Prevalence and Genetic Determinism of Viviparity in the Bottle Gourd *Lagenaria siceraria* (Molina) Standley (Cucurbitaceae)

Hermann Hippolyte Tro, Beket Séverin Bonny[*], Kouamé Kévin Koffi, Irié Arsène Zoro Bi

Breeding and Crop Husbandry Unit, Faculty of Natural Sciences, 02 BP 801, Abidjan 02,
Nangui Abrogoua University, Abidjan, Côte d'Ivoire
*Corresponding author: bonybekets@yahoo.com

Abstract Viviparity or early germination of seeds in fruits still attached to the parent plant is a factor in yield reduction and economic loss in agriculture. *Lagenaria siceraria* (Molina) Standl. is a plant of nutritional, medicinal and agronomic importance facing a decrease in production due to viviparity. The objective of this work was to study the genetic determinism of viviparity in *L. siceraria*. Eight accessions (4 viviparous and 4 non-viviparous) resulting from a screening of 100 accessions of two cultivars (Calabash and Egussi) of *L. siceraria* were used in direct and reciprocal crosses. Self-fertilisation of F1 progeny resulted in F2 progeny. Four field experiments in six cycles yielded the different individuals of each generation used in this study. Results indicated that accessions of the gourd cultivar were non-viviparous. The majority (96.67%) of accessions of the cultivar Egussi were viviparous and were present in all agro-ecological collection areas. F1 plants from direct and reciprocal crosses were all non-viviparous. Self-fertilization of F1 plants led to F2 progeny in 3:1 segregation (3 for non-viviparous and 1 for viviparous). The non-viviparous phenotype appeared dominant over the viviparous phenotype. Seed viviparity is controlled by a gene, with an allele pair (V/v). Plants with non-viviparous fruits can be, VV or Vv. Plants with viviparous fruits are vv.

Keywords: viviparous, non-viviparous, Lagenaria siceraria, self-fertilisation, allele, gene

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1. Introduction

Lagenaria siceraria (Molina) Standley is one of the five species of Cucurbits cultivated in Côte d'Ivoire. It is a herbaceous, annual, monoecious and bisexual plant that multiplies only by seeds. *Lagenaria siceraria is* the largest gourd group characterized by a diversity of size, berry shapes and seeds [1,2]. This large group can be divided into 2 subgroups. The first subgroup produces large fruits with a very hard pericarp and inedible seeds. The second subgroup with edible seeds is characterized by fruits with fragile pericarp [3]. This second subgroup is mainly cultivated for its seeds which are dried, peeled and made into a paste, cooked and eaten in sauces. The richness of these seeds in lipids, proteins and vitamins [4,5] makes them suitable for solving food problems, especially in rural areas. Thus, *Lagenaria siceraria* contributes significantly to food security and the promotion of the health of populations [6,7]. Although cultivated on a small scale, this minor species [8] has real economic potential. Indeed, *L. siceraria* has the capacity to produce large quantities of seeds and is therefore one of the most common species on local markets [9]. The species also offers important agronomic advantages in traditional farming systems that do not use fertilisers and herbicides. Indeed, *L. siceraria* is an essential component in intercropping and rotational cropping systems [10]. It thus contributes to the conservation and the sustainability of the production systems of thousands of small farmers in rural areas. However, in Côte d'Ivoire, as in many developing countries, farmers' access to locally adapted varieties is reduced, thus compromising the potential yield and performance of agricultural production [11]. Among all cucurbits cultivars grown locally, *L. siceraria* is the most productive and vigorous. Still, it shows poor yield performance. Mass selection practiced by farmers remain the only method used to improve production in the species. Several factors are at the root of the low yields recorded in this species. These include the lack of appropriate technical itineraries [12], the unsuitability of local varieties to changing climatic and environmental conditions, pest and disease attacks [13], but also post-harvest conservation problems [14]. In addition to all these constraints, there is the phenomenon of viviparity or germination of seeds in the fruit before harvesting. This phenomenon, which is characterized by a loss of seed

dormancy in the fruit occurs in various regions of the world and causes great economic losses in agriculture [15]. Indeed, viviparity leads to losses in yield, viability, nutritional quality and palatability of fruits and seeds [16,17]. Seeds in particular determine the maximum potential yield of cucurbits crops [18]. Viviparity, which is a factor in the depreciation of seed quality, has become a problem in recent years in some regions of the world due to climate change [19]. The effects of climate change and warming have been very noticeable over the last five decades in Côte d'Ivoire [20]. Rainfall has become less frequent, low and highly variable from season to season in all regions of Côte d'Ivoire [21]. Faced with this situation, local rural producers of *L. siceraria* do not yet have access to improved varieties. Cultivation is still traditional and farmers continue to take seeds from their own harvest for planting the following season. Where appropriate, seed supply is usually done between neighbours or through local markets. This reflects the inefficiency of local seed systems for food crops, which remain essentially informal. Yet, the sustainable production of any crop depends essentially on the quality of the seed sown, especially in no-till plants [22,23] such as *L. siceraria.* However, viviparity is frequently observed in the cultivation of *L. siceraria,* especially in genotypes with fine fruit pericarp and edible seeds compared to the hard fruit pericarp gourd type, generally used as a tool or utensil [24]. Indeed, N'Gaza et al. [24] reported a variable degree of prevalence of viviparity with 2.16% (non-viviparous), 89.19% (viviparous) and 8.65% (highly viviparous) in accessions from Côte d'Ivoire. However, sensitivity to viviparity of *L. siseraria* and many other crops is also related to harvest time [24,25], high temperatures and humidity during seed maturation [26]. For smallholders using traditional storage structures, spoilage or lack of good quality seed is a major problem [27], such as losses due to viviparity in *L. siceraria*. In addition to yield reduction, increased viviparity in production areas could also reduce species diversity or even cultivation due to continuous seed losses. Genetic diversity is crucial to ensure the long-term survival and evolution of species to environmental changes in their habitat [28,29]. Indeed, viviparity is controlled by environmental and genetic factors [30,31]. The adverse effect of viviparity in local food crops such as *L. siceraria* can compromise food security and the income of rural producers. Thus, the selection of genotypes tolerant or resistant to viviparity is a reliable way to ensure production, therefore yield and consequently to address the problem of food insecurity among producers of this crop. Assessing the genetic control of viviparity is a prerequisite to set up a reliable breeding program aimed realizing high yielding and viviparity tolerant varieties of *L. siceraria.*

2. Materials and Methods

2.1. Site Description

The survey of the genetic determinism of viviparity in *L. siceraria* was conducted at the experimental station of the University Nangui Abrogoua (05°17′ and 05°31′ north latitude and between 03°45′ and 04°22′ west longitude), in Abidjan, southern Côte d'Ivoire. This zone is defined by a sub-equatorial climate characterized by the alternation of four seasons including two rainy seasons (from April to July and from October to November) and two dry seasons (from August to September and from December to March). However, these periods have been less marked in recent years [32]. Rainfall is abundant (annual average > 2000 mm) with a relative humidity of 80% and an average annual temperature of 28°C for a thermal amplitude of 3.63°C [33]. Ferralitic soil is relatively deep and characterized by a sandy-clay texture and a cluster structure [34]. Vegetation is mainly represented by tropical rainforest [9].

2.2. Plant Material

The plant material consisted of 100 accessions of *Lagenaria siceraria* from the seed bank of the University Nangui Abrogoua (UNA). The accessions were collected from farmers' fields in three agro-ecological zones in Côte d'Ivoire (North: 27 accessions, North-East: 35 accessions, and South: 38 accessions) where cultivation is regularly practiced. These accessions are from two cultivars. The cultivars Calabash (inedible seeds) and Egussi (edible seeds) represented respectively by 10 and 90 accessions. These 100 accessions were screened and eight accessions were retained (Table 1), four of which were highly viviparous (Figure 1a) and four non-viviparous (Figure 1b). These eight accessions constituted the parental accessions used in the different crosses for the study of the genetic determinism of viviparity.

Figure 1. Sectioned fruits of *L. siceraria*; a: viviparous accession; b: non-viviparous accession

Table 1. Parental accessions of *Lagenaria siceraria* used in the different crosses

N°	Accessions	Origin	Type	Feature
1	NI002	Alépé (South)	*Egussi*	Non-viviparous
2	NI005	Bondoukou (North-East)	*Egussi*	Viviparous
3	NI022	Alépé (South)	*Egussi*	Viviparous
4	NI030	Alépé (South)	*Egussi*	Non-viviparous
5	NI031	Bondoukou (North-East)	*Egussi*	Viviparous
6	NI034	Ferké (North)	*Egussi*	Viviparous
7	NI079	Korhogo (North)	*Calabash*	Non-viviparous
8	NI189	Bondoukou (North-East)	*Egussi*	Non-viviparous

2.3. Field Experiments

Four field experiments in six cycles have produced plants of different generations. Screening of the 100 accessions was carried out from August to November 2016 in a randomized complete block design (RCBD) (56 m × 52 m). The spacing between sowing points was 2 m within and between lines. Each accession was represented by five plants. The retained eight parental accessions after screening were then seeded in an RCBD with two blocks (9 m×8 m) separated by 3 m. One block was allocated to non-viviparous accessions and the other block to viviparous accessions. Each block had four lines, each corresponding to one accession. The lines were spaced 2 m apart and had five sowing points equidistant by 2 m. Three cycles of self-pollination (April to July 2017, August to November 2017 and April to July 2018) of the eight parental accessions were carried out to obtain parental individuals (P_0). The same field experiment was used for reciprocal crosses of the eight parental accessions (P_0) to obtain F_1 hybrid seeds (August to November 2018). Thus, the 32 (16×2) generations of F_1 hybrids obtained were grown on a 1300 m^2 (50 m × 26 m) plot to assess viviparity (April to July 2019). This plot consisted of two separate 4 m blocks. The first block contained the F_1 hybrids (♀ non-viviparous accessions × ♂ viviparous accessions) and the second block contained the F_1 reciprocal hybrids (♀ viviparous accessions × ♂ non-viviparous accessions). Each block contained 16 lines separated by 2 m and corresponding to the 16 F_1 hybrids of a given crossing direction, i.e. 32 lines on the whole plot (August to November 2018). Five sowing points equidistant by 2 m per line were carried out giving a total of 160 F_1 hybrid plants evaluated for their viviparity. After self-pollination of the F_1 hybrids, the viviparity of the F_2 hybrids was assessed (August to November 2019) on the same plot using the same system. But it consisted of 32 lines of five sowing points per block, or 64 lines for the plot. Only F_2 plants that produced at least three fruits were selected for further study. Thus, 178 out of 320 plants of F_2 hybrids were used to study the genetic determinism of viviparity. For each trial, three seeds were sown per plot and only one plant was retained after demarriage. Regular hand weeding controlled the weeds. The fruits of each plant were harvested at the end of each growing cycle (50 days after anthesis) when the plant was completely dry [35] and were placed at the sowing point.

2.4. Parental Access Crossings

Before making the different types of crosses for the study of viviparity, the flowers were selected the day before. The flowers chosen to be manually pollinated were protected by cloths to avoid pollination by insects. Thus, three cycles of self-pollination were carried out from the eight accessions selected in order to purify and fix the characteristics of the parental individuals (P_0). During the purification of the accessions, only the fruits of plants with no viviparous seeds were selected as non-viviparous accessions. For viviparous accessions, plants with a large number of fruits whose seeds were viviparous were selected. Then, crosses between viviparous (P_{0v}) and non-viviparous (P_{0nv}) parental accessions were performed to obtain first generation individuals (F_1: P_{0v} × P_{0nv}), composed of F_{1v} (first generation viviparous individual) and F_{1nv} (first generation non-viviparous individual). The second generation individuals (F_2) were obtained by self-fertilisation of all F_1 individuals.

2.5. Data Collection and Statistical Analysis

Data were collected on each plant after harvest at the end of the growing cycle. All harvested fruits were grouped by plant. The fruits were then sliced crosswise into two parts using a knife. Two levels of viviparity observation were used: (i) the different faces of the fruits were examined for the presence or absence of viviparous seeds; (ii) the search for viviparity was carried out after exposing the fruits to room temperature for seven days for their decomposition (fermentation) in order to extract the seeds [35] which were then washed. In this study, any accession that produced at least one fruit with viviparous seeds was considered viviparous. The percentage of accession, viviparous and non-viviparous fruits was determined after screening 100 accessions of *L. siceraria according* to the agro-ecological zone of collection and cultivar. The phenotypic frequency distribution of viviparity was analysed with Chi-square tests (χ^2) [36]. The Chi-square test of independence was first performed to determine whether viviparity was dependent on the agro-climatic zone. Then, the Chi-square test of homogeneity was carried out to test the homogeneity of viviparity between the different zones. An analysis of segregations was performed using the Chi-square compliance test on the populations of F_2 individuals. This test was used to examine the quality of adjustment of the observed segregation ratio to that expected. The various tests were conducted using Statistica 7.1 software [37].

3. Results

3.1. Viviparity Prevalence of *L siceraria* Accessions According to Cultivar and Collection Area

The prevalence of viviparity of the 100 accessions was assessed through screening. Considering the cultivar, the prevalence rates of viviparity of the accessions are recorded in Table 2. No accessions of the gourd cultivar

produced viviparous seeds. In contrast, regarding the cultivar Egussi, 96.67% of accessions produced viviparous fruits while 3.33% produced non-viviparous fruits. Table 3 shows the distribution of viviparous and non-viviparous fruits of the cultivar Egussi in the three agro-ecological collection areas. The Chi-square tests of independence showed that viviparity was related to the agro-ecological zones ($\chi^2_{gk} > 5.991$; P < 0.0001). In addition, Chi-square tests of homogeneity showed a difference in the distribution of viviparous and non-viviparous fruit phenotypes of accessions from different areas ($\chi^2_g > 5.991$).

The detailed analysis in Table 3 showed a high rate of viviparous fruits than non-viviparous fruits in the North-East accessions (56.2% vs 43.8%) and in the North (54.2% vs 45.8%). Conversely, the southern accessions recorded a higher rate of non-viviparous fruits (62.8%) than viviparous fruits (37.2%). In sum, 96.67% of the accessions of the cultivar Egussi evaluated were viviparous and 52.51% of the fruits produced on the plot were non-viviparous.

3.2. Determinism Genetic of the Viviparity and Non-viviparity Character

The determinism genetic of viviparous and non-viviparous accessions was analysed based on direct and reciprocal crosses between the four viviparous and four non-viviparous accessions. All plants obtained at F_1 had produced non-viviparous fruits. Seeds from self-fertilization of F_1 plants led to segregating F_2 progeny composed of both viviparous and non-viviparous fruiting plants (Table 4). Segregation ratios (non-viviparous: viviparous) in F_2 were assessed on a total of 178 plants that had produced at least three fruits. The results of the Chi-square test (χ^2) (showed that the segregations obtained in F_2 were consistent with the theoretical 3:1 frequency ($\chi^2 < 3,841$; *P* > 0.05). Plants with non-viviparous fruits represented 75% of the F_2 population while those with viviparous fruits were 25% of the F_2 population. The non-viviparous phenotype dominated the viviparous phenotype.

Table 2. Prevalence of the viviparity of accessions of bottle gourd and "*Egussi*" cultivars of *Lagenaria siceration*

	Calebash		« *Egussi* »	
	Viviparous (%)	Non-viviparous (%)	Viviparous (%)	Non-viviparous (%)
Accessions	0	100	96.67	3.33
Fruits	0	100	47.49	52.51

Table 3. Enumeration and relative frequency of viviparous and non-viviparous fruits of the cultivar "*Egussi*" in the three agro-ecological zones of collection, as well as the results of chi-two tests carried out

	North	North-East	South	χ^2_g	χ^2_{gk}	P
viviparous	208 (54.2%)	365 (56.2%)	156 (37.2%)	19.955		
non viviparous	176 (45.8%)	284 (43.8%)	263 (62.8%)	20.121	40,077	< 0,001
χ^2_g	2,409	9,451	28,217			

$\chi^2_g > \chi^2_\alpha = 5.991$ (ddl = 2) is significant and indicates that the zone frequencies are significantly different for a particular phenotype; $\chi^2_{gk} > \chi^2_\alpha = 5.991$ (ddl = 2) is significant and indicates that zone frequencies are significantly independent for viviparity; α = 0.05.

Table 4. Segregation frequencies for the viviparity of F2 plants resulting from self-fertilization of F1 plants resulting from direct and reciprocal crosses of non-viviparous and viviparous parental individuals

Cross-breeding (self-fertilisation) $F_1 \times F_1$	Observed quantity			Theoretical frequencies	Statistical test	
	Total	nv	vi		dl	χ^2
F_1 : NI002×NI005	7	5	2	3:1	1	0,05[ns]
F_1 : NI005×NI002	21	18	3	3:1	1	1,28[ns]
F_1 : NI002×NI022	11	8	3	3:1	1	0,03[ns]
F_1 : NI002×NI031	18	15	3	3:1	1	0,66[ns]
F_1 : NI002×NI034	15	12	3	3:1	1	0,69[ns]
F_1 : NI030×NI005	20	17	3	3:1	1	1,06[ns]
F_1 : NI030×NI031	16	15	1	3:1	1	3,00[ns]
F_1 : NI030×NI034	14	13	1	3:1	1	2,38[ns]
F_1 : NI022×NI079	13	12	1	3:1	1	2,08[ns]
F_1 : NI079×NI031	13	10	3	3:1	1	0,03[ns]
F_1 : NI079×NI034	13	11	2	3:1	1	0,64[ns]
F_1 : NI189×NI05	8	7	1	3:1	1	0,67[ns]
F_1 : NI034×NI189	9	8	1	3:1	1	0,93[ns]

ns = non-significant (for the test χ2), nv : non-viviparous plant, vi: viviparous plant. $\chi^2 < \chi^2_\alpha = 3.841$ (ddl = 1) is insignificant and indicates that the theoretical frequencies are identical to the observed frequencies for the viviparity character; α = 0.05.

4. Discussion

Seed quality is vital for sustainable agricultural production and food security. Indeed, the potential yield of crops depends largely on the quality of the seed sown [38]. Seed quality is vital for sustainable agricultural production and food security. Indeed, the potential yield of crops depends largely on the quality of the seed sown [39]. One of the factors affecting seed quality is viviparity. The objective of this study was therefore to understand the genetic determinism of viviparity in *L. siceraria*. Viviparity has been reported in various Cucurbits species, including *Sechium edule* [40], *Cucumis melo* L. group [41], *Cucurbita maxima* [42], *Cucumis melo* var. *cantalupensis* [43] and *Citrullus lanatus* [44]. The present study showed that of the two cultivars of *Lagenaria siceraria* evaluated, only the cultivar Egussi was viviparous unlike the gourd cultivar. This prevalence of cultivar-related viviparity could be due to genetic factors. In addition, analysis of accessions of the cultivar Egussi revealed the presence of viviparity in all collection areas. However, accessions in the North and North-East zones, which are relatively less humid, showed higher rates of viviparity than accessions in the South zone where rainfall and humidity are higher. These observations are contrary to those of Baek and Chung [45] and Zhang et al. [46] who reported that rainfall and high humidity were conducive to an increase in viviparous seeds in rice and wheat respectively. The low viviparity rate recorded in the southern accessions could also be explained by their adaptation to the climatic conditions of the southern zone, which is the experimental area. Conversely, the favorable climatic conditions in the South could be a factor in triggering hormonal signals regulating viviparity in the accessions originating from the North and North-East zones. Andreoli et al. [47] indicated that moisture during seed maturation is a catalytic factor for viviparity. In any case, the effect of the environment in the expression of viviparity has been reported in some works [48,49]. Thus, the prevalence of viviparity would probably be related to the genotype or an adaptation of the genotype to the growing area or to the genotype×environment interaction [50]. Thus, for selection trials of viviparous and non-viviparous accessions, the choice of the southern region was therefore judicious. The high rainfall in this area was appropriate for selection of non-viviparous and viviparous genotypes. In the present study, a viviparity rate of 97.67% was observed in accessions of the cultivar Egussi. Similar results were obtained by [51] for the hardness of the seed coat, also in gourd and Egussi cultivars. These authors noted that this seed coat hardness trait was governed by a gene with a pair of alleles. A dominant allele and a recessive allele which would control the hard and soft seed coat respectively in *L. siceraria*. This study provided an understanding of the heritability of seed viviparity and non-viviparity in *L. siceraria*. The results obtained are a pathway for varietal improvement of *L. siceraria*. They will provide growers with seeds of good agronomic quality in order to optimize production. However, appropriate molecular analyses would make it possible to verify the results obtained.

5. Conclusion

The present study aimed at understanding the genetic determinism of viviparity in gourd and Egussi cultivars of *L siceraria*. Results indicated that accessions of the gourd cultivar were non-viviparous. Almost all accessions of the cultivar Egussi *were* viviparous. For this cultivar Egussi, viviparity was expressed in all growing areas. Analysis of the genetic determinism of viviparity revealed that this trait was governed by a pair of alleles with complete dominance. The non-viviparous phenotype was controlled by a dominant allele (V) while the viviparous phenotype was controlled by a recessive allele (v). The results obtained could be used in breeding programs for non-viviparous genotypes in *L. siceraria in* order to qualitatively and quantitatively improve yields in this species. However, this work opens up interesting prospects for the development of genetic markers such as SNPs that are more relevant for the selection of non-viviparous genotypes [46].

Conflict of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

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