible (Ehrlich and Raven, 1969; Burton, 1974), the effect of cross-pollination between millet fields is negligible, even though millet has a much higher outcrossing rate than rice. In maize, cross-pollination in the borders of neighbouring fields is considerable, up to 60%, but rates 15 m away from the border are very low (Gonzalez and Goodman, 1997). In another study on maize, cross-pollination rates between fields decreased from 10 to 20% in the first row to 1% after 2–3 m (Louette, 1999). For many other crops, distances greater than 15 m may effectively isolate plant populations (Ehrlich and Raven, 1969). This does not mean that no pollen flow occurs between fields at distances larger than 15 m from each other, but that the effect of pollen flow between fields will be very small in relation to that of pollen flow within a field.

Level of mixtures within varieties and the development of off-types

Gambian farmers discard off-types from their sowing seed, but often do not purify their seed completely. Up to one third of the seed may consist of off-types. Whereas Gambian women farmers do have clear descriptions of rice varieties, Gambian men farmers do not have clearly defined descriptions of millet varieties. This is not to be explained through any greater affinity of women for seeds. Experiments with both groups of farmers indicated that there is no difference in men's and women's capacity to distinguish and group rice panicles and millet spikes (Nuijten, 2010). Instead, men's lack of descriptors for millet aligns with the fact that morphological variation in millet is continuous, rather than discontinuous, as in rice. This continuous variation in millet is confirmed by molecular analysis (Nuijten and Van Treuren, 2007). As a consequence, it is more difficult for farmers of either gender (and scientists) to estimate the level of varietal mixture in millet.

The number and types of off-types to be found in rice varieties depend on the extent of farmer seed selection efforts, the distinctiveness and duration of cultivated varieties and off-types, farmer variety portfolios, and the range of varieties grown by other farmers in the village. Particular varieties are sown mixed and, for experimentation, new varieties are often sown in a mixed stand. Although some varieties seem to survive more easily as mix-ins than other varieties, the off-types found in farmers' fields can be considered a function of variety use and selection dynamics, both past and present.

Discovery of new varieties by farmers

In the research area, many more rice varieties exist than millet varieties. Because of the low cross-pollination rate in rice, new varieties develop, whereas the high cross-pollination rate in millet inhibits new distinct varieties from forming. Following Slatkin (1987), gene flow is a creative force in rice, whereas in millet, it is a constraining force. This partly explains why women more readily explained the possibility of strange off-types appearing in their fields. These plants will be easily recognized if they have distinct plant height, flowering period, husk colour or spikelet shape. Farmers with a sharp eye for detail even notice off-types that differ only slightly in spikelet appearance. Thus, recognizing a difference in plant morphology, particularly in relation to the inflorescence, is the first phase of the selection process for new varieties. The second phase is testing of the distinct off-type on farm to see whether it performs well and has the required height and flowering period. The third phase is testing in the cooking pot, once there is sufficient of the new rice to be eaten. The argument that off-types must be distinctive from existing varieties to be recognized and selected as types before they can be further selected for utilitarian characteristics has also been emphasized by Boster (1985) for cassava (*Manihot esculenta* Crantz).

This selection process explains the large variation in inflorescence morphology typical not only of rice in The Gambia, but also of various crop farming systems worldwide (Lambert, 1985; Voss, 1992; Bellon and Brush, 1994). For millet, farmers predominantly rely on spike and seed characteristics to differentiate varieties, particularly seed colour and presence of bristles. In millet, however, differences in spike shape, bristle colour and bristle length are not so clear, compared to rice, because of the genetic and morphological variation within varieties maintained by pollen flow. Morphological variation within varieties tends to be more continuous in millet, whereas in rice, it can be defined in distinct classes. Additionally, it is harder to see differences in seed shape and size of millet, because seeds are not that clearly visible when still attached to the spike in the field or during selection (Nuijten, 2005). Using inflorescence-related traits to differentiate varieties seems to be widespread among many food crop farmers. Lambert (1985) mentions that Indonesian rice varieties show large phenotypic diversity and that farmers distinguish varieties by traits related to the inflorescence, such as husk colour and grain size, shape, texture and colour. Voss (1992) notes that farmers growing beans (*Phaseolus vulgaris* L.) in Central Africa often use seed characteristics to differentiate varieties. For maize, farmers also predominantly use seed and cob traits to identify varieties and associate these traits with agronomic and use characteristics (Bellon and Brush, 1994).

Translation into a more general mechanism

It might be argued (following Slatkin (1987)) that the lower the rate of pollen (gene) flow the more it works as a creative force. However, it is obvious that as the rate of gene flow approaches zero, this creative force must also decrease and disappear. This suggests that there may be an optimum (low) level of gene flow for creativity. Given consistent, worldwide reports of farmer ability to select new rice types from among local stocks of planting material, it seems likely that the rate of pollen flow of rice approaches this optimum rate, but how close remains unclear. Possibly, the optimum rate is somewhat higher than that which normally occurs for rice (Fig. 2), as is suggested by observations on beans and sorghum. In the case of beans in Central Africa, the cross-pollination rate is 2% (Voss, 1992), higher than for rice, and farmers grow mixtures of beans, on average containing 20 varieties (Sperling *et al.*, 1993), even higher than the number of mixed-in rice varieties found in this study. In the case of sorghum in Ethiopia, which has an average cross-pollination rate of 5% (Doggett, 1988), Ethiopian farmers often plant mixtures of up to 20 sorghum varieties in their field (Teshome *et al.*, 1999; Seboka and Van Hintum, 2006). Compared to the average rate of cross-pollination of rice of 0.5%, a rate of 2–5% seems to promote gene flow and creation of new genotypes, but does not lead to varieties losing their distinct characteristics. A comparative study on millet and sorghum diversity in Niger found about twice as many variety names for sorghum than for millet (Bezançon *et al.*, 2009), which supports the observed pattern in varietal diversity found for rice and millet in this study.

Farmer action may in certain circumstances add to the creative force by artificially (if unintentionally) raising outcrossing rates, e.g. by tolerating or encouraging mix-ins. This seems to be the case for rice in The Gambia, but less for millet. In North-western Sierra Leone, some groups of farmers deliberately plant interspecific rice mixtures to stimulate variety adaptation (Longley and Richards, 1993; Jusu, 1999). The mixed cultivation of several subspecies and species promotes the development of new genetic diversity. This has been noted for rice in parts of West Africa (Nuijten *et al.*, 2009). Under certain conditions, farmer practices may also stimulate outcrossing between cultivated crops with wild and weedy relatives, such as for rice and millet in The Gambia (Nuijten, 2005), and for sorghum in Ethiopia, Niger (Tesso *et al.*, 2008) and Cameroon (Barnaud *et al.*, 2009).

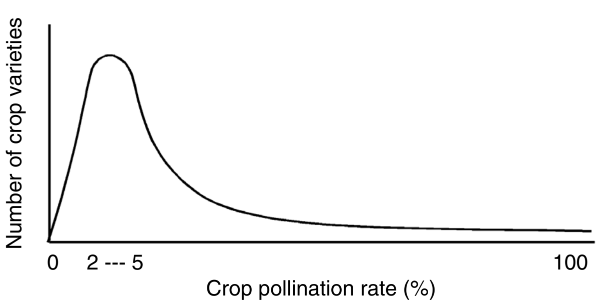

Fig. 2. Relationship between crop pollination rate and the number of varieties developing in farmers' fields for crops reproducing through seed.

This mechanism might also help to explain the large diversity in potato (*Solanum* sp.) farming systems in the Andes. Cross-pollination followed by human selection is suggested to explain the large diversity in these systems (Quiros *et al.*, 1992). The cross-pollination rate in potato is higher than in sorghum, but new potato genotypes become fixed in one generation because potato is (in cultivation) a vegetatively propagated crop. The high cross-pollination rate in potato does not lead, therefore, to a blurring of distinct characteristics, as in millet or maize. This explanation may also explain the large diversity in sweet potato (*Ipomoea batatas* (L.) Lam.) in Irian Jaya. Here, farmers are aware that sweet potato volunteer seedlings are potential new varieties, which in combination with the vegetative reproduction explains the existence of over 1000 local varieties in an area that is not part of the presumed centre of origin of sweet potato (Schneider, 1999).

Two further issues to be factored into any comprehensive model of crop varietal development under farmer management are seed multiplication rates and what happens to early selections (F1–F4 generations). Bray (1986) mentions that rice has a higher seed multiplication factor than the comparable cereals wheat (*Triticum aestivum* L.) or barley (*Hordeum vulgare* L.). The level of the multiplication factor is also related to the growth conditions, rice often being grown in more favourable areas than wheat and barley. Because of the high seed multiplication factor, often only one multiplication cycle is needed to obtain from a few rice panicles an amount of seed sufficient for testing. Consequently, in only a few years, farmers will know whether a rice variety has potential or not. Millet has an even higher multiplication rate than rice, but off-types lose their distinctiveness through cross-pollination. The multiplication rate of sorghum is also higher than of rice. This is presumably an important factor in facilitating the development of new sorghum varieties in Ethiopia, together with the cross-pollination rate approaching the presumed optimum in Fig. 2.

In The Gambia and South Senegal, a number of women said they never saw rice off-types change, when selected for testing. This would imply that they never select F1–F4 generation plants for testing. Allard (1988) indicated that the yields were low for first generation barley crosses, but increased tremendously from the F1 to the F5 generation through an increase in the number of seeds per inflorescence. Those women who claim that off-types show no further change may be missing earlier generations because they are not 'impressive to their eye' (as they sometimes say). The implication, however, is that selection pressures during F1–F4 generations are 'built-in' to on-going farming practices in ways not entirely clear. This matter requires further investigation and may provide important information for linking farmer crop development with formal crop development.

Acknowledgements

This research was financially supported by NWO–WOTRO (Science for Global Development). The authors thank the National Agricultural Research Institute of The Gambia, the field assistants and all collaborating farmers (particularly those from Tujereng) for their support. The authors want to thank Conny Almekinders and two anonymous reviewers for their comments on earlier versions of the manuscript.

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