Phenology and reproductive effort of cultivated and wild forms of *Pennisetum glaucum* under experimental conditions in the Sahel: implications for the maintenance of polymorphism in the species

J.-F. Renno and T. Winkel

Abstract: In the Sahel region of Africa, the wild and the cultivated forms of pearl millet, *Pennisetum glaucum* (L.) R.Br., are sympatric and interfertile and yet have remained distinct for millenia. Reproductive barriers are not sufficient to explain this situation. To elucidate other possible mechanisms, the two forms were compared under experimental conditions in the Sahel for their phenology and reproductive effort. The length of the flowering period of each type was much longer than the average individual flowering period. When the last cultivated plants were finishing flowering, 65% of the wild plants were still flowering and 30% were just starting to flower. Thus, the last group was completely isolated from cultivated pearl millet gene flow (endogamic reproduction). The two forms of pearl millet also differed in the distribution of aboveground biomass among different plant parts, except for the number of seeds per plant. Both phenological behaviour and reproductive effort contribute to the maintenance of distinct forms of wild and cultivated pearl millet.

Key words: *Pennisetum glaucum*, pearl millet, wild pearl millet, reproductive effort, phenology, endogamy.

Résumé : Dans les régions sahéliennes d'Afrique, les formes sauvage et cultivée du mil (*Pennisetum glaucum* (L.) R.Br.) sont sympatriques et interfertiles, mais demeurent néanmoins distinctes depuis des millénaires. Les barrières à la reproduction ne suffisent pas à expliquer cette situation. Dans le but d'identifier d'autres mécanismes en jeu, la phénologie et l'effort reproductif des deux formes de mil ont été comparés en situation expérimentale au Sahel. La durée de la période de floraison de chaque type était beaucoup plus longue que la durée moyenne de floraison d'un individu. Quand les dernières plantes cultivées finissaient de fleurir, 65% des plantes sauvages étaient encore en train de fleurir et 30% commençaient à le faire. Ces dernières se trouvaient ainsi totalement isolées du flux de gènes de mil cultivé, dans une situation de reproduction endogamique. Les formes sauvage et cultivée du mil se différenciaient également par la répartition de leur investissement dans la biomasse aérienne, à l'exception du nombre de graines produites par plante. Comportement phénologique et effort à la reproduction contribuent au maintien de deux formes distinctes de mil.

Mots clés : *Pennisetum glaucum*, mil cultivé, mil sauvage, effort reproductif, phénologie, endogamie.

Introduction

Archaeological traces of imprints of both wild and cultivated pearl millet (*Pennisetum glaucum*) seeds and bristles on pottery, found in southeast Mauritania and dating from around 3000 BP, are evidence of a neolithic agriculture with cultivated and wild pearl millet populations in sympatry (Amblard and Pernès 1989). The current wild form is distributed across the northern Sahel and is phylogenetically close to the ancestor of the cultivated pearl millet (Harlan 1975; Portères 1976).

Van der Zon (1992) recognized three subspecies in *Pennisetum glaucum* (L.) R.Br.: *P. glaucum* ssp. *glaucum*, the cultivated pearl millet; *P. glaucum* ssp. *violaceum* (Lam.) A. Rich., the wild and weedy forms; and *P. glaucum* ssp. *sieberianum* (Schlecht.) Stapf & Hubb., the intermediate form between the wild and the cultivated forms, known as shibra in Niger. These three taxa belong to the same gene pool of the allogamic and polymorphic annual species, *P. glaucum* (L.) R.Br. (Harlan and de Wet 1971).

Regarding the cultivated pearl millet, the farmer plays an essential selective role through agricultural practices: choice of seeds from spikes typical for a local cultivar, batches of seeds (called pockets) sown into holes favoring the growth of the biggest seeds, hoeing to eliminate weeds and pearl millet plants outside the pockets, thinning out to preserve the most vigourous plants, and elimination of the shibra. Nevertheless, in the field, the frequency of the remaining shibra varies between 5 and 30% in the areas where the wild and cultivated forms are in contact (Rey-Herme 1982). These wild populations are not subject to conscious selection pressure by humans. For two samples of seeds taken from wild pearl millet populations in Senegal and Niger, the proportion of descendants of the hybrid phenotype (shibra), supposedly the product of fertilization by cultivated pollen, was estimated at 31 and 19%, respectively (Marchais and Tostain 1992)

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How is the polymorphism of *P. glaucum* maintained? How is it that wild pearl millet does not disappear in contact with cultivated pearl millet under the effects of gene flow?

Many studies have addressed these questions. Studies of genetic distance indicated strong intermixing of genes between wild and cultivated pearl millet (Tostain 1993). Pernès (1983, 1985) underlines the fact that the two forms interact but can exchange alleles without a modification of phenotypes because the genetic control of domestication is supposed to depend on a few linked genes. Moreover, gene flow can be controlled by mechanisms that act at the pre- and post-zygote stages in favour of the maintenance of differentiation between the wild and cultivated forms. Pollen competition was observed as a prezygote barrier, giving the advantage to self-pollination (Sarr et al. 1988; Robert et al. 1991), while the reduction in viability of hybrid grains was observed as a postzygote brake (Amoukou and Marchais 1993). Genomic strategies in wild pearl millet in contact with cultivated pearl millet were mentioned by Joly-Ichenhauser (1984) and Pernès (1986), who assume the existence of two linkage groups of predomestication genes that would have the effect of favouring the maintenance of phenotypes in spite of hybridization. However, if these reproductive barriers limit gene flow, they do not entirely eliminate it and are not sufficient by themselves to explain the maintenance of two distinct interfertile forms in contact for millenia. Isolated reproduction in space and also in time, as well as selective pressures, could play an essential role in structuring the polymorphism of pearl millet.

Where wild and cultivated forms of pearl millet are in geographical contact, what is the proportion of plants in each form escaping the gene flow of the other form by asynchronic flowering periods? What are the differences in reproductive effort between wild and cultivated pearl millet? How are the differences maintained between sympatric wild and cultivated populations that have been exchanging genes for millenia?

In an attempt to address these questions, we compared, under Sahelian experimental conditions, the phenology of tillering and flowering of a wild pearl millet and a cultivated pearl millet from the same geographical region, as well as the distribution of aboveground biomass production between vegetative and reproductive organs in each of these two forms.

Materials and methods

Material

The seeds used for the study samples were collected from hundreds of spikes for each form, in six sites between Belbeji (14°43′N, 8°05′E) and Tanout (14°57′N, 8°49′E) in Niger, where wild and cultivated pearl millet (cv. Ankoutess) are sympatric. 'Ankoutess' is adapted to a short rainy season (3 months from June to September) and thus can be considered as minimally or not at all photoperiod sensitive (Clément 1985; Burton and Powell 1968 in Skerman and Riveros 1990). The seeds of wild plants were harvested near pearl millet fields.

Experimental protocol

The experiment was carried out at the Institut des Radio-Isotopes (IRI), University of Niamey (Niger) in 1993. The soil at this station is typical of farm land in the Sahel, with 93% sand in the 0- to 150-cm layer. The study took place in the hot dry season between February and May. The daily mean temperature varied between 26 and 37°C, and the daily mean incident radiation between 17 and 27 MJ/(m^2 · day). Irrigation was regulated to simulate the average rainfall regime during the rainy season in the region of Tanout. It was started on February 9, one day before sowing, then stopped 74 days after emergence (DAE, date at which 50% of the pockets had emerged). There was one natural rainfall at 71 DAE (7.5 mm). Weeds were controlled manually. Fertilizers were supplied at 30 kg · ha^{-1} N, P, and K 1 day before sowing and 15 kg · ha^{-1} N at 16 DAE.

The experimental field was divided into five replications with two subplots each. The subplots measured 4 × 10 m, sown either with cultivated or wild seeds, and were randomized per replication. Seeds were sown in pockets (1 pocket/m^2) and the development of eight pockets in the center of each subplot was observed. The first DAE was the same for wild pearl millet and cultivated pearl millet, 3 days after sowing. At 15 DAE, the cultivated plants were thinned out to three plants per pocket, a planting density considered to be optimal under Sahelian conditions (Institut National de Recherches Agronomiques du Niger 1987). In each pocket one randomly chosen plant was observed until the end of its cycle. For the wild plants, no standard density can be representative of the lack of homogeneity in density of natural populations. For the convenience of observations, taking into account the very important tillering of each plant, the wild plants were thinned to 1 plant/m^2. This experimental approach resulted from a compromise between the need to collect precise information on each individual plant and the need to observe the phenotypic expression of each plant form as it is found under natural conditions.

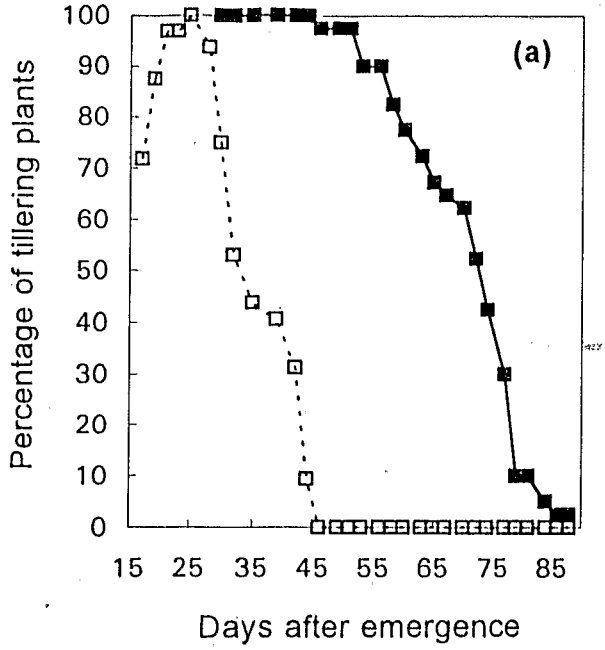
Observations

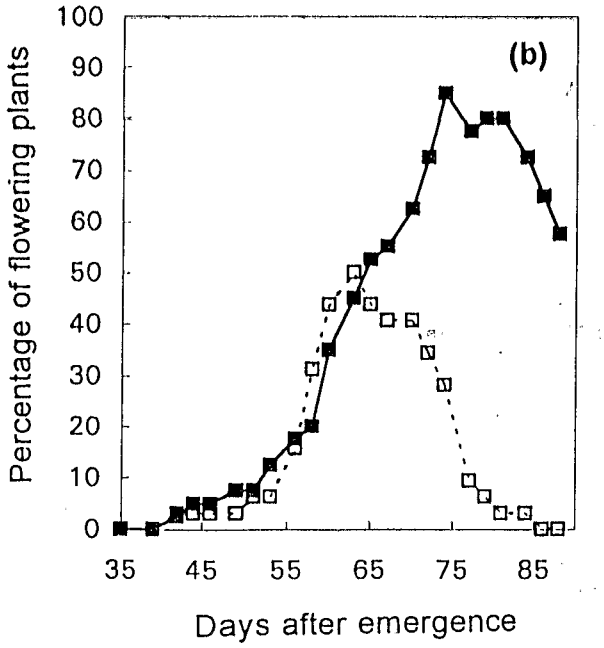
The observations of the phenology of flowering and tillering were planned for 40 plants of each form of pearl millet, but this number had to be reduced to 32 cultivated plants after the intermediate forms (the shibra type identified after flowering) had been discarded. The final production of aboveground biomass was planned to be measured on a subsample of 20 plants of each form harvested at 90 days. This number was reduced to 17 cultivated plants (after the shibra had been removed) and to 19 wild plants, one having died before the harvest. No shibra was identified in the sample of wild pearl millet. After flowering, envelopes were put over the spikes of the wild plants to prevent shedding of the seeds (the cultivated plants do not shed their seeds).

Phenology of tillering and flowering

Every 2 or 3 days during the development of the plants, the following observations were made. (*i*) The number of plants in the primary tillering phase: a plant was considered to be in the primary tillering phase during the whole period between the development of the first and the last primary tiller (the primary tillers are those growing out of the first stem that has emerged). The young pearl millet plants, particularly the wild plants, are too fragile to be frequently manipulated, so the observations began at 17 DAE (2 days after thinning) for the cultivated form and at 30 DAE (15 days after thinning) for the wild form. The observations were made until harvest. (*ii*) The number of plants in the flowering phase: a plant was considered to be in the flowering phase during the whole period between the first and the last flower. The flowering phase for the cultivated form begins with the flowering of the spike of the main stem (the first stem emerged) and ends with a spike of a primary tiller. Since the number of primary tillers was low and secondary tillers were very rare and always sterile, the flowering phase could be followed exhaustively for each plant. With the wild form, the flowering phase also begins with the flowering of the spike of the first stem (the equivalent of the main stem of the cultivated plant) but ends with the flowering of the spikes of the last additional tiller

Fig. 1. Phenology of tillering (*a*) and flowering (*b*) in cultivated (□) and wild pearl millet (■).





(derived from the *n*th rank of a primary tiller). For each wild plant, the flowering period of the first stem, of the first primary tiller, and of the last tiller were noted carefully. Thus, the whole of the flowering period of each plant was covered.

Aboveground biomass production at harvest

At harvest, the plants were separated out into stems, leaves, and spikes and dried at 80°C, until a constant weight was reached (72 h). For each plant, the measurements of the biomass and the following counts were carried out: (*i*) vegetative organs: mass of stems (mSt), mass of leaves (mL), total biomass (TAm), number of primary tillers (nbTi); (*ii*) reproductive organs: number of spikes (nbSp), mass of spikes before threshing (mSp), and after threshing, mass of seeds (mSd) and number of seeds (nbSd).

The reproductive effort was estimated by (*i*) the reproductive ratio (RR), which is the mass of the reproductive organs (spikes including seeds) divided by the total biomass and (*ii*) the seed ratio (SR), which is the mass of seeds divided by the total biomass.

An estimation was made of the potential number of seeds per plant (pSd/Pl), the potential number being the maximum number of seeds produced if all the ovules (one per spikelet in pearl millet) had produced seeds. A sample of spikes (40 and 63 spikes for the cultivated and wild forms, respectively) was taken at random from the total number of spikes produced by each form of pearl millet. The number of involucres on the central portion of each spike was counted for a length of 1.5 to 3 cm depending on the size of the spike. On each spike, the number of spikelets per involucre was counted (1 for wild, 1–3 for cultivated pearl millet). After measuring the total length of the spikes, the mean potential number of seeds per spike was calculated and multiplied by the number of spikes per plant to obtain the potential number of seeds per plant (pSd/Pl).

The differences observed between cultivated and wild forms were tested by a *t* test as a 5% probability level.

Results

Phenology of tillering

At the start of our observations at 17 DAE, 72% of the cultivated plants were at the tillering phase; this proportion was 100% at 25 DAE (Fig. 1*a*). The tillering period of cultivated plants was complete at 44 DAE. The proportion of wild plants in the tillering phase (Fig. 1*a*) was 100% at 30 DAE, at the beginning of our observations. All the plants remained in the tillering phase up to 44 DAE and at harvest (90 DAE) 2.5% of them were still producing new tillers. The tillering phase of the wild plants continued, therefore, well after that of the cultivated plants.

Phenology of flowering

The average flowering period of a cultivated plant was 7.5 days, whereas that of a wild plant was 21 days with strong individual variations for both (CV of 39% for the wild sample and 70% for the cultivated sample) (Table 1). However, the total flowering time of the samples was 45 days for cultivated pearl millet and more than 49 days for wild pearl millet, since the latter population had not finished flowering at harvest (Fig. 1*b*).

The distribution over time of the percentage of cultivated plants in the flowering phase followed a normal curve. Flowering began at 42 DAE, when the tillering phase was finished. The maximum level was attained at 63 DAE, with 50% of the plants flowering. At 77 DAE, about 10% of the plants were continuing to flower. There were no more flowers after 84 DAE.

The same type of distribution was observed for the wild plants. They began to flower at 42 DAE, well before the end of their tillering phase. The maximum number of plants in the flowering phase (85%) was at 74 DAE, when about 30% of the cultivated plants were flowering. When the last cultivated plants were finishing flowering at 84 DAE, 65% of the wild plants sample were going to exchange genes only among themselves; thus reproduction was endogamic. When irrigation was stopped (74 DAE), 30% of the wild plants were starting to flower and more than 80% of their flowering

Table 1. Distribution of aboveground biomass production, seed potential, reproductive ratio, seed ratio, and flowering duration of cultivated and wild pearl millet plants (means per individual).

	mSt	mL	mSp	mSd	TAm	nbSp	nbSd	nbTi	pSd/Pl	RR	SR	Flowering
						Cultivated						
Mean	63.4	43.7	38.2	22.6	146.9	1.6	3194	6.8	8365	0.25	0.14	7.5
N	17	17	17	17	17	17	17	17	17	17	17	32
CV	46	46	64	71	42	71	68	19	71	52	60	70
SE	7.0	4.9	5.9	3.9	14.8	0.3	525	0.3	1432	0.03	0.02	0.9
						Wild						
Mean	252.5	94.0	79.9	4.9	426.3	89.9	4158	16.2	32312	0.18	0.01	20.9
N	19	19	19	19	19	19	19	19	19	19	19	40
CV	52	41	67	108	44	75	108	21	75	54	98	39
SE	29.9	8.8	12.3	1.2	42.6	15.4	1026	0.8	5528	0.02	0.003	1.3

Note: Abbreviations are as follows: mSt, mass of stems; mL, mass of leaves; mSp, mass of spikes; mSd, mass of seeds; TAm, total biomass; nbSp, number of spikes; nbSd, number of seeds; nbTi, number of primary tillers; pSd/Pl, potential seed number per plant; RR, reproductive ratio; SR, seed ratio; flowering, mean duration per plant (days); *N*, sample size; CV, coefficient of variation (%); SE, standard error. Masses are in grams of dry matter per plant.

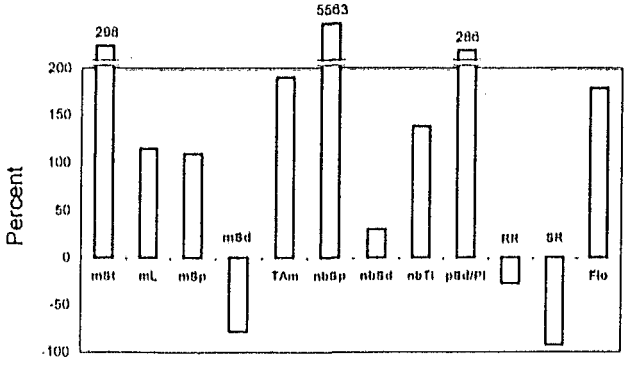


Fig. 2. Percentage differences in aboveground biomass production, seed potential, reproductive ratio, seed ratio, and flowering duration of wild pearl millet relative to cultivated pearl millet. See Table 1 for subheadings.

period took place between this date and the harvest. At harvest (90 DAE), 58% of the wild plants were still producing flowers. The flowering period of the cultivated pearl millet thus took place entirely within that of the wild pearl millet.

Reproductive effort

Except for the number of seeds per plant, all the results related to reproductive effort were significantly different ($P < 0.05$) between the two forms of pearl millet (Table 1; Fig. 2). Compared with a cultivated plant, a wild plant had the following characteristics: (*i*) the number of spikes was 57 times greater, but it represented a total mass only twice as much as the spikes of a cultivated plant because of the larger size of the spikes of cultivated plants; (*ii*) the number of seeds per plant was not significantly different from that of cultivated pearl millet (4158 as opposed to 3194) but corresponded to a mass 4.5 times less (4.9 g as opposed to 22.6 g for the cultivated pearl millet) because of the larger size of the seeds of the cultivated plants; (*iii*) the investment in the number of seeds produced compared with the total biomass was half (10 seeds/g of dry matter as opposed to 22 seeds/g of dry matter for a cultivated plant), this being due principally to the difference in the average number of seeds per spike (46 for a wild plant, 1996 for a cultivated plant).

The average reproductive ratios (RR) of wild and cultivated plants were significantly different (18 and 25%, respectively) but were still quite close compared with the seed ratio (SR), which was 14 times less for a wild plant than for a cultivated plant (1 and 14%, respectively). A wild plant had on average 16.2 primary tillers, each producing on average 5.6 spikes. A cultivated plant had on average 6.8 primary tillers and produced 0.3 spikes for each of them. Therefore, a large proportion of its tillers did not produce any spikes.

The cultivated pearl millet attained 40% of its estimated potential in terms of seed production (real number of seeds per plant (nbSd) divided by the potential number (pSd/Pl)). Although the wild pearl millet produced a quantity of seeds equivalent to that of cultivated pearl millet, it had attained only 13% of its potential, which was 3.8 times higher than that of the cultivated pearl millet.

Discussion

This study shows that under experimental conditions, the cultivated pearl millet was always influenced by the wild pearl millet pollenic cloud, whereas the wild pearl millet population escaped from the cultivated pollenic cloud for a large part of its flowering period. If there had not been a harvest, the length of the endogamous reproduction of the sample of wild plants would have depended on the availability of water in the soil. According to Marchais (1994), under natural conditions in Niger, the observation of the flowering of a sample of tillers in a population of wild pearl millet revealed that 40% of the spikes were still flowering when the plants of the cultivated and shibra phenotypes had finished. The latter observation does not provide any information on the fraction of individual plants that participate in the endogamous system but supports the idea of strong endogamy in a wild pearl millet population.

For cultivated as for wild pearl millet, the average flowering period of a single plant was much shorter than the total

flowering period of the whole population sample, particularly for the cultivated plants. One of the main effects of domestication is to synchronize the flowering of plants (Harlan et al. 1973). In the case of pearl millet, the larger variation (higher CV) of the flowering periods of cultivated plants compared with wild plants indicates that domestication has not selected strongly for uniform ripening. Another consequence of domestication is to prevent the shedding of seeds and provide for simultaneous harvesting. This character has been selected for in cultivated pearl millet. However, because the farmer could need early-ripened grain for food and also to avoid predation by birds or insects, the same field can be harvested up to three times in the same crop season. Under Sahelian conditions, the advantage for farmers having a crop with a large interindividual variability in the flowering period could be to escape the risks of short-term stresses (water or pests) during the flowering period.

The wild phenotype was characterized by the length of the tillering and flowering phases and also by an asynchronous flowering pattern among the plants. If the tendency to flower late has a genetic basis and an adaptive advantage, it might have been selected for during the course of evolution, maintaining a part of the wild populations isolated from the gene flow of the cultivated plants. However, in the farming environment, germination and growth patterns of the different populations of wild pearl millet and of the different fields of cultivated pearl millet are not simultaneous. Moreover, the shibra could play a bridging role in gene flow if their flowering periods overlap those of the two extreme forms. Then, under natural conditions, the global flowering periods of wild and cultivated populations of pearl millet should overlap more than under our experimental conditions.

If the integrity of the cultivated phenotype can be explained by anthropic selection, the integrity of the wild phenotype may result from the combination of the tendency for endogamous reproduction and a range of predomestication characters peculiar to it, like abundant tiller and spike formation, shedding of the seeds, seed dormancy, etc. Under natural conditions these characters offer adaptive advantages compared with those from deviant forms, like shibra, which tend to resemble the cultivated form. In this study, the morphological characters compared are often interdependent. For example, for a wild population, the high and extended tillering results in a spread-out appearance of a large number of spikes and so amplifies the progeny engendered in endogamous situations. Moreover, this strategy favours the chances of reproductive success in an unpredictable environment.

In our experiment, the cultivated sample attained 40% of its potential in seed production with a seed ratio of 14%, which corresponds to a yield of 678 kg · ha^{-1}, close to the upper limit in traditional farming conditions (Anand Kumar 1989). The wild sample attained only 13% of its potential in seed production, with a seed ratio of 1%, which corresponds to the lowest values mentioned for Sahelian monocotyledons (De Ridder et al. 1981). The seed production and seed ratio in the wild population are low partly because the latest spikes did not have the time to fully develop their seeds, and partly because there could be a difference between wild and cultivated plants in the sensitivity to external factors (temperature, humidity, factors of pollination, etc.) causing failure in pollination or abortion.

Genetic introgression does not eliminate the phenotypic differences among wild, weedy, and cultivated relatives in a large range of environments in diverse taxa, like *Oryza* (Second 1982; Bezançon 1993), *Zea* (Doebley et al. 1987; Doebley 1990), and *Citrullus* (Zamir et al. 1984). Differential selection gave rise to an agrosystem in which the ancestral and the derived form evolved. The undesirable deviants are counter-selected by the farmer, but in the case of pearl millet in the Sahel, these deviants have never been completely eliminated. It is interesting to consider that the continual introgression of wild genes in the cultivated forms could permit a "genetic adjustment" of the crop to the widely variable habitat conditions typical of the Sahel.

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