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Farmers' practices, metapopulation dynamics, and conservation of agricultural biodiversity on-farm: a case study of sorghum among the Duupa in sub-sahelian Cameroon

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Abstract

In many traditionally managed agroecosystems, populations of domesticated plants maintain high levels of genetic diversity. The threat of erosion of this diversity is a current conservation concern, motivating studies of how diversity can be maintained by in situ conservation measures. Precisely how the biological traits of plants and the cultural practices of farmers act on fundamental evolutionary forces – drift, migration, selection, and mutation – to create and maintain crop plant diversity has been little investigated in detail. We develop some elements of the framework required for studying such biocultural interactions, focusing on one component of management: farmers' decisions on what to plant, and the structure of germplasm exchange among farmers. We illustrate the approach with a study of Duupa farmers in northern Cameroon. Our results suggest that sorghum populations managed by the Duupa function like source–sink metapopulations. Fields of older farmers, larger and containing a greater number of varieties, act as sources, whereas fields of younger farmers act as sinks, becoming sources as their owners mature. In each field, seeds for sowing are selected from a small number of plants. The frequent exchange of germplasm among fields may counteract the genetic bottlenecks associated with the small number of genitors within each field. Identifying key processes and key individuals should facilitate the design of in situ conservation measures to maintain crop plant diversity against the threat of genetic erosion.

Keywords: Farmers' practices; Population biology; Evolutionary forces; Sorghum; Duupa

1. Introduction

In many traditional agroecosystems, genetic diversity within crop species has important functions. Varieties of the same species not only differ in their cultural roles, e.g., the uses to which they are put, but also in their ecological tolerances. As used here, a "variety" is a category of plants recognized as a separate entity by farmers, based on morphological and other traits (see for example Zeven, 1998).

Farmers cultivate crop populations in environments that are heterogeneous in space and often unpredictable in time, and varieties often differ in their response to such variation. Genetically diverse populations may also be less susceptible to high levels of attack by pathogens and herbivores. Thus, in systems where farmers have limited capacity to control spatial and temporal environmental variability with material inputs, planting a diverse assemblage of genotypes can lower the risk of failure and increase food security (Altieri, 1999). Diversity matters not only within farmers' fields, but also

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at the level of farmer communities. Farmers count on the diversity present in other farms, to get new seed lots when they need them. Seed exchange may even extend as far as cyclic renewal of seed lots (seed change), a frequent feature in traditional agricultural systems (Louette et al., 1997; Zeven, 1999; Louette and Smale, 2000).

The positive valuation of agricultural biodiversity has progressively led to an extraordinary store of genetic diversity. Nevertheless, recent socio-economic changes threaten this diversity. Modern varieties, created to satisfy particular criteria, and environmental modifications that favour these varieties, may leave little place for local varieties. Longer-term adaptation to a fluctuating and heterogeneous environment, or to a rich cultural context, may thus be compromised (Brush, 2000).

There are two broad approaches to conserving agricultural biodiversity. First, the ex situ approach attempts to maintain genetic resources outside of agroecosystems, in germplasm banks. Whereas such preservation may prevent the extinction of abandoned varieties, it stops or greatly alters the evolutionary processes that mould the populations' diversity (Oldfield and Alcorn, 1987; Brush, 1995). Second, in situ approaches (or on-farm conservation) aim to maintain the existing genetic resources on-farm, allowing evolutionary processes to maintain and continue to create diversity (Cleveland et al., 2000; Maxted et al., 2002). The two approaches have complementary advantages and drawbacks (Brush, 2000). However, the scientific basis for in situ dynamic conservation remains weak. All agree that cultural practices of farmers are important in maintaining diversity, but much information is anecdotal (Louette and Smale, 2000). Which practices are important, and how they affect fundamental evolutionary forces to maintain genetic diversity, are poorly understood.

1.1. First understand, then manage

In the past decade, agronomists have carried out studies on how innovations they consider desirable could be propagated in traditional agroecosystems, e.g., by examining the insertion of new varieties into local seed systems (e.g. Cromwell, 1990; Voss, 1992; Almekinders et al., 1994), or by developing participatory management approaches in which plant breeders work with farmers to develop new varieties (e.g. Witcombe et al., 1999). In contrast, too few studies have considered how traditional systems work. The enormous socioeconomic and ecological changes facing many farming communities surely modify the functioning of crop populations in many ways. Developing effective on-farm programs to maintain adaptation in the face of such change depends first of all on a solid understanding of how farmers have through ages created and maintained crop diversity and persist in doing so without outside help in large parts of the world. Farmers' plant breeding must be understood in terms of the same theoretical principles that underlie both professional plant breeding (Soleri and Cleveland, 2001) and the functioning of wild plant populations.

Few studies examine how farmer practices affect evolutionary forces acting on crop plant populations, and only a small proportion of the possible interactions have been treated. These studies focus, for example, on farmers' criteria in seed selection and the goals of selection (Louette and Smale, 2000); on choices among varieties (Bellon, 1996; Cleveland et al., 2000); and on spatial arrangement of planting in ways that encourage hybridization between varieties (Cleveland et al., 2000; Perales et al., 2003). As numerous aspects of crop-plant ecology and population genetics remain unexplored, there are large gaps in our understanding of the evolutionary genetics of crop plants in traditional agroecosystems. These gaps limit the effective application of in situ conservation approaches.

1.2. Natural and human factors interact to shape evolutionary forces

Natural factors and human management are inextricably linked and jointly shape the genetic diversity of crop plant populations. Natural factors comprise both environmental pressures and biological traits of the plant that affect its population structure. Human management modifies not only selection pressures but also population structure, thereby affecting drift, migration, and metapopulation dynamics (Jarvis and Hodgkin, 1999). Natural and human factors interact. For example, the breeding system of many crops depends not only on inherited traits of the plant (e.g. self-incompatibility), but also on the number and the disposition of varieties planted in the same field (Cleveland et al., 2000; Perales et al., 2003).

Farmers make many kinds of decisions all through the chain of agricultural operations that affect genetics of crop plants. Research generally focuses on the selection of seeds for planting, but other segments of the chain, e.g. how varieties are associated (or segregated) in space during planting, are often neglected. Even for seed selection, many aspects are poorly studied, such as the proportion of seeds that are planted by the farmer who produced them, the proportion that migrate through farmer exchange, the period and modalities of selection, and the structure of the local system of seed exchange.

1.3. Populations and metapopulations of crop plants

Crop populations must be considered as structured populations. Subpopulations are managed by different farmers in spatially discrete fields, which are submitted to different evolutionary forces and exchange migrants.

Subpopulations sometimes go extinct, as farmers replace seeds from sources other than their own seed (Zeven, 1999; Louette and Smale, 2000). Here, population extinction is immediately followed by massive migration, in a way different from natural structured populations in wild plants. Hence, there is a need to model this structure and examine its consequences for the population genetics of crop plants. Such a model should incorporate the following parameters:

1. Variation among farmers in their practices or knowledge, which may be a function of social categories (age, sex, social status) or other sources of variation (individual preference, familial history). In studies of structured crop populations, the average farmer does not exist.
2. Exchanges among farmers. If certain patterns are predictable, the migration web among subpopulations can be estimated.
3. Impacts of social or economic changes, which may act at a larger scale of time and space. Contemporary patterns and mechanisms at the local scale must be placed into the context of the regional history of diffusion of crop germplasm (for sorghum see Seignobos, 2000), and even the history of initial domestication and diffusion of the crop (Harlan, 1989).

1.4. Applying the approach: a preliminary case study

We conducted a preliminary study among the Duupa, farmers in sub-sahelian northern Cameroon, with the goal of clarifying some of these parameters, and examining how farmer practices related to planting and harvesting can influence crop population structure and the action of selection. We investigated the local seed system with particular emphasis on the structure of exchanges, and on the way the germplasm for planting is selected. We also analysed variations in Duupa farmer practices and longer-term changes, whose impacts on population processes is less predictable. By identifying fundamental questions and the kinds of data needed to answer them, we aim to design more precise studies of the knowledge and practices of farmers, and thereby to plan the population genetic studies required to test the hypotheses generated.

2. Methods

Our study was conducted in the Duupa village of Wanté (8°27′N, 13°18′E). The Duupa comprise 4000 people occupying about 1000 km^2, in the Bénoué plain and mountainous Poli massif. The Duupa are mostly sedentary farmers, cultivating a great diversity of subsistence crops, such as yams, cowpea, groundnuts, okra, and cereals. The latter include pearl millet, eleusine, and most important of all, sorghum (Garine, 1995). Accounting for more acreage than any other crop, sorghum grown by the Duupa is also highly diverse. We found about 25 locally recognized and named 'varieties' in this single village, and perhaps twice this number occur in the region occupied by the Duupa (Garine, 1995). These varieties are planted in polyvarietal mixtures, with a mean of around nine in a single field. Several races of sorghum, including guinea, guinea-caudatum, and kafir-durra, are represented among Duupa varieties, which collectively exhibit great morphological diversity (Garine, 1995).

2.1. Sorghum cultivation among the Duupa

Sorghum (*Sorghum bicolor* [L.] Moench) is at the centre of Duupa diet, and is also an important element of the social system, since all social and ritual occasions, e.g., exchange of services and bouts of communal work (*kombuma*), are articulated around the invitation to drink sorghum beer, called in the Duupa language *buma*.

Wanté village is a relatively isolated settlement, where approximately 20 families share flat to gently rolling lands covering a total surface of almost 10 km^2.

In the Duupa society, every active adult works in his/her own field. However, some women and many children work in the field cultivated by the head of the household. The location of a farmer's field may change from year to year, and the same parcel may be used by different farmers in successive years. Land is collectively owned by the village community as a whole. Agricultural work is performed in different ways. For some tasks, the farmer works alone or with his household. For other tasks, such as harvest, a farmer organises *kombuma*, where his extended family, neighbours, and affines are invited to work. This "employment" is free, except for the rule of reciprocity. Sorghum beer, produced from germinating sorghum seeds, is an indispensable ingredient of every social meeting, including collective work parties like *kombuma* (Garine, 2001).

Such a conservative society provides good conditions to study the impact of farmers' practices on the continuing evolution of crop plants. The Duupa agricultural activities begin with the planting period, from late April–May. This period corresponds to the first rain of the rainy season. During the growing season (April–October), fields are weeded two (or three) times, and sorghum is harvested from early December to late January (Garine, 1995). Threshing of the harvested crop can take place from early February to late March. In March and April, the stocks of seeds are set aside for planting, and can thus be observed. Hence, we conducted the interviews during the months of March and April 2001, a time corresponding both to the period when seed stocks are present and to the lowest activity in the Duupa agricultural calendar. Nevertheless, we were sometimes unable to examine the granaries, since many Duupa farmers believe that to show seeds to strangers can cause misfortune.

Interviews were conducted with the help of a Duupa interpreter. We interrogated 32 Duupa farmers (19 men and 13 women) belonging to 19 of the 20 households present in Wanté. The interviews were carried out separately with each person, to avoid collective answers that rarely reflect individual strategies. Despite the relatively small sample size, our study is exhaustive in Wanté, including almost all households of the village. Increasing the sample size would have required extension of the study to other villages, which was infeasible given our logistical limitations and the time-consuming nature of the ethnobiological approach. For each farmer, we recorded gender and age, which crops he/she cultivated, and the total area cultivated. During the inquiries, we focused on determining the modalities of several key factors, all partially or completely dependent on farmer behavior, capable of modifying selection pressures and crop plant population structure. These include the *local seed system* (seed exchanges leading to immigration and emigration events), *seed selection practices*, which determine the percentage of plants that play the role of female genitors for the next generation (and thereby influence selection and genetic drift) and the *way crops are propagated*, which influences the plant's breeding system. In the results, we consider only sorghum, which is cultivated by 90% of the farmers we interviewed.

2.2. Local seed system

The structure of the local seed system depends on several factors, most of them based on human social factors. We focused our interviews on the following questions:

1. Do you give seeds away (or sell seeds)?
2. Do you receive seeds from others (or buy seeds)?
3. What was (were) the source(s) of the seeds you used for your most recent planting?

The pertinence of farmers' answers was directly tested during inquiries by asking the same question in different ways. Responses to the third question enabled verification of the concordance of responses to questions 1 and 2. Strictly quantitative answers were neither expected nor obtained. We classified each farmer's answer in categories (*never*, *rarely*, *sometimes*, *at least once a year* for questions 1–2 and in *own seeds used*, *seeds obtained elsewhere*, or *both* for question 3. We then examined the relationship of answers to these questions to the following factors, which present two or three modalities: farmer's gender, farmer's age (distributed over three roughly equally sized groups: *less than 36 years old; between 36 and 56 years old; 56 years old or more*), destination of the last harvest (*farmer's own use only* versus *own use and exchange*), number of varieties cultivated (*less than the mean number of varieties per farmer; more than the mean number of varieties per farmer*), and area cultivated over the previous years 1999–2000 (*less than half the mean area cultivated by all farmers sampled; between half the mean and 1.5 times the mean; more than 1.5 times the mean area cultivated.* "Area cultivated" (see Table 1) was estimated by the farmer him/herself. From inspection we made of parcels cultivated in the previous year, such estimates appeared realistic. However, an imprecision in these estimates arises from the fact that crops are planted in polycultural associations. Sorghum is by far the dominant crop in fields, so estimates of field size for this crop are probably less affected by this bias than those for other crops.

2.3. Seed selection practices

The way farmers select the seeds to plant in the following year is directly linked to the proportion of plant individuals that will play the role of female genitors (i.e., mothers of the next generation) in the field. This proportion depends on several factors, but most importantly on the moment in the crop cycle at which seeds are selected. Duupa farmers choose sorghum seeds before panicles are threshed. They preferably choose infructescences of a few individuals, which provide them with all the seeds required, and the proportion of plants serving as female genitors is low. Consequently a few individuals provide the bulk of seeds for the next generation. We estimated the proportion of plants selected as female genitors in the fields of five Duupa farmers: We first estimated the total number of panicles harvested, by asking each farmer how many baskets -the standard measure used locally – he/she had filled with panicles during harvesting. According to our observations, one full basket contains about 150 panicles. The number of panicles conserved to provide seeds for the next planting was simply counted during interviews with each farmer. As a sorghum plant produces almost always only one panicle, the proportion of plants selected as female genitors can thus be estimated by the number of panicles selected to provide seeds divided by the total number of panicles harvested.

2.4. Propagation of crops

Sorghum is self-compatible, but substantial levels of outcrossing (up to 15%) occur under traditional farming systems (Dje et al., 1999). Mating structure is affected by the spatial patterns in which varieties are planted in fields. We interviewed farmers to obtain descriptions of

Table 1
Frequency of cultivation, number of varieties, and area cultivated for crop plants grown in Wanté village

Crop species	Total area cultivated	Sorghum	Cowpea	Groundnut	Okra	Yam	Cassava	Bambara groundnut	Maize	Finger millet
		Sorghum bicolor	*Vigna unguiculata*	*Arachis hypogaea*	*Abelmoschus esculentus*	*Dioscorea* spp.	*Manihot esculenta*	*Voandzeia subterranea*	*Zea mays*	*Eleusine coracana*
Percentage of farmers cultivating the crop ($N_{tot} = 30$)		90	73.3	63.3	50	33.3	30	13.3	13.3	13.3
Total number of varieties cultivated in the whole village		25	4	4	?[a]	6[b]	3	1	3	1
Mean number of varieties per farmer cultivating the crop		9.1 ± 5.1	2.2 ± 0.9	2.1 ± 0.9	?[a]	3.5 ± 1.3	2.0 ± 0.9	1.0 ± 0	1.4 ± 0.5	1.0 ± 0
Mean area cultivated (ha) per farmer cultivating the crop	0.75 ± 0.59	0.5 ± 0.49	0.08 ± 0.05	0.23 ± 0.08	–	0.11 ± 0.5	0.12 ± 0.1	0.03 ± 0.03	0.08 ± 0.03	0.12 ± 0.1

[a] Only one okra variety was cited by the farmers interviewed, but in previous years many farmers had more than one variety (E. Garine, unpublished field notes). The reason for this discrepancy is unclear.

[b] Previous field work had shown the presence of more than 10 varieties in Duupa villages. This value (6) may therefore be underestimated.

Table 2
Differences related to sex and age of farmers in the proportion of individuals that cultivate different crops, and in the total area cultivated

Cultivated crop		Total area cultivated		Proportion of farmers that cultivate or not cultivate (in %; $N = 30$)									
				Sorghum		Cowpea		Groundnut		Okra		Yam	
		<3/4 ha	$\geqslant$ 3/4 ha	Cultivate	Do not cultivate	Cultivate	Do not cultivate	Cultivate	Do not cultivate	Cultivate	Do not cultivate	Cultivate	Do not cultivate
Farmer's sex	♀ ($n = 12$)	66.7	33.3	75.0	25.0	66.7	33.3	91.7	8.3	41.7	58.3	0	100
	♂ ($n = 18$)	33.3	66.7	100	0	77.8	22.2	44.4	56.6	55.6	44.4	55.6	44.4
	P	(0.143) *0.603*		(0.056) *0.292*		(0.679) *0.999*		(0.014) ***0.081***[MNS]		(0.710) *0.999*		(0.002) ***0.012*** *	
Farmer's age	< 36 years ($n = 14$)	71.4	28.6	85.7	14.3	57.1	42.9	78.6	21.4	64.3	35.7	14.3	85.7
	36–56 years ($n = 10$)	50	50	90	10	90	10	50	50	30	70	50	50
	$\geqslant$ 56 years ($n = 6$)	0	100	100	0	83.3	16.7	50	50	50	50	50	50
	P	(0.015) ***0.089***[MNS]		(1.000) *1.000*		(0.116) *0.521*		(0.289) *0.870*		(0.175) *0.684*		(0.116) *0.521*	

The number in parentheses corresponds to the *P*-value calculated with a generalised Fisher's exact test (performed with 10^6 iterations). The number in italics refers to the *P* obtained after correction for multiple tests with the method of Dunn–Šydák (Bonferroni procedure). Bold numbers indicate *P* less than 0.1. The '*' sign indicates a significant result ($P < 0.05$ after Bonferroni correction). The 'MNS' sign indicates a marginally non-significant result ($0.05 < P < 0.1$ after Bonferroni correction).

planting practices that could affect mating structure of sorghum populations. These included how seeds from different varieties were mixed before planting (which could affect their spatial distribution at very local scales) and whether different sets of varieties were planted in different kinds of fields (e.g., large fields vs. home gardens).

3. Results

3.1. Description of the agricultural system: differences related to gender and age of farmers in the cultivation of different crops and in the total area cultivated

Gender and age of farmers were correlated with several traits, including which crops an individual grew. As stated above, Duupa farmers cultivate numerous species of crop plants. Sorghum, cowpea, okra, groundnut, and yam were the crops planted by the highest proportions of farmers. Of these, all except okra are represented by multiple varieties (Table 1). As confirmed by a generalised Fisher's test (Raymond and Rousset, 1995), yam was exclusively cultivated by men in Wanté, whereas groundnut was a women's crop (Table 2).

Age of the farmer seemed not to affect preferences for any crop species. However, there was a relationship (marginally non-significant after Bonferroni correction) between the total area cultivated by a farmer and his/her age: older Duupa farmers cultivated bigger fields of sorghum than did younger ones (see Table 2).

3.2. Proportion of plants serving as female genitors of the next crop generation

Quantitative data concerning sorghum are shown in Table 3. Duupa farmers employ mass selection in choosing seeds for planting. Farmers select entire panicles, either before harvesting of the crop, or between harvesting and threshing. They select large panicles with well-filled grains. For sorghum, we estimated that 1.01% of plants contribute to the next generation. Despite the small number of farmers ($N = 5$) on which this estimate is based, variation among farmers was relatively low (standard deviation = 0.199%), justifying use of this estimate as a broad approximation.

3.3. Local seed system

The relationships between responses to the three initial questions for sorghum and the factors listed were analysed using a generalised Fisher's test. Results are presented in Table 4. Interviews reveal that exchange of seeds selected for planting is never a matter of monetary transaction, whereas some farmers may sell part of their harvest in markets. 'To give seeds away (or to sell part of the harvest)' was significantly associated with the farmer's gender (more frequent in men), age (more frequent for older farmers), destination of harvest (more frequent among farmers whose yield covered need), and surface of fields (frequency increased with surface). Furthermore, 'to give seeds away' showed a strong trend to positive correlation with the number of varieties cultivated (marginally non-significant after Bonferroni correction). 'To receive seeds from others' showed the opposite pattern for all variables examined. Its frequency was significantly negatively correlated with the area cultivated; farmers that gave seeds away – or that sold part of their harvest – tended to be less likely to receive seeds; young farmers were more likely to receive seeds than older farmers; and farmers with few varieties were more likely to receive seeds than those with many varieties. Farmers who reported that they received seeds planted fewer varieties. Source of the seeds for the most recent planting showed a trend to association with field surface: farmers cultivating large fields were more likely to use exclusively their own seeds.

Farmers reporting that they received seeds usually reported also that they did not use exclusively their own seeds in their most recent planting (χ^2 tests before Bonferroni correction, $P = 0.01$). This significant relationship further attests to the internal consistency of the responses to our questionnaires. Nevertheless, farmers that gave away seeds showed no preference in using exclusively their own seeds or not (χ^2 tests before

Table 3
Proportion of plants (percent) selected as female genitors in the sorghum fields of five Duupa farmers

Size of field (ha)	Number of panicles harvested	Number of panicles selected to provide seeds for next planting	Percentage of plants selected as female genitors
0.5	2250	30	1.33
0.75	2250	20	0.89
1	3000	25	0.83
1	3750	40	1.07
2	7500	70	0.93
			Mean = 1.01%

See text for methods used to estimate number of panicles harvested.

Table 4
Correlations between farmer practices relating to seed exchange and several other variables, for sorghum

Variable		Proportion of cultivators (in %; $N = 27$) categorized in classes for several variables, according to their practices relating to seed exchange											
		Farmer's sex		Farmer's age (in years)			Sorghum area cultivated (in ha)			Number of cultivated varieties		Destination of the last harvest	
		♀ ($N = 9$)	♂ ($N = 18$)	< 36 ($N = 12$)	36–56 ($N = 9$)	$\geqslant$ 56 ($N = 6$)	$\leqslant$ 1/4 ($N = 14$)	1/4–3/4 ($N = 5$)	>3/4 ($N = 8$)	<10 ($N = 17$)	$\geqslant$ 10 ($N = 10$)	Only own consumption ($N = 19$)	Consumption and market sales ($N = 8$)
1. Do you give seeds away (or sell seeds)?	Never or rarely	88.9	22.2	75.0	11.1	40.0	71.4	20.0	12.5	52.9	30.0	57.9	12.5
	Sometimes	11.1	22.2	0	55.6	0	21.4	20.0	12.5	29.4	0	26.3	0
	At least once a year	0	55.6	25.0	33.3	60.0	7.2	60.0	75.0	17.7	70.0	15.8	87.5
	P	(0.003) ***0.013****		(0.002) ***0.012****			(0.005) ***0.025****			(0.021) ***0.100***MNS		(0.002) ***0.011****	
Do you receive seeds from others (or buy seeds)?	Never	22.2	22.2	0	22.2	60.0	0	20.0	62.5	11.8	40.0	10.5	50.0
	Rarely	66.7	38.9	50.0	55.6	20.0	50.0	60.0	37.5	41.2	60.0	47.4	50.0
	Sometimes or at least once a year	11.1	38.9	50.0	22.2	0	50.0	20.0	0	47.0	0	42.1	0
	P	(0.322) *0.857*		(0.019) ***0.090***MNS			(0.004) ***0.020****			(0.015) ***0.072***MNS		(0.017) ***0.082***MNS	
What was the source of the seeds you used for your most recent planting?	Seeds obtained elsewhere included	33.3	33.3	50.0	33.3	0	57.1	20.0	0	47.1	10.0	47.4	0
	Exclusively own seeds used	66.7	66.7	50.0	66.7	100	42.9	80.0	100	52.9	90.0	52.6	100
	P	(1.000) *1.000*		(0.104) *0.423*			(0.016) ***0.077***MNS			(0.092) *0.380*		(0.026) *0.122*	

The number in parentheses corresponds to the *P*-value calculated with a generalised Fisher's exact test (performed with 10^6 iterations). The number in italics refers to the *P* obtained after correction for multiple tests with the method of Dunn–Šydák (Bonferroni procedure). Bold numbers indicate *P* less than 0.1. The '*' sign indicates a significant result ($P < 0.05$ after Bonferroni correction). The 'MNS' sign indicates a marginally non-significant result ($0.05 < P < 0.1$ after Bonferroni correction).

Bonferroni correction, $P = 0.23$), and there was no correlation between frequency of receiving and frequency of giving (χ^2 tests before Bonferroni correction, $P = 0.16$).

3.4. Planting practices

In Wanté village, the number of varieties of sorghum varied among farmers (mean ± standard error of 9.1 ± 5.1 varieties per farmer; see Table 1). While panicles of different varieties are collected and managed separately, at planting time seeds of all varieties are mixed in a common bowl and sown randomly. Thus seeds of several varieties are commonly mixed in a single planting hole.

In addition to large fields, Duupa sometimes plant small "house gardens" of a few particular sorghum varieties in small plots near dwellings. According to our informants, the varieties planted in these parcels are relatively demanding of nutrients and more susceptible to bird predation. These varieties often flower precociously.

4. Discussion

4.1. Description of the agricultural system

Our study in Wanté shows that Duupa agriculture maintains high diversity, not only at the interspecific level, but also in terms of the number of local varieties of each crop, particularly in the case of sorghum. Our analysis of how the Duupa manage crop plants illustrates the importance of taking into account not only specific farming practices, but also the larger web of social relations within which exchanges of germplasm take place.

4.2. Proportion of plants serving as female genitors of the next crop generation

In contrast with other seed-propagated plants grown by the Duupa, only few sorghum plants serve as female genitors, since farmers obtain all the seeds for the next planting from a limited number of individuals. These are selected either before the harvest or from the harvest pile before threshing. Maize farmers in Mexico also select a small proportion of ears to supply seed. In maize populations in Jalisco, Louette and Smale (2000) estimated that about 1% of ears provided all seeds for the next generation. This is similar to our estimate for sorghum. However, since each maize plant may produce several ears, the proportion of plants serving as female genitors could be less than 1%. Louette and Smale (2000) note that farmers usually select ears for next year's seed from the harvest pile, and point out that this precludes direct selection on traits not observable in ears. It is not known whether Duupa farmers use different criteria for seed selection, depending on whether they choose panicles from plants in the field or from the harvest pile. Some farmers of sorghum select seeds in a way that should have very different population-genetic consequences (Almekinders and Louwaars, 1999).

However, consequences may be more complex. Mass selection in outcrossed crops is thought to favour highly heterozygous individuals. Even though the number of plants that contribute to the next generation is small, the genetic diversity of the seeds produced may be high (Ollitraut et al., 1997). Moreover, the number of fathers (pollen donors) that sired the seeds in a single panicle is unknown. In a wind-pollinated crop such as sorghum, with genetically diverse individuals planted in close spatial proximity, this number could be substantial. As stressed by Louette and Smale (2000) for maize in Mexico, the lack of control of the pollen source in open-pollinated crops could contribute to the maintenance of diversity.

We have shown that sorghum seed exchanges among Duupa farmers are extensive, leading possibly to an equilibrium between migration and drift. This high rate of migration favours the maintenance of the great varietal diversity we observed in Wanté village. Given the low proportion of plants serving as female genitors and the repeated bottlenecks this implies, we assume that any long-term reduction in the scale or intensity of seed exchange could alter the migration/drift equilibrium of sorghum and diminish the genetic diversity of its local populations.

4.3. Local seed system

Our observations provide an image of patterns of exchange of sorghum seeds in a Duupa village at a single point in time, and do not address phenomena acting at greater temporal and spatial scales. The village is not a closed system, and the set of varieties available is not static over time. Exchanges of seeds are attested between Duupa farmers from Wanté and Duupa from other villages, as well as with farmers of other ethnic groups. Even at low frequency, such long-distance exchanges could have long-lasting effects on the structure of crop diversity at the village level.

4.3.1. Variation in farmer practices depending on the farmer's age

Age of the farmer appears to be related to the area the farmer cultivates. In an agrarian civilization where cereal agriculture plays a central role in ethnic identity and the foundations of society (Garine, 2002), several advantages are associated with having a large sorghum field. First, having a larger field means that a household's food security is increased. This is an important advantage in a region where the growing season is short and where droughts and other events lead to great variation in harvest between years. Secondly, farmers with large fields can more often sell some grain or display it on ritual or social occasions. Third, and not least, owners of large fields play bigger roles in social exchanges, e.g., by their greater capacity to organise collective activities by offering sorghum beer. Farmers thus strive to have large fields, and their ability to accomplish this increases as they become older and acquire experience, resources, and prestige.

4.3.2. Structure of the local seed system

The most important result of our inquiries is that the local seed system appears to be structured like a source–sink metapopulation: older farmers provide seeds, whereas young farmers most often receive seeds. As the size of the cultivated area is correlated with the farmer's age, larger fields (i.e., larger plant sub-populations) tend to play the role of source in the metapopulation, whereas smaller fields (i.e., smaller plant sub-populations) tend to be sinks. As said an old Duupa farmer, "an older farmer will never ask a younger one for seeds; in the field, older people must help younger ones, not the opposite". This view of the social roles appropriate for individuals of different age is not restricted to seed exchange. Older Duupa are reluctant to be indebted in any way to younger individuals.

A corollary inference is that sink populations become source populations over the farmer's lifetime. A further finding is that larger fields, which generally belong to older farmers and function as sources, also contain the largest number of varieties. Thus, sorghum populations managed by the Duupa seem to mimic the functioning of some wild plant populations, in which after initial establishment both population size (through growth and immigration) and genetic diversity (through immigration (e.g. Giles and Goudet, 1997)) often increase over time, until at some point the population declines or disappears.

Similar source–sink dynamics might characterize other situations in which individual farmers vary in the roles they play in seed exchange. Among maize farmers in Jalisco, Mexico, for example, individuals covered the spectrum between those who always used their own seeds and those who almost never did so (Louette et al., 1997). This variation was related to several factors, including the size of the area farmed, as in the Duupa. In other respects, the two cases appear different. For instance, in the study by Louette et al. (1997), there is no indication that "sink" farmers become "source" farmers over time, as in the Duupa.

Source–sink dynamics in Duupa sorghum populations might be strengthened by the apparent rarity of "seed change" in favour of seeds obtained by exchange (Zeven, 1999; Louette and Smale, 2000). Duupa farmers rarely abandon a variety, but a farmer may neglect his own seeds when he considers them too "tired" to provide good yields. During the period of the study, no case was reported in which "tired" seeds were changed. However, we did record a few exceptional situations, e.g., when illness prevented a farmer from cultivating and replenishing his seed stock.

The farmer's gender may also influence his/her role in the local seed system. We have shown that men more often provide seeds to other farmers than do women. Many farmers organize *kombuma* during the sorghum harvest and threshing. Every helping participant of the *kombuma* is allowed to bring back home a reasonable quantity of seeds. This practice is underlain by a strong moral sentiment expressed by the Duupa that access to seeds must remain free to anyone in the community. Because men more frequently organize *kombuma* than do women (a difference anchored in the Duupa social code), men have more occasions to provide seeds to other farmers. Source and sink populations are thus also linked to the gender of farmers.

Our results indicate that seed exchanges can occur at a large spatial scale, and not only between neighbours. Spatial proximity among sorgum metapopulations is thus likely to exert less influence on gene flow than among structured populations of wild plants (Zimmerer, 1998). In addition, seeds from major 'source' farmers (i.e., those who provide seeds; see Table 4) may travel far away from their native site of production, through long-distance social exchanges or regional market stands. Farmers reported acquisitions of seeds of new varieties during trips to Ngaoundéré, 150 km to the south. Such acquisition could contribute signitifcantly to large-scale gene flow.

4.3.3. Will seed systems change?

These findings all indicate that older farmers play key roles in maintaining diversity. In view of recent social and economic changes affecting the region, it is not easy to predict whether young farmers will continue to assume the role of guardians of agrobiodiversity when they become older. The seed system we describe currently depends on a relatively small number of key individuals and might therefore be inherently fragile.

Cash crops such as cotton are being introduced in the region, and along with them new practices – e.g., the use of chemical fertilisers and herbicides – that could also affect the management of subsistence crops. For example, farmers who develop a mixed economic strategy combining the production of cotton and sorghum take advantage of the residual effect of chemical fertilizers spread on cotton to plant sorghum in the same field the next year, creating by the same occasion a new type of crop rotation. This new rotation could affect farmers preferences for varieties that better respond to increased nutrient levels.

Such large-scale changes could lead not only to the direct loss of diversity, but also to changes in the evolutionary forces, especially migration and drift, affecting crop metapopulations. Changing the sizes of populations and the migration patterns will modify the equilibrium between migration and drift. Crop genetic diversity could thus be threatened not only by abandonment of varieties and modification of the selective environment, but also by reduction of gene flow and increased fixation of genes by drift.

4.4. Planting practices: possible effects on mating structure

Our inquiries indicate that even with one general biological breeding system (i.e. sexual reproduction with frequent allogamy), practices of Duupa farmers could have substantial impacts on the "observed" breeding system of sorghum. This variation should affect the breeding system (e.g., relative proportion of outcrossed and inbred matings), assuming that there is substantial genetic variation among varieties. A striking feature of Duupa sorghum cultivation is that seeds of many different varieties are mixed in a common bowl before sowing. Thus plants of different varieties are found in close proximity in fields. This pattern, in which numerous varieties occur closely mixed in a single field, should lead to extensive gene flow among varieties, which all flower at about the same time (Garine, E., personal observation). How Duupa varieties of this partially outcrossed crop (Dje et al., 1999) are preserved, despite a planting pattern that encourages extensive hybridization between different varieties, remains unclear. Three explanations can be proffered. First, as yet unidentified barriers may minimize the frequency of intervarietal crosses. Second, individuals of a given variety may share a few major genes responsible for the variety's distinctive traits, and exhibit little differentiation at other loci. Third, panicles chosen for planting might be a nonrandom subset corresponding to distinctive ideotypes, with the population of panicles in the field including individuals with intermediate characters. Louette and Smale (2000) found evidence for such a pattern for maize grown by Mexican farmers.

Another feature of Duupa planting patterns is the segregation of a group of nutrient-demanding, rapidly growing, bird-susceptible varieties of sorghum in home gardens. These varieties should exchange genes more frequently with each other and less with the varieties planted in large fields. By affecting mating structure, planting patterns could thereby facilitate a kind of local adaptation of these ecologically similar varieties. Their precocious flowering could further increase the likelihood of homogamy.

4.5. Limitations of the study

This study is the first step in the examination of effects of farmers' practices on evolutionary forces acting on sorghum. Its principal limitation, aside from the restriction to a single village in our interviews, is the absence thus far of data on molecular and phenotypic diversity of Duupa sorghum varieties, and on the ecology and genetics of these polyvarietal populations. Studies building on this work are currently in progress and should overcome these limitations.

5. Conclusion

In this study, we have shown how Duupa seed selection, seed exchange, and planting patterns could influence genetic processes in the sorghum populations they manage. Like many other groups, the Duupa are faced by changes that could disrupt the social and ecological conditions that underlie their farming practices, including the local seed system. Understanding the consequences of these changes depends on understanding the links between farmers' practices and fundamental evolutionary forces. The role of farmers' practices in the continuing evolution of crop plants must be taken into account to produce models that combine concepts from natural sciences (e.g., dynamics of source–sink metapopulations) and knowledge of the impact of cultural diversity, which together shape the peculiar functioning of populations of domesticated plants.

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