

Prevalence of viviparous germination as a function of seasonal conditions and seed phenotypic characteristics in the bottle gourd *Lagenaria siceraria* (Molina) Standley (Cucurbitaceae)

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Abstract

Selection for resistance to viviparous germination is an important step and one of the most effective strategies for solving the problem of vivipary in orthodox seed species. Vivipary generally occurs when mature fruits are exposed to rain. To understand the existing relationships between seed phenotypic characteristics, seasonal conditions and the prevalence of vivipary in *Lagenaria siceraria*, experiments were carried out under natural conditions during the short and long rainy seasons of 2014 and 2015. Three main conclusions were drawn from the results. Firstly, yellowish seeds with a soft seed coat without a cap and yellowish seeds with a soft seed coat with a thin cap were more susceptible to vivipary with prevalences of 37.64% and 29.75% respectively. The whitish seeds with a hard seed coat and no cap, the brown seeds with a hard seed coat and no cap, the yellowish seeds with a soft seed coat and a thick cap and the seeds with a soft seed coat and a brown cap did not show vivipary whatever the intensity of the rain preceding harvest. Secondly, although the prevalence of vivipary was affected by the interaction of phenotype and rainy seasons, it explained only 7.57% of the variation. Most of the variation in vivipary prevalence was related to seed phenotype (68.33%) indicating that seed phenotype is the main factor influencing vivipary prevalence in *L. siceraria*. Finally, vivipary prevalence was strongly and positively correlated with rainfall and humidity in viviparous genotypes, whereas non-viviparous genotypes were not affected by climatic parameters.

Keywords: *Lagenaria siceraria*; Vivipary; Rainy season; Seed phenotypic characteristics.

1. Introduction

The agricultural policy adopted in Africa since the colonial period, and particularly in Côte d'Ivoire, has led to the considerable expansion of cash crops (*Coffea* L., *Theobroma cacao* L.) and certain food crops (*Zea mays* L., *Oryza sativa* L., *Manihot esculenta* Crantz), which are currently grown over very large areas to the detriment of other so-called minor crops. The latter are relegated to second or even third place, and have long been absent from research and extension programmes. Yet they represent a considerable asset for increasing farmers' incomes, especially as their market value is sometimes much higher than that of so-called export crops [1]. This is the case of the oleaginous Cucurbitaceae commonly known as 'pistache' in Côte d'Ivoire and 'Egussi' in several West and Central African countries [2].

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In Côte d'Ivoire, there are five species of oil-bearing Cucurbitaceae, including *Lagenaria siceraria* (Molina) Standley [1]. This species has two botanical forms, the calabash form and the "egusi" oilseed form. Molecular studies carried out by [3] have shown that these two botanical forms are in fact two distinct varieties. The main difference observed between the calabash variety and the oleaginous egusi variety is the hardness of the fruit pericarp and seed coat due to their lignification [4]. The calabash variety has fruits with a hard pericarp used as cooking utensils or decorative objects. Its seeds also have hard seed coats and are therefore not consumed as a sauce condiment in Côte d'Ivoire. The "egusi" variety has a fragile pericarp. The seed coat is also fragile and can be easily shelled.

Lagenaria siceraria is one of the most widespread and abundant cucurbit species on urban markets [5]. They play an important role in the culinary habits of the people who grow them in both rural and urban areas of Côte d'Ivoire. In addition, the high lipid and protein content of its seeds [6] makes it an ideal choice for solving food quality problems, especially in rural areas. Despite the importance of *L. siceraria* in the culinary habits of local communities, it is produced on small plots of land with low yields, partly due to the germinative quality of the seeds [1].

Vivipary in plants is the germination of fresh seeds of orthodox species, without having first undergone the dehydration phase of maturation [7]. This malfunction, leading to a loss of germination capacity and a drop in yield and nutritional quality of the seeds, has been widely reported in cereals (*Triticum aestivum* L., *Zea mays* L., *Oryza sativa* L.) and *Solanum lycopersicum* L. [8, 9, 10]. In the Cucurbitaceae family, only one plant species [*Sechium edule* (Jacq.) Sw.] is known to be naturally viviparous [11]. However, viviparous germination is often observed within this family in certain species such as *Citrullus lanatus* (Thunb.) Matsum. & Nakai [12] and the bottle gourd *L. siceraria* [13]. Selection for resistance to viviparous germination is an important step and one of the most effective strategies for solving the problem of viviparous germination in orthodox seed species, particularly in the bottle gourd *L. siceraria*. Seed genotype has been reported to be the main factor determining resistance to vivipary in most plant species. Nevertheless, environmental factors have been recognized as factors that can reduce vivipary resistance and consequently bias vivipary prevalence estimates [14]. Thus, to be relevant, varietal selection for vivipary tolerance/resistance should not only consider genotype, but also climatic factors. The present study was conducted to investigate the variation in vivipary prevalence as a function of bottle gourd *L. siceraria* seed genotype and seasonal growing conditions.

2. Materials and methods

2.1. Material

Six accessions of *L. siceraria* selected from the basic collection of the Nangui Abrogoua University were used in this study. These accessions were characterized by different seed phenotypes (Figure 1.):

- yellowish with a soft seed coat and without cap (YSCWC),
- yellowish with soft seed coat and thin cap (YSCTC),
- yellowish with soft integument and thick cap (YSITC),
- yellowish with soft integument and brown cap (YSIBC),
- whitish with hard integument without cap (WHINC),
- brown with hard integument without cap (BHIWC).





Figure 1 Phenotypic characteristics of *Lagenaria siceraria* seeds

A: yellowish seeds with soft seed coat and without cap (YSCWC), B : yellowish seeds with soft seed coat and thin cap (YSCTC), C : yellowish seeds with soft seed coat and thick cap (YSITC), D : yellowish seeds with a soft seed coat and brown cap (YSIBC), E: whitish seeds with a hard seed coat and without cap (WHINC), F: brown seeds with a hard seed coat and without cap (BHIWC).

3. Methods

3.1. Experimental design

The experimental design consisted of randomized complete blocks with two replicates. Each replicate consisted of six (06) elementary plots. Each elementary plot was represented by three rows of five plants, i.e. 15 plants. The sowing points were 3 m apart, both in rows and between rows. Three seeds were sown per plot. The plants were removed as soon as they had reached the tendril stage, leaving just one plant in each bunch. Organic fertilizer (chicken droppings) was applied as a fertilizer base in all the bunches. Weeds were controlled by regular manual weeding three times after the plot was set up. Insecticide treatments with cypermethrin were also carried out to protect the plants. Two cropping cycles were carried out during the long and short rainy seasons of 2014 and 2015. For the first crop cycle corresponding to the long rainy season of 2014, the seeds were sown on 31 March. For the second crop cycle, which corresponds to the short rainy season, the seeds were sown on 30 August 2014. In 2015, sowing for the first crop cycle corresponding to the long rainy season was carried out on 27 March, while the seeds were sown on 15 September for the second crop cycle corresponding to the short rainy season. The berries were harvested at the end of July for the first crop cycles and at the end of December for the second crop cycles. Climatic data for the crop cycles corresponding to the short and long rainy seasons in 2014 and 2015 are shown in Table 1.

Table 1 Climatic data for the two cropping cycles corresponding to the short and long rainy seasons of 2014 and 2015

Year	Season	Rtot (mm)	Tmin (°C)	Tmax (°C)	Tmoy (°C)	PR (mm)	HRU (%)	HRH (%)	TH (°C)
2014	S1	1533.65	25.6	28.3	27.63	354.81	84.88	88.2	25.6
	S2	471.43	24.7	27.4	26.16	101.86	84.3	81.7	27.4
2015	S1	1317.04	25.5	28.7	27.85	93.48	83.96	88.7	25.5
	S2	761.76	24.8	27.5	26.38	12.19	81.82	74.4	27.4

Rtot: total rainfall from sowing to harvesting, Tmin: minimum temperature, Tmax: maximum temperature, Tmoy: average temperature, RH: rain during harvesting, RHU: relative humidity, RHH: relative humidity during harvesting, TH: temperature during harvesting, S1: first crop cycle corresponding to the long rainy season, S2: second crop cycle corresponding to the short rainy season.

3.2. Parameters measured

Data was collected on the percentage of viviparous seeds. This is expressed as the ratio of the number of germinated seeds (NoGV) in a fruit to the total number of seeds in that fruit (NoGT) multiplied by 100.

3.3. Data statistical analysis

The data were analyzed using Statistica 7.1 software. Three-way analysis of variance following the Generalized Linear Model (GLM) was used to test the effects of the factors year, growing season, phenotype and their interactions on the prevalence of vivipary. The significance of these factors and their interactions was determined by comparing the probability P associated with the Fischer-Snedecor test statistic with the theoretical threshold of $\alpha = 0.05$. When $P \geq 0.05$, it is considered that the factors 'year', 'growing season', 'accession' and their interactions 'year x growing season x phenotype' do not influence the percentage of vivipary. However, when $P < 0.05$, these factors influence the percentage of vivipary. Depending on the significance of the interactions, the prevalence of vivipary was compared either for each factor, for the double interactions or for the triple interaction.

This analysis was completed by the non-linear correlation ratio or percentage variation (η^2) linked to each variable analyzed according to the factors considered. This parameter measures the degree of dependence of the variable on the different factors. It was calculated using the ratio between the sum of the squared deviations of the factor considered and the total sum of the squared deviations of all the factors considered, multiplied by 100 [15, 16].

$$\eta^2 = \frac{SS}{SSt} \times 100$$

SS: sum of squared differences. This expresses the variability explained, i.e. the *variation* that the factor explains;

SSt: sum of total squares. It expresses the total variability of the observations.

In addition, Pearson correlation coefficients (r) were calculated to analyze the correlations between the climatic parameters measured during the trial and the prevalence of vivipary in each of the four accessions studied. The significance of the correlation was determined by comparing the probability P with the theoretical threshold of $\alpha = 0.05$. When $P \geq 0.05$, there was no significant correlation between the climatic parameters and the prevalence of vivipary, whereas when $P < 0.05$, there was a significant correlation between the percentage of vivipary and the climatic parameters.

4. Results and discussion

4.1.1. Viviparous germination in *Lagenaria siceraria*

Two stages of vivipary have been observed in berries. Partial vivipary marked by the rupture of the seed coat due to the emergence of the hypocotyl or the cotyledonary leaves and complete vivipary characterized by the emergence of the cotyledonary leaves, the radicle and the hypocotyl and therefore a whole plantlet (Figure 2.). The emergence of cotyledonary leaves is recognized as the most detrimental type of vivipary in orthodox seed species because seeds with this type of vivipary can neither be consumed [17] nor serve as seeds [10].



Figure 2 Vivipary in *Lagenaria siceraria*

A: non-viviparous fruit, B: viviparous fruit, C, D: partial vivipary marked by the emergence of the cotyledonary leaves and/or the tigella, E, F: complete emergence characterised by the emergence of the cotyledonary leaves, the tigella and the radicle.

4.2. Effect of climate on the prevalence of vivipary in different seed phenotypes of *L. siceraria*

The analysis of variance used to study the effects of year, rainy season, phenotype and their interactions showed that all the factors mentioned, their double interactions 'year x phenotype', 'year x rainy season', 'phenotype x rainy season' and the triple interaction 'year x rainy season x phenotype' significantly ($P < 0.001$) influenced the percentage of vivipary. The effects of year (1.64%) and rainy season (3.79%) were relatively small compared to phenotype (68.33%). Although the triple interaction 'year x rainy season x phenotype' was statistically significant, it accounted for only 1.44% of the total variation (Table 2). This result suggests that most of the variation in vivipary prevalence was related to seed phenotype.

Table 2 Analysis of variance of the prevalence of vivipary of four accessions of *Lagenaria siceraria* during the long and short rainy seasons of 2014 and 2015.

Variation sources	SS	DF	F	p	% variance
year (Yr)	4439.33	1	86.06	< 0.001	1.64
Rainy season (Rs)	10267.69	1	199.06	< 0.001	3.79
Phenotype (Ph)	185361	5	602.96	< 0.001	68.33
Yr x Rs	1870.34	1	36.26	< 0.001	0.69
Yr x Ph	8978.23	5	29.11	< 0.001	3.31
Rs x Ph	20537.07	5	66.36	< 0.001	7.57
Yr x Rs x Ph	3910.68	5	12.81	< 0.001	1.44

SS: Sum square, DF: Degrees of freedom

A study of the prevalence of vivipary as a function of seed phenotype (Table 3) showed that accessions with yellowish seeds with a soft seed coat and no cap (YSCWC) and yellowish seeds with a soft seed coat and a thin cap (YSCTC) are more susceptible to vivipary than accessions with whitish seeds with a hard seed coat and no cap (WHINC), brown seeds with a hard seed coat and no cap (BHIWC), yellowish seeds with a soft seed coat and thick cap (YSITC) and yellowish seeds with a soft seed coat and brown cap (YSIBC). This resistance to viviparous germination could be explained by the hardness of the integuments, the colouration and the thickness of the caps. Studies carried out on the degree of tolerance to vivipary in orthodox seed species have shown that the hardness and colouration of the seed integument increase the degree of resistance to vivipary [18]. This resistance due to coloration is thought to be due to lignin and polyphenols, whose role is to modify the physical properties of the integuments or act as germination inhibitors [19].

Table 3 Mean values of the effect of phenotype on the percentage of viviparous seeds in *Lagenaria siceraria*

Phenotype	PoGV*
Whitish seed with hard integument without cap (WHINC)	0.00 ± 0.00 ^c
Brown seed with hard integument without cap (BHIWC)	0.00 ± 0.00 ^c
Yellowish seed with soft integument and brown cap (YSIBC)	0.00 ± 0.00 ^c
Yellowish seed with soft integument and thick cap (YSITC)	0.00 ± 0.00 ^c
Yellowish seed with soft seed coat and thin cap (YSCTC)	29.75 ± 18.57 ^b
Yellowish seed with a soft seed coat and without cap (YSCWC)	37.64 ± 19.42 ^a

*PoGV: Percentage of viviparous seeds. Values bearing the same letters are statistically identical.

Table 4 Mean values of the effect of the interaction 'year x rainy season x accession' on the percentage of viviparous seeds.

Phenotype	Year	Season	PoGV
Whitish seed with hard integument without cap (WHINC) NV	2014	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
	2015	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
Brown seed with hard integument without cap (BHIWC) NV	2014	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
	2015	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
Yellowish seed with soft integument and brown cap (YSIBC) NV	2014	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
	2015	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
Yellowish seed with soft integument and thick cap (YSITC) (NV)	2014	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
	2015	Season 1	0.00 ± 0.00 ^g
		Season 2	0.00 ± 0.00 ^g
Yellowish seed with soft seed coat and thin cap (YSCTC) V	2014	Season 1	51.79 ± 18.26 ^b
		Season 2	21.31 ± 8.03 ^e
	2015	Season 1	30.20 ± 13.23 ^d

		Season 2	15.69 ± 7.77 ^f
Yellowish seed with a soft seed coat and without cap (YSCWC) V	2014	Season 1	62.81 ± 18.15 ^a
		Season 2	28.64 ± 6.35 ^d
	2015	Season 1	35.27 ± 13.45 ^c
		Season 2	23.80 ± 7.31 ^e

Values with the same letters are statistically identical. PoGV: percentage of viviparous seeds; NV: non-viviparous; V: viviparous; season 1: long rainy season; season 2: short rainy season.

The post ANOVA test carried out on the triple interaction 'year x rainy season x phenotype' showed that the percentage of vivipary varied according to year, rainy season and accessions. In fact, the major rainy season of 2014 resulted in the highest percentage of viviparous germination, followed by the major rainy season of 2015, while the lowest vivipary rates were observed during the minor rainy seasons of 2014 and 2015 in the YSCWC and YSCTC accessions (Table 4). The percentages of vivipary of YSITC, YSIBC, WHINC, BHIWC accessions remained constant. The prevalence of vivipary of *L. siceraria* accessions susceptible to vivipary (YSCWC and YSCTC) therefore tended to depend on the year and rainy season, whereas the latter had little or no influence on non-viviparous accessions (YSITC, YSIBC, WHINC, BHIWC). This observation is similar to that made by Biddulph *et al.* (2007) [9] and Barnard and Smith (2009) [20] on wheat. These researchers showed that viviparous lines of wheat seemed to be more strongly influenced by the environment than tolerant lines. The prevalence of vivipary in YSCTC varied according to year and season from 15.31 to 51.79%, while it varied from 23.80 to 62.81% in YSCWC for the same seasons and years. Seasons and years with low rainfall associated with high temperatures produced a low rate of vivipary in phenotypes susceptible to vivipary. These results are in line with those of Biddulph *et al.* (2005) [21] who showed that the prevalence of viviparous germination in viviparous genotypes decreased with water stress and high temperatures. Studies by Ober and Setter (1992) [22] showed that water deficit increases ABA concentrations in maize kernels, while high humidity decreases ABA content, leading to earlier germination of kernels in the fruit. Correlation studies between climatic parameters and the prevalence of vivipary have shown that rainfall during the fruit harvest period is strongly and positively correlated with the percentage of vivipary in viviparous accessions. According to de Oliveira *et al.* (2014) [23], the influence of rainfall during harvest on seed germination in the fruit is due to the permeability of the fruit and seed pericarp. In fact, this permeability of the fruit pericarp leads to an exchange of water and moisture between the external environment and the seeds, thus keeping the seeds in a high humidity.

Given that the year and the rainy season influenced the percentage of vivipary, the effect of climate on the prevalence of vivipary of the different accessions, particularly those that do not appear to be stable such as the viviparous accessions YSCWC and YSCTC, was studied. The Pearson correlation coefficients between climatic data and the prevalence of vivipary in viviparous accessions are presented in Table 5.

Table 5 Pearson correlation coefficients between the percentage of vivipary and climatic characteristics

Climatic characteristics	Correlation coefficient	P
Total rainfall (mm)	0.80*	0.018
Minimum temperature (° C)	0.79*	0.019
Maximum temperature (° C)	0.57 ^{ns}	0.140
Mean temperature (° C)	0.68 ^{ns}	0.066
Rain during harvest (mm)	0.76*	0.029
Relative humidity (%)	0.65 ^{ns}	0.079
Humidity during harvest (%)	0.72*	0.046
Temperature during harvest (° C)	-0.73*	0.038

* : significant correlation; ns: non-significant correlation

The results showed that there was a significant positive correlation between the percentage of vivipary and total rainfall from sowing to harvest ($r = 0.80$; $P = 0.018$). A significant positive correlation was also observed between the percentage of vivipary and minimum temperature ($r = 0.79$; $P = 0.019$). It was also shown that total rainfall during harvest and total

humidity during harvest were positively and significantly correlated with vivipary percentage ($r = 0.76$; $P = 0.029$, $r = 0.72$; $P = 0.046$). A significant negative correlation was also observed between the percentage of vivipary and the average temperature during harvest ($r = -0.73$; $P = 0.038$). These results imply that the percentage of vivipary increases with high rainfall and humidity during harvest and decreases with high temperatures during harvest. Under these conditions, *L. siceraria* must be selected for vivipary tolerance over several years and in an environment where the genotypes are capable of expressing their true vivipary tolerance. In the absence of tolerant genotypes, genotypes susceptible to vivipary should be grown during low-rainfall growing seasons.

5. Conclusion

The interaction between the seed phenotypic characteristics of *Lagenaria siceraria* and climatic parameters determines tolerance to viviparous germination. The study of climatic effects on the prevalence of vivipary also showed that phenotypic characteristics explains most of the total variation in this prevalence. However, climatic characteristics had a strong influence on the percentage of vivipary. The prevalence of vivipary remained the same for non-viviparous accessions (whitish seeds with a hard seed coat and no cap, brown seeds with a hard seed coat and no cap, the yellowish seeds with a soft seed coat and a thick cap and the seeds with a soft seed coat and a brown cap) whereas it varied greatly from one season to the next for viviparous accessions (yellowish seeds with a soft seed coat without a cap and yellowish seeds with a soft seed coat with a thin cap). Analyses of climatic parameters showed strong positive correlations between total rainfall, rainfall during harvest, relative humidity during harvest and minimum temperature and the prevalence of vivipary. To control viviparous germination in *L. siceraria*, it is necessary either to select accessions capable of resisting vivipary whatever the climatic parameters, or to avoid heavy rainfall and humidity during harvest periods.

Compliance with ethical standards

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Disclosure of conflict of interest

The authors declare that no competing interests exists

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