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Sahelian smallholders' varietal mixtures reconcile yield and agrobiodiversity conservation

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Abstract

In the current setting, marked by the major challenges of growing food demand and climate change impacts, the ability of sub-Saharan agriculture to meet population needs depends on the resilience and adaptation capacity of this system. Using agrobiodiversity to promote agricultural sustainability is a strategy that has garnered much attention lately. Research suggests that mixing species or varieties within crop fields could increase the yield and/or stability. This mixing is also geared towards the conservation of crop diversity while ensuring that the various associated products and services will be available at the farm level.

Few recent research studies have highlighted the benefits of varietal mixtures for Africa. This lack of research is a concern, given that this continent is considered to be highly vulnerable to climate change. This study was carried out to test whether plots with varietal mixtures would outperform monovarietal plots in terms of yield and pathogen regulation under smallholder farming conditions in Senegal. Together with farmers, we conducted 30 experiments in which mixtures of early- and late-flowering pearl millet landraces were grown in these farmers' fields, while monitoring their low input management. We noted a significant positive effect of varietal mixtures on grain yield (mean gain of 63 ± 31.5 kg ha⁻¹ for mixture plots, $p = 0.046$) with a relative yield total (RYT) averaging 1.87 ± 0.94 . Both early- and late-flowering landraces benefited from mixtures, with a greater

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impact on late-flowering landraces. Higher fertility in terms of the seed number, percentage of fertile tillers and number of panicles per tiller, was documented in mixture plots. We did not find a significant effect of mixture on fodder, striga or weed infestation.

In water and nutrient resource limiting conditions, such as in Sahelian agroecosystems, growing mixtures of early- and late-flowering landraces appeared to be an efficient way to increase productivity while ensuring agrobiodiversity conservation. Perhaps even more importantly, mixtures allowed farmers to harvest multiple products with different uses in an agrosocioecosystem context with constantly increasing land pressure.

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Keywords: Agrobiodiversity; Varietal mixtures; Pearl millet; Sahel; Flowering; Phenology

Introduction

Almost 100 years after the term was coined, agrobiodiversity and agroecology are more than ever viewed as levers to achieve the UN Sustainable Development Goals in a global change context (Burlingame, 2019). With four times more species cultivated compared to large farms, smallholder-farming systems (<2 ha) manage the greatest extent of agrobiodiversity on Earth (Ricciardi et al., 2018). Smallholders use a highly diverse portfolio of crop species and varieties to ensure a complementary range of products, stagger harvests, adapt to diverse climatic and agroecological conditions and support sociocultural services (Bellon & Ollivier, 2011; Caillon & Lanouguère-Bruneau, 2005; Labeyrie et al., 2021; Lalou et al., 2019; Radanielina et al., 2014). Smallholders have therefore developed many association practices ranging from agroforestry, crop rotation, intercropping and, notably, varietal mixtures to enable them to maintain such diversity in <2 ha plots. Varietal mixtures consist of a combination of several varieties of the same crop within a plot. Varietal mixtures combining up to 9 bean landraces or 11 sorghum landraces have been reported (Barnaud et al., 2008; Joshi et al., 2020). Indian farmer's motivations for mixing varieties range from food taste enhancement, having access to multiple harvestable products with different uses and insurance against crop failure (Joshi et al., 2020). Beyond phenotype preference (panicle form, grain colour, etc.) and social meaning considerations, Indian and Mexican smallholder farmers also take advantage of the functional diversity in mixtures, particularly flowering cycle diversity, to cope with rainfall variability (Clawson, 1985; Joshi et al., 2020). By growing landraces with short, intermediate and late flowering cycles, farmers temporally spread out the risk of being impacted by a damaging climate event, while boosting harvest security. The practice of taking advantage of diversified flowering cycles within a plot has also been observed in Sahelian Africa with regard to both cereals and legumes (David, 1976; De Rouw & Winkel, 1998). Despite the fact that many research and breeding programmes focus on developing and promoting short-cycle varieties because earliness is viewed as an efficient strategy to avoid

midseason dry spells, farmers have continued to grow late-flowering landraces in mixtures with short-cycle landraces (Lalou et al., 2019).

Research tools such as meta-analyses help synthesize knowledge and bridge knowledge gaps in agroecological practices (Beillouin et al., 2019; Tamburini et al., 2020). For instance, the benefits of varietal mixtures have still received less research attention than other diversification strategies (Beillouin et al., 2019). Several gaps have been identified in varietal mixture analyses, such as mixing criteria, representativeness of environmental conditions or crops.

Mixing criteria that have been evaluated were focused on disease resistance and weed suppression (Beillouin et al., 2019; Kiær et al., 2009). Few studies have considered phenology as a mixing criterion, yet contrasting results were obtained when they did. In a meta-analysis of wheat cultivar mixtures, Borg et al. (2018) reported that wheat phenological mixtures overyielded phenologically homogeneous mixtures by 3.3% on average. Fletcher et al. (2019) concluded that wheat phenological mixtures provide a good way of coping with across-season variability in water availability and of stabilizing crop yields, particularly in risky environments. But contrasting and variable effects on grain yield and disease resistance were found for wheat (Giunta et al., 2020; Vidal et al., 2020), as well as soybean (Gizlice et al., 1989; Mumaw & Weber, 1957; Schweitzer et al., 1986).

A second gap identified concerns the relevance and representativeness of regions where mixtures are investigated. Indeed, agroecological research should focus more closely on regions where varietal mixtures are most needed, where environmental conditions are harsher and where the development of compensatory infrastructure is very complicated, e.g. in developing countries. Few studies have been conducted in Africa (Beillouin et al., 2019), which—in addition to prevailing soil fertility issues—is now considered to be one of the most climate-vulnerable continents, with the Sahel being a climate change hotspot (Niang et al., 2014). In addition, few conditions have been assessed and when they are it is almost always on a one-at-a-time basis (Borg et al., 2018). One way to take realistic multiple-limiting conditions and their interactions into account is to focus studies in real

farm settings. Overall, meta-analyses have revealed that the way research has assessed the impact of mixtures is poorly representative of smallholder farmers' practices and conditions. By not building on existing farmers' practices, research misses out on potentially interesting practices resulting from farmers' experience, and well suited to their constraints and objectives, despite the fact that the resulting technological innovations could have a higher acceptance rate by farmers (Périnelle et al., 2021; Salembier et al., 2016).

Overall, smallholder farming systems represent 85% of farms (Samberg et al., 2016) and produce 30–53% of calories at the global scale. They are thus key systems for food and nutrition security (Ricciardi et al., 2018; 2021; Samberg et al., 2016) and deserve greater research attention to gain further insight into and identify local practices that encompass the multiple aspects of food, nutrition and cultural values. As agroecology is transdisciplinary (Ruiz-Rosado 2006), adopting an agroecological approach implies creating favourable conditions for hybridizing scientific and farmers' knowledge, perceived as both expert and contextualized knowledge (Doré et al., 2011; Leclère, 2019) while fostering collective and generic learning (Girard & Magda, 2018). This study was co-designed with farmers' organizations in Senegal with the aim of assessing the impacts of a traditional practice involving the mixing of early- and late-flowering pearl millet landraces on in situ yield, i.e. in poor soil conditions with limited fertilization on smallholder plots. In Sahelian agrosystems, pearl millet (*Cenchrus americanus* (L.) Morrone syn. *Pennisetum glaucum* (L.) R. Br.) is the staple food for over 90 million people, while yielding less than 1 t. ha⁻¹ (Satyavathi et al., 2019). We have sought empirical evidence that this traditional practice is a sustainable and valuable strategy to boost crop yields without compromising landrace diversity conservation while remaining embedded in ecological and cultural values.

Material and methods

Study sites

The study was carried out in Senegal during the 2019 cropping season (June–December) in two villages (Fig. S1) that are members of a local farmers' association (ASPSP, *Association Sénégalaise de Producteurs de Semences Paysannes*) network. The two villages, i.e. Lissar (15° 07' 97" N, 16° 62' 10" W) and Mbane (14° 38' 42" N, 16° 42' 55" W). They are located in two contrasting agroclimatic zones (ACZ) within the peanut growing area of Senegal. Lissar is in the northern ACZ, situated within 300–400 mm isohyets, where the number of rainy days averaged 23 ± 6 days/year over the 1995–2008 period (Salack et al., 2011). Mbane is in the central northern ACZ, situated within 400–500 mm isohyets, where the number of rainy days averaged 34 ± 6 days/year over the 1995–2008 period (Salack et al.,

2011). In both ACZ, the soils were sandy, slightly acidic, with a low cation exchange capacity. They are classified as aridisols in the American soil taxonomy, while in the FAO soil classification the soils of Lissar are described as 'weakly leached ferruginous', those of Mbane are 'leached ferruginous'. Cultivation pressure is heaviest within these ACZ in Senegal. Over the years, the sustainability of smallholder farms has diminished because of this increased cultivation pressure, since both the length of fallows and the availability of manure generated by livestock herds have been reduced, which means that the soils can no longer be replenished in nutrients.

Experimental design

During the 2019 wet season, 15 farmers' fields per site were made available for this study. A network of experiments was set up in a randomized block design with 15 blocks or replications (Fig. S1). Each block was nested in one farmer's field. Two groups of treatments were randomly distributed within each block:

- T1: monovarietal pearl millet with landrace 1, or 2, 3 and 4.
- T2: mixture of all four landraces (1 + 2 + 3 + 4) at equal proportions (25% each).

The four pearl millet landraces, i.e. two early-flowering (EF) and two late-flowering (LF), were obtained from the collection of the French National Research Institute for Sustainable Development (IRD). Information on these landraces is reported in Table 1. The plot size per treatment was 7.5 m × 2 m, with the plots separated by 2 m walkways. Before sowing, 10 kg per plot of organic manure was added and no pesticides were applied over the crop cycle. Pearl millet seeds were sown in hills with 0.3 by 0.3 m spacing and thinned to one plant per hill 15 days after sowing, with a final mean density of 3 plants/m². Plants were sown on 6/07/2019 at Mbane and 9/07/2019 at Lissar. Crops were harvested from 6 to 8 November in Mbane and from 11 to 13 November in Lissar.

Measurements

Soil characteristics of experimental sites

Soils were sampled before the start of the experiments for chemical analysis. Five soil samples per block were randomly collected from 0 to 20 cm depth and then bulked to obtain a composite sample, so 15 samples per village were collected for analysis. The samples were analysed for total soil organic carbon (SOC) and total nitrogen (by CHN elemental analyser), available P (Olsen method), water pH and mineral nitrogen (N_NO3 and N_NH4) using standard methods at the IRD Analytical Laboratory (US IMAGO Senegal) in Dakar (<https://imago.ird.fr/moyens-analytiques/>

Table 1. List and information of pearl millet landraces used.

N° Accession	Code	Landrace name	Cycle	Ethnic group	Collection Date	Country	Longitude	Latitude	Isohyet (mm)	Days to harvest
PE00853	Early_Nig1	NA	Early	NA	1975	Niger	10° 00' E	13° 51' N	400–500	80–90
PE02643	Early_Nig2	Tamangagi	Early	Haoussa	1976	Niger	09° 05' E	12° 53' N	500–600	80–90
PE02822	Late_Nig	Somna	Late	Djerma	1976	Niger	02° 54' E	12° 27' N	500–600	120–140
PE01228	Late_BF	Kazouya	Late	Mossi	1975	B. Fasso	00° 30' W	12° 32' N	500–600	100–130

dakar). The soil chemical analysis reported in Table 2 indicates that the soil fertility was very low in both sites, particularly at Mbane; pH values were below neutral, and significantly lower at Mbane. Phosphorus availability for the crops was remarkably low at both sites, but significantly higher in Lissar, and close to the values reported by Tounkara et al. (2020) for sandy soils in central western Senegal, and by Fofana et al. (2008) for sandy soils in Niger. The carbon (C) and nitrogen (N) contents were under the values 0.5% and 0.05% potential values generally expected for sub-Saharan sandy soils. The C/N ratios were not significantly different between sites, suggesting that low soil biological activity was not limiting for the carbon recycling processes in soils. The low soil C content was likely due to low organic amendments.

Collected pearl millet traits at harvest

In addition to grain yield, we measured seven morphological traits and three variables related to weeds (all species together without taxonomic identification) and pathogens (Table 3). The number of tillers per plant (NbT) was calculated as the total number of tillers on the plot divided by the number of plants. Fodder was sundried in the plot for 10 days and weighed. The rate of productive tillers was estimated as the number of tillers bearing panicles in the plot divided by the total number of tillers (PrT). The number of panicles per plant (NbP) was calculated as the number of panicles in the plot divided by the number of plants. The harvested panicles were classified as mature (i.e. panicles with grains) or immature (i.e. no grains), and these data were used to estimate the maturity ratio. Mature panicles were then classified as filled panicles or spoiled panicles if they were less than half full of grains'. Mature panicles were sundried for a month at the research station. All panicles in a plot were threshed together and then the panicle weight

(DwP), total grain weight and 1000-grain weight (W1000) were measured. In pearl millet landraces, first generation hybrids of wild and cultivated millet were sometimes noted in the grown seed batches. These hybrids were often left in the field and used for fodder or grain in case of shortages. In our experimental study, hybrids were therefore left until harvest and counted separately (HyBR).

The most common pearl millet diseases in Senegal are downy mildew (*Sclerospora graminicola*), smut (*Tolyposporium penicillariae*) and ergot (*Claviceps fusiformis*) according to Mbaye (1992). Downy mildew can lead to 40% yield loss (Thakur et al., 2011). Striga (*Striga hermonthica*) is a persistent, hemi-parasitic weed that attacks several grasses in many countries throughout sub-Saharan Africa, particularly maize, sorghum and pearl millet grain crops. In West African countries, 40–77% of grain fields have been estimated to be infested by witchweed. Yield losses average 10–31% but it can reach 90–100% in some years (Sauerborn, 1991). The relationship between disease resistance and flowering is unclear, with early- or late-flowering varieties being more resistant depending on studies (Ramaiah, 1991, Wilson et al., 2000). Striga infestation also depends on the climate and soil fertility conditions. Control recommendations for subsistence farmers include reducing the number of Striga seeds in the soil and enhancing soil fertility (Hess et al., 1996). In our study, we visited each plot 70 days after sowing to count the number of plants infected by downy mildew and the number of Striga plants in the plot. However, the prevalence of downy mildew was too low to be analysed in our studied plots. Fig. 2, Eqs. (1)–(3)

Assessing mixture effects on landrace productivity

We estimated three different indexes to test for mixture effects on crop productivity. We first estimated the relative

Table 2. Organic soil nutrient statistics per village.

	N (NO ₃) mg/kg	N (NH ₄) mg/kg	N%	C%	C/N	P available mg/kg	pH
Lissar	0.82 ± 0.42	1.84 ± 0.49	0.017 ± 0.005	0.201 ± 0.068	11.82 ± 0.87	4.74 ± 1.32	6.45 ± 0.50
Mbane	0.93 ± 0.61	1.52 ± 0.28	0.021 ± 0.002	0.268 ± 0.035	12.52 ± 1.06	2.72 ± 0.38	5.73 ± 0.39

For each site, the 15 individual experimental unit values were averages. T-tests were performed to test if the soil compositions were significantly different between the two sites. Significant measurement data ($p < 0.05$) are in bold.

Table 3. Summary statistics of plant traits measured across the four landraces in monovarietal plots.

Trait	Description & Unit	min	max	mean	sd	CV
Density	plant/m ²	1.07	4.8	3.13	0.93	0.3
NbT	nb of tillers per plant	1.44	7.75	3.48	1.08	0.31
FYind	kg of dried tillers per plant	0.01	0.55	0.13	0.08	0.67
PrTR	nb fertile tillers/nb tillers	0.27	0.95	0.61	0.14	0.23
NbP	nb of panicles per tiller	0.28	1.53	0.71	0.2	0.28
MatP	nb mature panicles per plant	0.39	4.73	1.95	0.84	0.43
SpoP	nb spoiled panicles per plant	0.17	3.91	1.25	0.69	0.55
GYind	grain weight per plant	0.38	37.2	8.31	6.59	0.79
DwP	weight of dried panicles per plant	3.27	121.25	32.34	20.29	0.63
W1000	weight of 1000 seeds g	3.74	12.13	8.66	1.35	0.16
NbS	nb of seeds – DwP/(W1000×10 ⁻³)	45	4421	948	736	1
HybR	nb hybrid/nb plant	0	0.7	0.11	0.13	1.3
Striga	nb striga/nb plant	0	0.4	0.05	0.1	2.01

Minimum (Min), maximum (Max), mean, standard deviation (SD) and coefficient of variation (CV) are reported for each trait.

yield total (RYT) by adding the relative yields (RY) of each landrace in a mixture (De Wit 1960):

$$RYT = \sum_{i=1}^s RY_i \quad \text{and} \quad RY_i = \frac{O_i}{M_i} \quad (1)$$

where s is the total number of landraces, O_i is the observed mixture yield of landraces i and M_i is yield of landrace i in a monovarietal plot. While $RYT > 1$ indicates overyielding, $RYT < 1$ indicates yield penalties for mixtures while $RYT = 1$ indicates no change in yield for mixture compared to monovarietal yields. The second index was the proportional deviation of yield, defined respectively as D_T for total and D_i for each landrace:

$$D_T = \frac{O_T - E_T}{E_T} \quad \text{and} \quad D_i = \frac{O_i - E_i}{E_i} \quad (2)$$

where O is the observed yield and E the expected yield of the mixture if each yield had been the same as in the monovarietal plot, with T standing for total and i for landraces.

Because of global warming, governmental policies promote early-flowering crop varieties to secure harvests. We thus estimated the yield difference between mixtures and monovarietal plots of early-flowering landraces. We hence estimated D_{Early} as follows:

$$D_{Early} = \frac{O_T - \text{mean}(ME_i)}{\text{mean}(ME_i)} \quad (3)$$

where O_T is the observed total yield of a given mixture, and $\text{mean}(ME_i)$ is the mean of early-flowering monovarietal yields.

We performed a principal component analysis using measures related to yield in order to compare monovarietal and mixture plots. We then tested whether traits of plants in mixtures differed from traits of plants grown in monovarietal plots. The effect of mixtures on traits was tested with an

analysis of variance according to eq. (4), with all effects being fixed except residual error:

$$Y_{imkl} = \mu + \alpha_m + \theta_k + \tau_l + \varepsilon_{ikl} \quad (4)$$

where Y_{imkl} is the trait measured on landrace i , in treatment m at the k site in plot l ; μ : overall mean; α_m : treatment effect ($m \in [1:2]$), θ_k : site effect ($k \in [1:2]$), τ_l : plot effect ($l \in [1:30]$); ε_{ikl} : random error term. All statistical analyses were performed with the R software v.3.6.3 package (R Core Team 2017), as well as the stats v.4.2.1 and factoMineR v.2.4 packages.

Results

Landrace traits and yield measurements

The descriptive statistics of traits measured across the four landraces in monovarietal plots are reported in Table 3. The PCA of yield component data explained 62% of the variance (Fig. S2). The first component had a large positive association with the grains number component, so this component primarily reflected the agroecological conditions prevailing during the period before millet flowering. The second component had a positive association with the 1000-grain weight (W1000), and a negative association with the number of tillers/plant (NbT), so this component primarily reflected the conditions prevailing during the post-flowering period since the W1000 was mainly affected by the conditions during this period. The opposition between W1000 and NbT might have been related to increased water stress during the grain filling period, as a consequence of the higher water needs of the plant to sustain higher vegetative biomass. Many experimental studies have highlighted this mechanism in central Senegal (Affholder, 1997). The data structure did not allow separation of the two treatments

(monovarietal (T1) and mixture (T2)). However, the mixture of varieties (T2) seemed to be more associated with higher grain yield components compared to the monovarietal crop stands (T1).

Under traditional Sahelian farming conditions, pearl millet yields have been reported to vary within the 150–550 kg.ha⁻¹ range, depending on the rainfall conditions (McIntire & Fussell, 1989). In the monovarietal treatment (T1), EF landraces had a higher grain yield (288 ± 205 kg ha⁻¹) compared to the LF landraces (174 ± 146 kg.ha⁻¹, $t = 3505$, $p = 0.0007$; Fig. S3A). With all landraces considered together, grain yield in the monovarietal plots (T1) averaged 231 ± 186 kg.ha⁻¹, while it averaged 297 ± 133 kg.ha⁻¹ in mixture plots (T2) (Fig. S3B). We found a significant positive impact of mixture on grain yield, with mixture plots showing an average surplus of 65.6 ± 31.2 kg.ha⁻¹ ($t = 2099$, $p = 0.038$). However, this significant difference was not recorded for dry fodder yield ($t = -0.921$, $p = 0.359$). Dry fodder yield estimates for monovarietal plots averaged 4.6 ± 4 t.ha⁻¹ and 4 ± 2 t.ha⁻¹ for mixture plots.

The positive impact of the mixture of landraces on millet yield was confirmed by the RYT estimates, which were significantly >1 ($t = 5$, $df = 29$, $p = 1.9 e^{-05}$, Fig. 1), thus reflecting overyielding in mixture plots compared to monovarietal plots. RYT averaged 1.87 ± 0.94. Five plots showed RYT <1, with >2 RYT in 11 plots (Fig. S4).

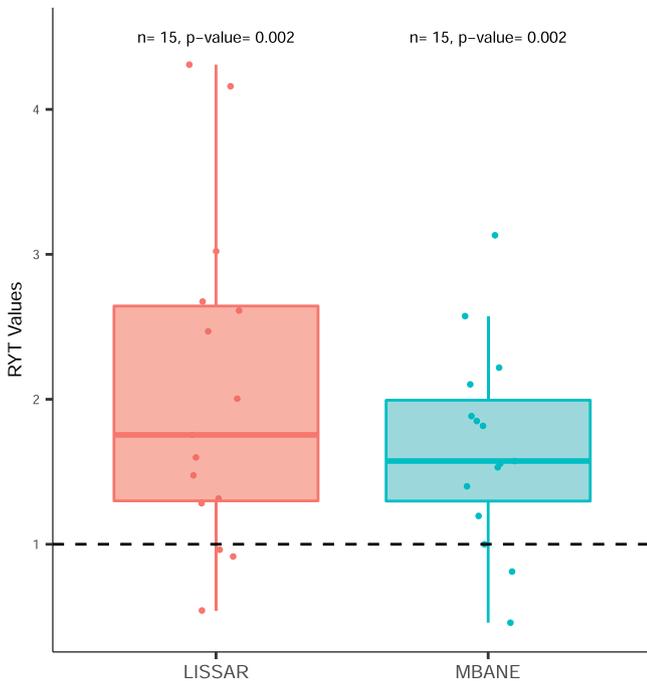


Fig. 1. Boxplots of RYT values for the Lissar and Mbane sites. RYT > 1 indicates overyielding, a RYT < 1 indicates a yield penalty for mixtures and RYT = 1 indicates no change in yield from mixing compared to monovarietal yields. For each boxplot, the number of observations (n) and the p -value of the T-test for a mean significantly different from 1 are shown.

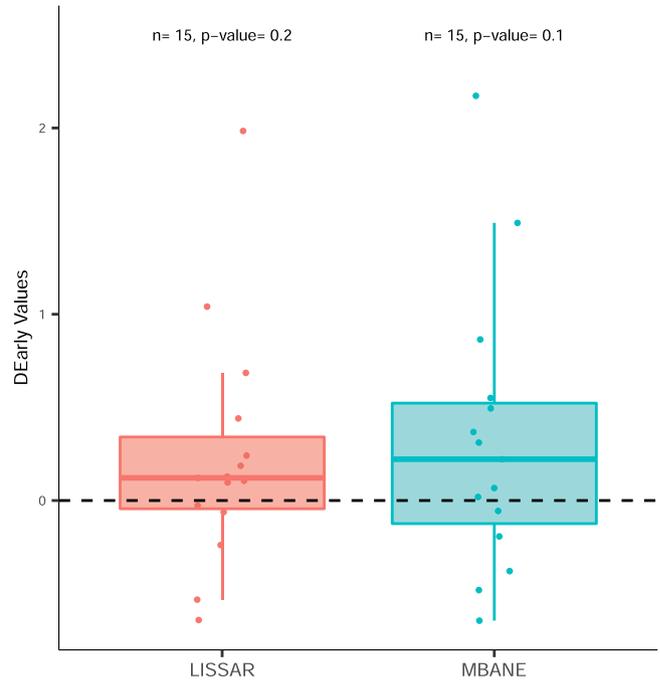


Fig. 2. Boxplots of D_{Early} values for the Lissar and Mbane sites. D_{Early} measures the proportional deviation of yield of mixtures compared to the mean yield observed in monovarietal plots with early-flowering landraces. D_{Early} values above 0 indicate overyielding. For each boxplot, the number of observations (n) and the p -value of the T-test for a mean significantly different from 0 are shown. As noted in the main text, when grouping observations from both villages, D_{Early} averaged 0.28 ± 0.69 ($t = 2222$, $df = 29$, $p = 0.034$).

Farmers are usually encouraged to grow EF landraces or EF cultivars as they were expected to complete their cycle before the midseason dry spell. We therefore investigated if the mixture plots overyielded compared to EF monovarietal plots based on the D_{Early} estimate. D_{Early} , as well as D_i and D_T , measured the proportional yield deviation in mixture plots relative to the monovarietal plots, with values >0 indicating overyielding. We found that D_{Early} averaged 0.28 ± 0.69 ($t = 2$, $df = 29$, $p = 0.034$), which meant that mixture plots had 28% higher production on average than EF monovarietal plots. Regarding the conventional D values, mean D_i for EF landraces was 0.56 ± 1.23 ($t = 4$, $df = 59$, $p = 9e^{-04}$) and was 1.19 ± 1.93 for LF landraces ($t = 5$, $df = 59$, $p = 1e^{-05}$). D_i of LF landraces were found to be significantly higher than for EF landraces ($t = -2$, $df = 100$, $p = 0.02$), indicating that beneficial effects of mixtures were higher for LF landraces (Fig. 3). Overall, D_T averaged 0.51 ± 0.66 and was significantly higher than 0 ($t = 4$, $df = 29$, $p = 0.0002$). No significant differences between sites were observed for any of the indexes.

Mixture effects seemed to benefit grain yield for both EF and LF landraces and this impact was related to different traits. For both EF and LF landraces, the yield increases could be explained by an increase in the grain number (Table 4). In EF this process was accompanied by an

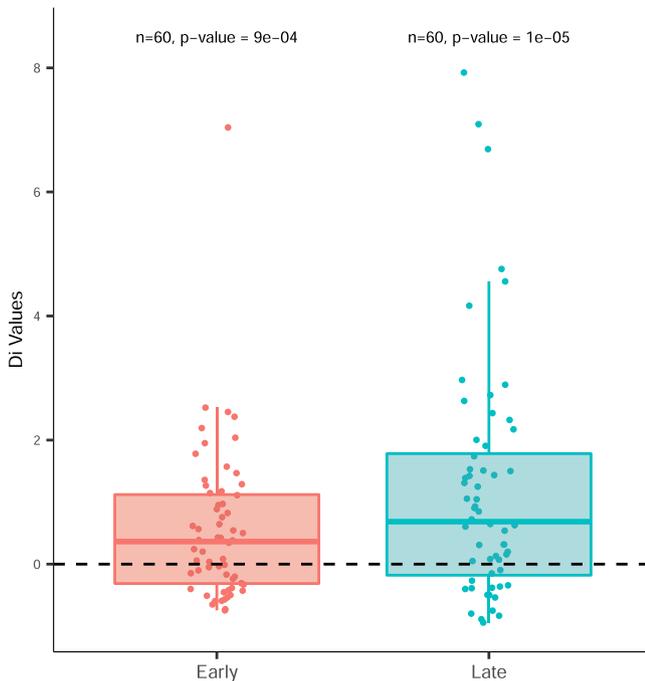


Fig. 3. Boxplots of D_i values per flowering group. D_i is the proportional deviation of yield of the landrace observed in mixtures compared to its expected yield in a monovarietal plot. D_i values above 0 indicate overyielding. For each boxplot, the number of observations (n) and the p -value of the T-test for a mean significantly different from 1 are shown.

increase in the number of panicles reaching maturity, while in LF it was accompanied by an increase in the number of fertile tillers and an increase in panicles per tiller. We did not note a significant effect of mixture on fodder, striga or other weed infestation.

Discussion

Fostering mixtures to boost crop yields

In this study, we investigated the effects of phenological mixtures by growing one flowering cycle landrace per plot compared to growing early- and late-flowering landraces on the same plot under Sahelian farmers' field conditions, with low fertilization and rainfed limiting conditions.

Our results revealed no effect of mixtures on fodder yield, but a highly significant impact on grain yield was noted. Therefore, phenology could be a useful mixing criterion with potential to increase the crop yield without jeopardizing the fodder yield. This is an important aspect considering the dual use of pearl millet, i.e. for human nutrition and livestock fodder. We estimated an average 87% grain overyield in the mixture plots compared to all of the monovarietal plots, and 28% when only compared to early-flowering landraces in monovarietal plots (e.g. D_{Early}). Previous meta-analyses revealed high variability in mixture effects on grain

yield, i.e. ranging from 30 to 100% according to Kiaer et al. (2009), from 40 to 60% according to Reiss and Drinkwater (2018) and with a mean of <6% according to Borg et al., 2018; Kiaer et al., 2009; Reiss & Drinkwater, 2018 and Smithson & Lenné, 1996. Yet few studies have investigated the impact of the phenological criterion in mixture plots and, when it is taken into account, it is often combined with the plant height criterion (Borg et al., 2018). Reported impacts ranged from no effect to a positive effect on biomass or grain yield (Borg et al., 2018; Giunta et al., 2020; Hooper & Dukes, 2004; Montazeaud et al., 2020; Smithson & Lenné, 1996; Thiaw et al., 1993; Vidal et al., 2020).

Different ecological mechanisms could explain the positive impact of biodiversity on productivity, including: 1) a sampling effect, and 2) complementarity (Barot et al., 2017). The sampling effect relies on the assumption that more diverse plant communities are more likely to host varieties that perform best in a given environment. Short-cycle varieties are considered more suitable for arid environments and our findings are in agreement with this statement. In monovarietal plots, higher yields were observed for short-cycle varieties, so it is likely that these short-cycle varieties would have the highest overyielding values (D_i). Yet, contrary to those expectations, we observed that late-flowering landraces benefited the most from mixtures. Similar results were found by Thiaw et al. (1993), where medium cycle cowpea varieties benefited more than early ones, and by Hooper and Dukes (2004), with late-season annual plants benefiting the most in phenological mixtures of serpentine grassland species. In all three studies, the presumed 'most' adapted variety was not the outperforming one, thereby suggesting that the sampling effect is *a priori* not the main cause of overyielding in phenological mixtures.

Otherwise, strong differentiation at phenological stages could lead to an increase in yield through improved resource use. Complementarity is based on the principle that components utilize different resources, i.e. niche partitioning (Loreau M. & Hector. A., 2001). Phenological differences could allow nutrient uptake to occur at different times, hence reducing competition at key physiological stages (Meilhac et al., 2020). This is in line with observations of Turner et al. (2020) where, in *Arabidopsis*, phenological mixtures had a positive impact in low-resource conditions but not in high resource conditions. Reducing resource competition through phenological mismatching could enable late-flowering landraces to have access to more resources for better performance, notably in unfavourable conditions such as an excessively dry growing season.

This complementary process does not exclude other mechanisms such as facilitation. Facilitation mechanisms could also be involved in the nutrient cycling process through an increased availability of nutrients for other varieties in the mixture (Barot et al., 2017 and reference therein). For instance, pearl millet genotypes are known to impact rhizobacterial diversity and thus soil microbial communities (Ndour et al., 2017; P.M.S., 2021). Research on pearl millet

Table 4. Summary of the results for an analysis of variance on 12 traits.

		All landraces combined			Late-flowering landraces			Early-flowering landraces		
		Estimate	SE	Pr (> t)/Pr (> z)	Estimate	se	Pr (> t)/Pr (> z)	Estimate	se	Pr (> t)/Pr (> z)
Grain yield per plant	Intercept	3.08	2.15		1.46	2.14		4.68	3.10	
	Mixture effect	2.07	0.80	0.01	2.35	0.82	0.01	1.84	1.13	0.11
Productive tillers rate	Intercept	0.11	0.08		−0.03	0.12		0.21	0.10	
	Mixture effect	0.07	0.04	0.04	0.16	0.05	0.00	0.00	0.05	0.96
Nb of panicles	Intercept	0.53	0.06		0.50	0.09		0.56	0.08	
	Mixture effect	0.06	0.02	0.01	0.08	0.04	0.03	0.05	0.03	0.12
Mature panicle rate	Intercept	1.20	0.27		0.89	0.43		1.49	0.32	
	Mixture effect	0.21	0.10	0.04	0.19	0.17	0.26	0.25	0.12	0.04
Spoiled panicle rate	Intercept	0.87	0.23		0.59	0.35		1.13	0.27	
	Mixture effect	−0.02	0.08	0.82	−0.07	0.14	0.59	0.06	0.10	0.54
Dried weight of panicles	Intercept	14.62	6.59		11.60	10.24		17.81	8.45	
	Mixture effect	5.76	2.45	0.02	7.55	3.93	0.06	3.65	3.09	0.24
Nb of seeds	Intercept	412.00	242.80		185.00	267.00		641.00	350.00	
	Mixture effect	256.00	90.20	0.01	239.00	102.00	0.02	266.00	128.00	0.04
Weight of a 1000 seeds	Intercept	8.14	0.45		8.47	0.51		7.77	0.55	
	Mixture effect	−0.06	0.17	0.71	0.19	0.20	0.34	−0.23	0.20	0.26
Nb of tillers per plant	Intercept	2.80	0.34		2.51	0.54		3.10	0.44	
	Mixture effect	−0.03	0.13	0.80	−0.27	0.21	0.21	0.20	0.16	0.21
Fodder yield per plant	Intercept	0.06	0.02		0.06	0.04		0.07	0.03	
	Mixture effect	0.00	0.01	0.82	−0.02	0.02	0.11	0.01	0.01	0.28
Hybrid rate	Intercept	−2.20	0.13		−2.14	0.20		−2.24	0.16	
	Mixture effect	−0.04	0.06	0.52	−0.01	0.09	0.91	−0.04	0.09	0.65
Witchweed rate	Intercept	−4.51	0.58		−2.14	0.20		−4.51	0.58	
	Mixture effect	−0.11	0.15	0.45	−0.01	0.09	0.91	−0.11	0.15	0.45

Three datasets were used: 1) a first dataset with all four landraces corrected for site and plot effects; 2) a dataset with the measurements on the two LF landraces, and 3) a dataset with measurements on the two EF landraces. Estimates, standard error and *p*-values are reported. Pr (>|z|) values are from a logit distribution for rate measures and Pr (>|t|) values are from a Gaussian distribution for remaining variables. *P*-values in bold indicate a significant effect.

root architecture suggests that the root angle, and thus will define the resource usage strategy either in the soil upper or lower layers. This trait is strongly correlated with flowering in pearl millet during drought experiments, in other words it seems that early and late-flowering varieties may not exploit the similar soil layers. To unpack the role of each mechanism, further experiments should be focused on investigating phenotypic and plasticity differences in root systems and microbiomes. A number of studies are underway on these topics, yet few studies have compared early- and late-flowering pearl millet.

In addition to the impact of phenology, we identified at least three other possible explanations for why we observed strong mixture effects: i) the number of components (i.e. varieties), ii) the stress gradient hypothesis, and iii) the genetic diversity (crop types, landraces vs. improved varieties). In our study, we tested mixtures with four landraces. Most studies (up to 96% of trials in Reiss & Drinkwater 2018) used fewer than three components, while the number of components > 4 has been found to be positively correlated with overyielding (Kiær et al., 2009; Reiss & Drinkwater 2008; Smithson and Lenne 1996; but not by Borg et al., 2018). As on average 11 sorghum landraces are grown within the same field (Barnaud et al., 2008), research is far from exploiting the potential number of components that smallholders would agree to mix.

Species biodiversity is a key component in the resistance to harsh climate events, while also stabilizing ecosystem productivity (Isbell et al., 2015) and biodiversity–ecosystem functional relationships (Craven et al., 2016). Indeed, the stress gradient hypothesis (Lortie & Callaway, 2006), predicts that through facilitation, biodiversified systems such as mixtures could be more beneficial when abiotic conditions are not optimal, i.e. when low fertilizer quantities are used under climatic stress conditions (heat/cold, flood/drought) or in infertile/degraded soils. The results of a meta-analysis of global plant communities showed that most plant interactions respond to stress and shift toward facilitation and reduced competition (He et al., 2013). Evidence of a greater benefit of varietal mixtures in biotic stress conditions has been reported (Borg et al., 2018; Reiss & Drinkwater, 2018). Latter authors found that grain overyielding was higher in tropical climatic conditions when no fertilizer was used and when the P concentration was suboptimal. In our study, soils were notably characterized by suboptimal P concentrations. We added some farmer-produced organic manure but the quality and quantity used would not have been sufficient to offset the very low quality of this type of soil. Considering that low water availability markedly limits crop yields in Sahelian rainfed agriculture (Affholder, 1997), it is surprising that only few studies have investigated the impact of crop mixtures in low water or drought conditions. Under experimental drought conditions, genetic diversity has been found to have a beneficial effect on grain yield stability, but not on productivity (Brooker et al., 2021; Prieto et al., 2015). This is a gap that should be explored in future

research and our results were in line with the gradient stress hypothesis, which suggests that mixtures could be beneficial in limited nutrient and water conditions.

Moreover, from quantitative and qualitative perspectives (i.e. composition), we believe that genetic diversity would have an impact on the mixture outcome. A growing number of studies are investigating the genetics underlying plant–plant interactions, even though studies on positive interactions remain marginal (Subrahmaniam et al., 2018). Recent studies have shown that allelic diversity at specific DNA regions are positively or negatively associated with mixture outcomes (Turner et al., 2020; Montazeaud et al., 2022). The impact of allelic diversity within and between components would warrant further in-depth assessment. The potential effects of mixtures may so far have been underestimated because mainly self-pollinated species have been considered: wheat, barley and oats (e.g. 80% in Reiss & Drinkwater, 2018), with the remaining share being legumes. Self-pollinated species naturally have relatively lower genetic diversity and higher homozygosity rates than cross-pollinating species such as pearl millet. Homozygosity could be further increased by the domestication genetic loss observed in cultivated forms: 69% in bread wheat, 84% in durum wheat and 50% in barley (Haudry et al., 2007; Pankin et al., 2018), compared to about 30% in pearl millet (Cloutault et al., 2012; Varshney et al., 2017). This domestication genetic loss may impact the ability of cultivated forms to benefit from biodiversity effects (Chacón-Labela et al., 2019) and it is becoming increasingly clear that the ability to interact in communities has shifted during crop evolution (Fréville et al., 2022). It could therefore be assumed that the mixture effects would vary depending on whether the mixture components are autogamous vs. allogamous crops, or improved varieties vs. landraces.

Enhancing biodiversity conservation for sustainable and fair agroecological transitions

Megavarieties, i.e. improved varieties highly promoted by agricultural services, tend to increasingly dominate agricultural landscapes. For instance, only six maize varieties prevail in 71% of the world's total maize-growing area, while four rice varieties account for 65% of the rice-growing area (Ceccarelli et al., 2013). From a conservation standpoint, as long as varietal mixtures do not lead to a loss of yield, they are a relevant solution for the conservation of local landraces and maintenance of their environmental and human co-evolution. Studies have shown how quickly adaptations through natural and human selection can take place and that co-evolution is a dynamic solution to climate change (Bocci et al., 2020). Promoting agroecological practices favouring agrosystem diversification or changing the plant breeding paradigm from ideotype to ideomix (Litrice & Violle, 2015) would also serve to preserve agrobiodiversity.

A bibliographic survey suggests that 98% of agricultural research published so far is not relevant to the needs of smallholder farming systems (Nature Editorial, 2020). The crop and varietal portfolio is rooted in the multiple values embedded in diversity, and productivity is far from being the only factor driving farmers' choices. In Vanuatu, cassava varieties are kept for product/gift exchanges so as to preserve family heritage and facilitate acceptance in social networks. (Caillon & Lanouguère-Bruneau, 2005). Despite drought episodes, Sahelian late-flowering pearl millet landraces have not been abandoned (Bezançon et al., 2009; Lalou et al., 2019), while late-flowering landraces are viewed as tastier and easier to digest and their tillers are better for roofing and fences (Lalou et al., 2019). Agroecological innovations—while fulfilling a diverse range of biodiversity values for a fair and sustainable transition—need to be based on better knowledge of smallholder farming systems and the values borne by local communities. The agroecological transition, as Leclère (2019) reports, must: (i) adapt locally the generic solutions from agronomic sciences; (ii) complement scientific knowledge with local knowledge derived from farmers' experience; and (iii) inspire and produce new agronomic knowledge. It is thus a question of promoting collaborative research to mainstream stakeholders' different visions and values. Altieri and Toledo (2011) thus stress the importance of direct farmer involvement in the research process. The joint mobilization of scientific and farmers' knowledge—i.e. both expert and contextualized (i.e. within the socio-agro-economic context) knowledge—constitutes a key approach. In this respect, experimental networks with farmers, such as that discussed in this paper, create favourable conditions for hybridizing knowledge (Doré et al., 2011; Hazard et al., 2018; Leclère, 2019), while allowing for collective learning (Girard & Magda, 2018). Yet it is not only a question of farmer involvement, it involves a shift from top-down to bottom-up approaches to knowledge production guided by farmers' needs and aspirations. This has the greatest potential for enabling transformation to foster sustainability and social justice (Anderson et al., 2019). The results presented here were the outcome of a joint venture, which is why the non-academic partners are associated as co-authors. Moreover, the key finding of this study was not solely the impact of the mixture *per se*, but rather that we—a collective of researchers and farmers—were able to effectively address farmers' questions. These farmers will thus directly benefit from the research findings, while impacting the transformation trajectory regarding farmers' practices. The joint participation approach is an essential way to foster sovereignty and food security while building fair and sustainable agroecosystems. Indeed, as pointed out by IPBES in, 2019, “Recognizing the knowledge, innovations, practices, institutions and values of indigenous peoples and local communities (IPLCs), and ensuring their inclusion and participation in environmental governance, often enhances their quality of life and

the conservation, restoration and sustainable use of nature, which is relevant to broader society.”

Conclusions

In this study, we have demonstrated the significant impact of phenology-based varietal mixtures under real field conditions on Sahelian farms, thereby allowing smallholder farmers to maintain their diverse range of species and varieties, while being in line with their diversity of values and uses. A growing body of research advocates the use of varietal mixtures in the 21st century agriculture. This highlights that arguments against this practice, i.e. in favour of mechanization and homogenization, no longer stand (Wuest et al., 2021) and that the economic and nutritional benefits varietal mixtures should be sufficient proof (Snyder et al., 2020). Yet questions remain regarding the associated know-how, i.e. which varieties, how many and how to crop them. Here we argue that answers to these questions based on smallholder farmers' knowledge should eventually emerge, especially in developing countries where varietal mixtures have been long been used.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available on the dataverse deposit under <https://doi.org/10.23708/SVJS1T>

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Supplementary materials

Supplementary material associated with this article can be found in the online version at [doi:10.1016/j.bae.2022.12.006](https://doi.org/10.1016/j.bae.2022.12.006).

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