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Effect of Seasonal Temperature on the Genotypic Variability of Flowering Duration in Pearl Millet (*Pennisetum glaucum*) in Niger

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Abstract: Heat stress is a major contributor to crop losses worldwide. Millet [*Pennisetum glaucum* (L.) R. Br.] is a staple crop for inhabitants of arid and semi-arid regions of the world, due to its extraordinary adaptation to drought and high temperatures. Climate change points to an overall increase in temperature, the effect of which on crop growth and productivity remains to be determined. The most sensitive phase is the flowering period when the reproductive organs are exposed to excessive temperatures. A better understanding of the durations of this phase and the genetic mechanisms underlying the variability of these exposure durations will provide an important step toward the development of efficient breeding strategies for high and stable production of millet in semi-arid environments. This study evaluates the variability of flowering time in millet, as well as its relationship to yield components. Eleven varieties of millet, four of which came from the research center, were evaluated at two time periods with different minimum and maximum temperatures during flowering to see the impact on flowering time, set and grain yield. The device is in randomized complete blocks of 11 varieties with 4 repetitions. The results of the analysis of variance show significant variations between genotypes and between seasons, for most of the parameters measured. This wide variability could offer a new way to improvement for the species.

Keywords: Pearl Millet, Early Morning Flowering, Heat Stress, Seasonal Temperature Variation, Niger

Introduction

Millet (*Pennisetum glaucum* (L.) R. Br.) provides food and nutritional security to more than 500 million people in arid and semi-arid regions of West and East Africa and South Asia. Its culture extends over more than 29 million hectares in the world. Production has increased over the past 20 years, mainly due to the adoption of improved hybrids in India and the expansion of cultivated areas in West Africa. Niger is the second-producing country in Africa after Nigeria. Millet is grown on more than 6.5 million hectares, with an average yield of 450 kgha-1 and a production of around 3 million tons of grain (INS, 2016). Millet is rich in protein and micronutrients. It offers real hope for the fight against iron and zinc malnutrition, which affects almost 25% of the world's population (Anuradha *et al.*, 2017; Anuradha *et al.*, 2018; Govindaraj *et al.*, 2020). Millet is the crop that is "still" capable of growing and producing food seeds, in agro-climatic conditions where any other cereal would fail (Daouda Ousmane, 2017; Varshney *et al.*, 2017; Kadri *et al.*, 2019). It is the cereal proven to be the main crop to minimize the adverse effects of climate change in arid and semi-arid zones (Azare *et al.*, 2020). Millet is almost exclusively grown under strict rainfed conditions, in the Sahelian zone where there is only one rainy season. Its irrigation is not yet possible due, first of all, to the scarcity of water, then to the low economic and technical level of the farmers, the low fertility of the soil, and the increased climatic risk. Unfortunately, the rainy season in Niger is characterized by very high temperatures, which can sometimes exceed 45°C (Fig. 1), far from optimal production temperatures (Gupta *et al*., 2015). A drop of 15 to 35% in yields is envisaged in Africa and Asia, for a temperature increase of 3 to 4°C (Ortiz *et al*., 2008; Iizumi *et al*., 2017), which seems inevitable given the current trend.

Although heat stress can occur at any time during the cycle, its effect is more significant at the flowering and grain-filling stage (Kumar, 2004; Kholova *et al*., 2010; Gupta *et al*., 2015) and makes the crop productivity depends on effective sexual reproduction. Most of the previous work has focused on the length of the sowing-heading or sowing-flowering cycle and its relationship with the final grain yield (Naoura *et al*., 2020; Anuradha *et al*., 2017; Anuradha *et al*., 2018). Very few works have focused on the duration of sexual reproduction (and therefore the time of exposure of floral organs to high temperatures) and its genotypic variability, knowledge of which could help improve efficiency for the selection of millet varieties more tolerant to thermal stress. This is an essential question for the improvement of the thermal tolerance of the species. This study examines the genotypic variability of the duration of flowering and its involvement in heat stress tolerance in pearl millet.

Materials and Methods

The plant material includes a collection of 11 varieties of pearl millet promoted by the official agricultural extension services in Niger and coming from approved multipliers. Four are from the National Institute of Agronomic Research of Niger (INRAN), three from the International Research Institute for Crops in Semi-Arid Tropical Zones (ICRISAT), and four M2 lines from the Laboratory of Biotechnology and Plant Breeding (LABAP) of the Institute of Radioisotopes of Abdou Moumouni University of Niamey. The detailed characteristics of the varieties are given in Table 1.

The trials took place in the field, on the experimental plots of LABAP (latitude 13°29 North and longitude 2°10 East at an average altitude of 205 m). The soil is deep sandy of wind origin (95%), with moderate acid pH (5.5) and low organic carbon content (< 0.2%). The available phosphorus is about 3 ppm (Bray I), the CEC of 2 meq/100g of soil. The water retention capacity is 0.1 cm3 of water per cm3 of soil. A first trial in the dry Season (SS) was conducted from September to December 2019 and a Second (SP), in the rainy season from July to October 2020. During the period of fertilization and seed formation, daily temperatures are higher in the dry season than in the rainy season (Fig. 1). On the other hand, the morning temperatures are lower there. The sensitivity of plants to heat stress is such that even a change of one degree, beyond the norm, can trigger morpho-physiological responses in the reproductive organs. This work will allow us to understand the effect of this temperature difference between the dry season and the rainy season, on the duration of flowering and seed formation, as well as the genotypic responses in pearl millet.

The experimental device is in complete randomized blocks, with 11 varieties and four repetitions. Each variety corresponds to a 5 m seeding line with 5 pockets 1 meter apart (Fig. 2). All agronomic recommendations concerning pearl millet were applied during cultivation. Fertilization in four fractions of 20 units each, in the form of NPK (15-15-15), was applied. The first fraction was followed by manual plowing 30 cm deep (before sowing). The other three were brought in the form of a circle around the seedling and incorporated by light scarification. Irrigation was done manually using watering cans. In the dry season, the daily intake was 3 liters per pocket during the juvenile phase, which increased to 5 liters from the bolting. In the rainy season (second trial), irrigation was carried out as needed, at the rate of three liters per day, if necessary.

Observations were recorded from the main strand of the 3 central pockets of each line, for four parameters, namely, the Duration of Female Flowering (DFF), the Duration of Male Flowering (DFM), the Duration of Formation of First Seeds (DFG) and grain yield at harvest (Rdt). The Excel spreadsheet was used for data entry and the development of certain graphs. Yield components were analyzed using GENSTAT 12 software (analysis of variance and separation of means). The separations of the means were made, using the least significant difference, according to the "Student" test. All the probabilities were assessed at the 5% threshold.

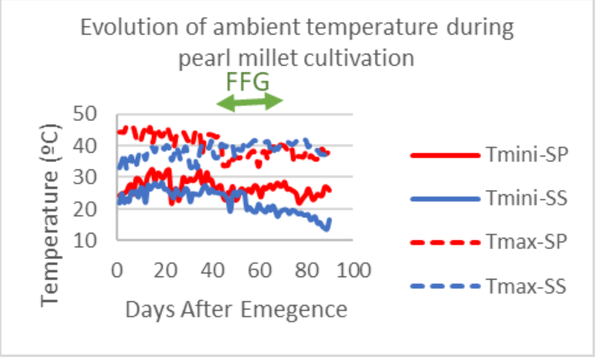

Fig. 1: Temperature variation during the millet crop cycle, in the dry Season (SS) and the rainy Season (SP). FFG: Fertilization and seed formation.

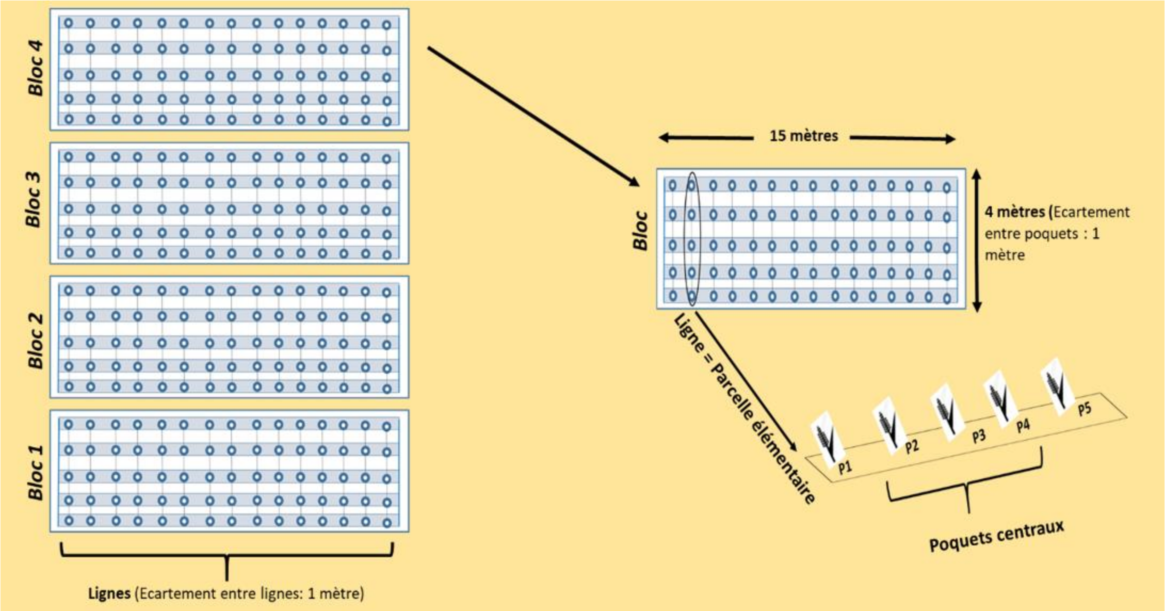

Fig. 2: Schematics of the experimental device

Table 1: Characteristics of the tested pearl millet varieties

Variety	Local denomination	Breeder	Production zone	Sowing-maturity cycle (Days)	Plant height (cm)	Tillering	Ear length	Yield (Tha^{-1})
Ankoutess	ANK P1	INRAN	300-350 mm	80-85	145-150	Medium	Short	1.25-1.45
H80-10GR	Hative Guerguera	INRAN	300-400	80-85	200-230	Good	Medium	2.5
Chakti		ICRISAT	350-700	68	190	Small	Medium	1.5
HKP	Haïni Kiré Precoce	INRAN	350-800	75-90	190-200	Medium	Medium	1.5-2.5
ICMV IS 99001	Nakowa	ICRISAT	350-700	90	250	Medium	Medium	2
MI 02-82	Mil Irradiated 1272	IRI	300-800	80-90	200-250	Good	Medium	1.5-2.5
MI 10-54	Mil Irradiated 1272	IRI	300-800	80-90	200-250	Good	Medium	1.5-2.5
MI 12-72	Mil Irradiated 1272	IRI	300-800	80-90	200-250	Good	Medium	1.5-2.5
MI 13-63	Mil Irradiated 1272	IRI	300-800	80-90	200-250	Good	Medium	1.5-2.5
SOSSAT-C88		ICRISAT	350-600	80	200	Medium	Short	1.5-2
Zatib	Zanwarfa da Tchinan Bijimi	INRAN	350-800	90-95	190-200	Medium	Medium	2-2.5

Results

Grain Yield

Millet grain yields varied between 0.89 and 5.52 to-1, with an overall average of 2.31 tha-1 for all varieties and all seasons combined (Table 2). The results of the statistical analyzes on grain yield are given in Table 3. The yield is significantly higher in the dry season than in the rainy season (p = 0.024). A very highly significant difference was obtained between genotypes (p<0.001), as well as a very highly significant interaction (p<0.001) between seasons and genotypes.

Duration of Female Flowering (DFF)

The duration of female flowering varies from 1.3 to 4.1 days and is 2.4 days on average, for all varieties and all seasons combined (Table 2). It is longer in the dry season than in the rainy season for all the varieties (2.7 days on average for the dry season against 2.1 for the rainy season). The results of the statistical analysis (Table 4) show very highly significant differences for each of the two factors studied (p < 0.001).

Duration of Male Flowering (DFM)

The duration of male flowering varies between 1.2 and 3.5 days, with an average of 2.0 days for all varieties and all seasons combined (Table 2). The results show great variability between the genotypes and between the two seasons. Female flowering lasts longer in the dry season (2.2 days) than in the rainy season (1.8 days). Statistical analysis shows a very highly significant difference (p<0.001) between varieties and between seasons (Table 5).

Total Flowering Time

The total duration of flowering was obtained by adding the duration of female flowering to that of male flowering for each variety and each season. It varies between 2.4 and 7.3 days, with an average of 4.4 days for all varieties and all seasons combined (Table 4). The total duration of flowering is also longer in the dry season than in the rainy season (4.9 days against 3.9). Statistical analysis shows a very highly significant difference ($p<0.001$) for the two factors studied (Table 6)

Time to First Seed Formation (DFG)

The duration of formation of the first seeds varies between 2.0 and 5.6 days, with an average of 4.4 days for all varieties and all seasons combined. The first seeds form more slowly in the rainy season (4.9 days against 3.9). Statistical analysis (Table 7) showed a highly significant difference between seasons ($p<0.001$) and between varieties ($p = 0.003$). A significant interaction ($p = 0.002$) between the genotype x Season factors are also highlighted.

Correlation Between Grain Yield and its Components

Grain yield is significantly and negatively correlated with the duration of the formation of the first seeds (R = -0.199; α = 0.05). A negative and highly significant correlation (R = -0.451; α = 0.01) was obtained between the duration of the formation of the first seeds and the duration of flowering (Table 8). For a given genotype of pearl millet, the longer flowering is spread over time, the faster the first seeds are formed. Thus, the longer the flowering, the higher the grain yield.

Table 2: Duration of flowering and formation of the first seeds in pearl millet (*Pennisetum glaucum* (L.) R. Br.). *DFF: Female Flowering Duration, DFM: Male Flowering Duration, DTF: First seeds Formation Duration, Rdt: Yield*

	DFF (Days)		DFM (Days)		DTF (DFF + DFM)		DFG (Days)		Rdt (Tha^{-1})	
Variety	SP	SS	SP	SS	SP	SS	SP	SS	SP	SS
MI 02/82	2.25	2.25^{ab}	1.33	2.00^{abc}	3.58^{abcd}	4.25^{ab}	5.33	4.25^{ab}	2.65	2.99^{ab}
MI 13/63	2.33	2.50^{ab}	1.33	1.75^{abc}	3.67^{abcd}	4.25^{ab}	4.21	4.00^{ab}	2.30	5.52^{c}
MI 12/72	2.21	4.08^{b}	2.33	3.25^{bc}	4.54^{bcde}	7.33^{c}	5.50	2.33^{a}	2.44	2.87^{ab}
MI 10/54	2.29	2.75^{ab}	2.12	3.50^{c}	4.42^{bcde}	6.25^{bc}	5.58	2.00^{a}	1.62	2.30^{ab}
ANKOUTESS	2.11	2.67^{ab}	1.22	1.25^{a}	3.33^{abcd}	3.92^{a}	5.29	5.67^{b}	2.62	1.69^{ab}
ICMVIS 99001	2.22	2.37^{ab}	1.92	2.75^{abc}	4.29^{bcde}	4.97^{ab}	4.54	3.00^{ab}	1.64	3.31^{b}
ZATIB-R1	1.17	2.62^{ab}	1.83	1.50^{ab}	3.00^{abc}	4.12^{ab}	5.50	4.75^{ab}	1.89	2.37^{ab}
H80-10GR (G4)	2.75	2.67^{ab}	2.50	2.25^{abc}	5.25^{e}	4.92^{ab}	4.08	4.00^{ab}	1.83	1.50^{ab}
HKP-R1	2.33	2.75^{ab}	1.92	2.25^{abc}	4.25^{bcde}	5.00^{ab}	4.75	4.25^{ab}	2.14	3.26^{b}
HKP R2	1.42	2.62^{ab}	1.58	2.00^{abc}	3.00^{abc}	4.62^{ab}	5.54	4.75^{ab}	1.87	1.68^{ab}
CHATKI (R1)	1.38	1.50^{a}	1.00	1.67^{abc}	2.38^{a}	3.17^{a}	4.88	5.33^{b}	2.09	0.89^{a}
ICMVIS 89305	2.67	3.00^{ab}	1.67	2.25^{abc}	4.34^{bcde}	5.25^{ab}	4.54	2.00^{a}	2.68	2.52^{ab}
SOSSAT-R1	2.39	2.83^{ab}	1.94	2.25^{abc}	4.33	5.08^{ab}	5.38	4.00^{ab}	1.56	1.71^{ab}
Average	2.13	2.55	1.75	2.21	3.87	4.86	4.93	3.87	2.10	2.51
Probability	<0.001	0.045	0.011	0.006	<0.001	<0.001	0.253	<0.001	0.523	<0.001

Table 3: Analysis of variance on grain yields. DF: Degree of Freedom; MS: Mean Square; VR: Variance Ratio

Source of variation	DF	SS	MS	VR	F pr.	Lsd 5%
Blocs stratum	3	2.2749	0.7583	0.95		
Blocs*Units* stratum						
Season	1	4.2836	4.2836	5.34	0.024	0.350
Varieties	12	41.6821	3.4735	4.33	<0.001	0.892
Season X Varieties	12	31.5800	2.6317	3.28	<0.001	1.261
Residual	75	60.1266	0.8017			
Total	103	139.9473				

Table 4: Analysis of variance on the duration of female flowering. DF: Degree of Freedom; MS: Mean Square; VR: Variance Ratio

Source of variation	DF	SS	MS	VR	F pr.	Lsd (5%)
Season	1	7.1208	7.1208	16.29	<0.001	0.258
Varieties	12	18.1956	1.5163	3.47	<0.001	0.658
Varieties	12	9.2269	0.7689	1.76	0.070	0.931
Residual	78	34.0973	0.4371			
Total	103	68.6406				

Table 5: Analysis of variance on male flowering duration in pearl millet. DF: Degree of Freedom; MS: Mean Square; VR: Variance Ratio

Source of variation	DF	SS	MS	VR	F pr.	Lsd (5%)
Blocs stratum	3	7.3617	2.4539	5.00		
Blocs.*Units* stratum						
Saison	1	5.4679	5.4679	11.15	<0.001	0.274
Varieties	12	24.4261	2.0355	4.15	<0.001	0.698
Season x Varieties	12	5.2953	0.4413	0.90	0.551	0.986
Residual	75	36.7795	0.4904			
Total	103	79.3305				

Table 6: Analysis of variance on the total duration of flowering in pearl millet. DF: Degree of Freedom; MS: Mean Square; VR: Variance Ratio

Source of variation	DF	SS	MS	VR	F pr.	Lsd (5%)
Blocs stratum	3	9.0315	3.0105	4	19	
Blocs.*Units* stratum						
Season	1	25.0685	25.0685	34.88	<0.001	0.331
Varieties	12	70.1582	5.8465	8.13	<0.001	0.844
Season X Varieties	12	13.6365	1.1364	1.58	0.116	1.194
Residual	75	53.063	0.7188			
Total	103	171.8009				

Table 7: Analysis of variance on the duration of the formation of the first seeds. DF: Degree of Freedom; MS: Mean Square; VR: Variance Ratio

Source of variation	DF	SS	MS	VR	F pr.	Lsd (5%)
Blocs stratum	3	2.919	0.973	0.80		
Blocs.*Units* stratum						
Season	1	29.267	29.267	24.38	<0.001	0.428
Varieties	12	39.870	3.322	2.77	0.003	1.091
Season X Varieties	12	42.796	3.566	2.97	0.002	1.542
Residual	78	93.618	1.200			
Total	103	205.550				

Table 8: Correlation between duration of flowering, first seed formation and grain yield in pearl millet (P. glaucum). DFF: Female flowering duration, DFM: Male flowering duration, DTF: Total flowering duration; DFG: First seeds formation duration, Rdt: Yield

	DFM	DFF	DFT	DFG	RDT
DFM	1				
DFF	0.161	1			
DTF	0.782^{**}	0.742^{**}	1		
DFG	-0.373^{**}	-0.312^{**}	-0.451^{**}	1	
RDT	0.143	0.073	0.144	-0.199^{*}	1

** Highly significant correlation at the 0.01 level; * Significant correlation at the threshold of 0.05

Discussion

The yield is significantly higher in the dry season than in the rainy season. During fertilization and seed formation, the average maximum temperatures are 38.9 and 40.3ºC, for the rainy season and the dry season respectively. That is a difference of 1.44ºC. Higher dry season temperatures are expected to produce more damage to fertilization and lead to a greater drop in grain yield compared to the rainy season. The temperature difference between the two seasons did not produce a measurable differential negative impact on millet grain yields. The consequences of heat stress on male and female cereal gametes have been the subject of several previous works (Djanaguiraman 2018; Lohani *et al.*, 2020; Jiang *et al.*, 2019; Bheemanahalli *et al.*, 2017; Santiago and Sharkey, 2019; De Storme and Geelen, 2020; Kranner 2010; Chaturvedi *et al.*, 2021). Pearl millet is protogynous and the stigmas appear first. The emergence of the stigmas begins in the terminal third of the panicle, then continues simultaneously upwards and downwards. The emergence of the stigmas took on average 2.13 and 2.55 days in the rainy season and the dry season respectively. Unpollinated stigmas may remain fresh for several days. With the prevailing temperatures of 38 to 40ºC, a negative impact on fertilization and seed formation could be expected as reported by some authors (Gupta *et al*., 2015). It is only during pollination that the stigmas shrivel up within a few hours. The emergence of the anthers took 1.75 and 2.21 days respectively for the rainy season and the dry season. The hot daytime temperatures of up to 40.3ºC had no negative impact on fertilization and grain formation. On the contrary, the morning temperatures, which increase from 19.7 to 26.9°C, seem to have had a significant effect on the efficiency of fertilization in millet. In addition, a recent study, using ROS probes coupled with cytometry, shows that exposing flowers to a temperature of 35°C for 30 min resulted in a 60% reduction in pollen germination potential in *Lycopersicum esculentum* (Luria *et al*., 2019). In addition, we note in wheat varieties, a peak of flowering during the coolest hours of the day (i.e., early morning or late evening), to reduce the damage caused by heat stress at flowering (Aiqing *et al*., 2018). Similarly, sorghum (*Sorghum bicolor* [L.] Moench) and pearl millet (*Pennisetum glaucum* (L.) R. Br.), known for their ability to survive in extremely hot and dry environments, achieve their floral opening the first hours after dawn (Chiluwal *et al*., 2020). In our experience, the minimum average temperatures (observed very early in the morning), during flowering, were 26.9 for the rainy season and 19.7°C for the dry season. This temperature difference of 7.2ºC may be related to the significant drop in yield observed in the rainy season, compared to the cooler dry season. This heat avoidance strategy, which effectively attenuates heat stress-induced spikelet sterility, has been well documented in rice (Ishimaru *et al*., 2010), where the introduction of this trait, from the wild form to cultivated forms significantly reduced ear infertility and lower grain yields (Bheemanahalli *et al*., 2017). This is an opportunity that should be explored for pearl millet, given that a very highly significant difference was obtained between the genotypes tested ($p<0.001$). A very highly significant interaction ($p<0.001$) is also highlighted between the season and the millet genotypes. This genetic diversity recorded for this trait, even in a small set of 11 pearl millet genotypes, is encouraging and highlights the need for further research in this area.

The duration of the formation of the first seeds is negatively correlated with the durations of female and male flowering. When it is long, the yield is low, and vice versa. Similarly, the grain yield is low when flowering lasts a long time. The duration of exposure of the floral organs to the high temperatures of the day hurts the formation of grains and yield. From this point of view, varieties with short flowering times should be sought (CHATKI and ANKOUTESS). The comparison between the two seasons shows that the cool temperatures of the dry season led to an extension of the duration of flowering. Morning temperatures may play a more important role in fertilization efficiency and grain yield in millet.

Conclusion

In the current pattern of climate change, the sensitivity of fertilization to heat stress in pearl millet is a threat to food security in semi-arid areas of the world, especially with the increase in night temperature. Thorough knowledge of the vulnerability of gametes to the duration of exposure to thermal stresses is vital to develop cultures with increased thermo-tolerance. Many studies describe the sensitivity to high temperatures of different stages of development or different reproductive organs. The present work shows the genotypic variability of the duration of flower exposure to high temperatures and their relationship with grain yield. It shows that the high daily temperatures certainly harm the final grain yield, but that the cool and fleeting morning temperatures play an essential role in the efficiency of fertilization. It opens the door to a way of improving the productivity of pearl millet in restrictive environments, through a better understanding of the molecular mechanisms involved in the duration of flowering under heat stress.

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Author's Contributions

Sani Daouda Ousmane: Principal researcher, head of this research unit, supervised all the work, from its conception to the final drafting of this publication

Mouhamadou Mounkaila Boureima: Conducted the experiment in the field, collected and processed the data

Maman Nassourou Lawali: Directed the experimental device and the statistical analysis of the data

Abdoul Razak Sani Daouda and Illiassa Soumaila Sounakoye: supported the data collection and the first computer processing

Ethics

All methods used in this study were approved by the institutional ethics committee.

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