African Crop Science Journal, Vol. 21, No. 3, pp. 245 - 254
ISSN 1021-9730/2013 $4.00

INTER-FERTILITY AMONG FEMALE PARENT CLONES OF PINEAPPLE INVOLVED IN A 6X6 COMPLETE DIALLEL CROSSING SYSTEM BASED ON TYPOLOGICAL APPROACH

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(Received 9 February, 2013; accepted 9 July, 2013)

ABSTRACT

Pineapple (*Ananas comosus* L. Merr) breeding programme in Côte d'Ivoire considers fruit diversification as key component in the international pineapple industry. The objective of this study was to determine the sexual compatibility of female pineapple clones recently developed in Côte d'Ivoire. Three female hybrid clones, 410-106-33, 410-200-15, 103-104-6; one variety, known as Queen Victoria RE43; as well as two Smooth Cayenne varieties HA10 and HA25 used as controls, were tested in this study. They were inter-crossed according to a 6x6 complete diallel mating system with selfings. Results showed that female hybrid clone 410-200-15, was the least inter-compatible; implying that it can be indifferently cultivated in single or mixed-crop fields. This was followed by the genitors RE43 and 410-106-33. The response pattern could be due to the relatedness existing among these three clones. Conversely, hybrid clone 103-104-6 was the most inter-compatible. In this case, it needs to undergo successive back-crosses, using the parent HA10 as donor, before on-farm evaluations. The female clones 410-106-33 and RE43 produced the heaviest and the lightest fruits, respectively.

Key Words: *Ananas comosus,* back-cross, Côte d'Ivoire

RÉSUMÉ

Le programme d'amélioration génétique de l'ananas (*Ananas comosus* L.) en Cote d'Ivoire considère la diversification fruitière comme une composante clé pour l'industrie internationale de l'ananas. L'objectif de la présente étude était de déterminer la compatibilité sexuée de clones femelles d'ananas récemment crées en Côte d'Ivoire. Trois clones hybrides femelles désignés 410-106-33, 410-200-15, 103-104-6, une variété, connue sous le vocable de Queen Victoria RE43, ainsi que deux variétés Cayenne lisse HA10 et HA25 utilisés comme témoins, ont été testés dans cette étude. Ils ont été inter-croisés selon un plan de croisements diallèle complet 6 x 6 avec autofécondations. Les résultats ont montré que le clone hybride femelle 410-200-15 a été le moins inter-compatible, suggérant qu'il peut être cultivé indifféremment en parcelles mono ou multiclonales. Il a été suivi par les géniteurs RE43 et 410-106-33. Un tel comportement pourrait être dû à la parenté existant entre ces trois clones. A l'opposé, le clone hybride 103-104-6 a exprimé la plus haute inter-compatibilité. Il devrait être soumis à des back crosses successifs, utilisant le parent HA10 comme donneur, avant les évaluations en milieu réel. Les clones femelles 410-106-33 et RE43 ont produit respectivement les fruits les plus lourds et les plus légers.

Mots Clés: *Ananas comosus,* back-cross, Côte d'Ivoire

INTRODUCTION

Pineapple (*Ananas comosus* L. Merr) is a monocotyledonous, herbaceous, perennial and diploid (2n=2x=50) species of the Bromeliaceae family originated from South America (Guyot, 1992). World pineapple production is estimated at higher than 14.6 million tonnes annually (FaoStat, 2004). The pineapple processing industry is dominated by a single cultivar, known as 'Smooth Cayenne'. Due to the predominance of this cultivar in international market of fresh fruits, a policy of fruit diversification was adopted in Côte d'Ivoire (Cabot, 1988). For this purpose, a varietal breeding programme was initiated in 1978. From the 40,000 hybrids developed, nineteen designated as C1, C2....C19 were preselected (Atse and Coppens d'Eeckenbrugge, 1997); among which three, 103-104-6, 410-106-33 and 410-200-15, were identified as superior genotypes. Before these are multiplied for varietal release, their sexual compatibility needs to be known.

Since seminiferous fruits are not appreciated by consumers and traders (Py *et al*., 1984), such seeds negatively affect the quality of fruit (Py *et al*., 1984). All pineapple populations belong to the same species complex (Coppens d'Eeckenbrugge *et al*., 1997). Based on the absence of reproductive barriers among the species of the genus Ananas, the three assessed female hybrid genitors, including the variety RE43, could be inter-fertile. The objective of this study was to evaluate sexual compatibility among four clones including three hybrid clones developed in Côte d'Ivoire and one valued cultivar.

MATERIALS AND METHODS

The experiment was conducted from September 1997 to April 1998, at the Research Station of Anguededou belonging to DFA/IDEFOR (Département des Fruits et Agrumes/Institut Des Forêts) in Côte d'Ivoire. This Station is located at 5°25'N, 4°08'W and 25 m above sea level. Four common testers and parents, 103-104-6, 410-106-33, 410-200-15 and RE43; as well as two controls, HA10 and HA25, were used. The first three hybrids were created just over 20 years ago (Cabot, 1988) and were identified as superior hybrids (Atse and Coppens d'Eckenbrugge, 1997; Coppens d'Eckenbbrugge *et al*., 1997,). Clones 410-200-15 and 410-106-33 came from Cayenne x Perolera inter-varietal crosses, while clone 103-104-6 came from Perolera x Perolera intra-varietal cross (Cabot, 1988). Clone Queen Victoria RE43, which is sweeter than cultivar Smooth Cayenne, has high value on international market. Clones HA10 and HA25 belong to the Smooth Cayenne variety. They are also well valued on international market, because they dominate on the fresh fruits market and that of the processing industry.

All parent clones belonged to a pre-existent planting design, which consisted of plants laid out into two rows. Six pineapple plants per clone were chosen based on their vigour, and used as male and female, that is to say common testers and parents. One was used for selfings and the other five for crossings. They were planted in two rows on ridges, with a 40 cm x 25 cm spacing. A gap of 90 cm was maintained between ridges to allow to manager to move easily between ridges.

The clones were planted in three different sites: (i) Genebank field for clone Queen Victoria RE43, (ii) plants multiplication field for the hybrid clones 410-200-15, 410-106-33 and 103-104-6; while (iii) clones HA10 and HA25 were planted in field on monthly basis. The six clones were involved in a complete diallel mating system with selfings. Single crosses are analysed in this paper. Four variables were measured including: (i) seeds number deriving from cross-pollinations per week (Nbseed), (ii) seeds number obtained per self-pollinated flower per week (Seedflow), (iii) ripe fruit weight (Weigfruit), and (iv) bloomed flowers number per week (Blooflow).

Calcium carbide solution was applied on the leafy crown of each plant chosen as parents to induce flowering. Two months later, the inflorescences emerging from plant were covered with pollination bags. Daily, in the morning, the anthers surmounting the filament of each stamen were collected in petri-dishes using tongs and were used either to self-pollinate or cross-pollinate manually the bloomed flowers. Bloomed flowers were counted and, thereafter, marked with red oil painting. At maturity, the fruits were harvested, weighed and the seeds contained in each fruits scored after dissection.

Collected data were treated with Xlstat 2007.6 package. ANOVA, Principal Component Analysis (PCA) and Hierarchical Cluster Analyses (HCA) were run to analyse the variability. With respect to ANOVA, the clones were separate via two approaches. First, the Dunnett's test was used to identify at most three classes: (i) the class of female clones whose means were below those of the controls, (ii) the class of the female clones with means similar to those of the controls; and (iii) that of parent clones whose means were above those of the controls.

Second, within each class, the Newman-Keuls or the Student t tests were performed at 5% likelihood. The bloomed flowers number per week (Blooflow) and seeds number obtained per cross-pollinated flower per week (Seedflow) were square root transformed, because they were not normally distributed. The PCA allowed the a priori clustering of variables and individuals represented by the six female parent clones. The factorial axes number was determined by Kaiser's and Angle criteria. Likewise, the choice of variables was guided by the representation quality termed QLT_{kl} (QLT_{kl} of a variable1 = $\cos^2$ axis1 + $\cos^2$ axis2) and the Pearson's linear coefficient of correlation. The Hierarchical Cluster Analysis (HCA) refined the clustering of individuals obtained from the PCA and displayed the relatedness among identified groups.

RESULTS

Variability by descriptor of inter-fertility. All four female clones, including the two control clones, were not significantly different ($P>0.05$) for the number bloomed flowers per week (Blooflow), with respect to the Dunnett and Newman-Keuls tests. Consequently, they presented the same rhythm of anthesis. Moreover, the untransformed averages ranged from 62.410 to 156.275. In the same way, the dispersion of observations around the mean varied from 8.86 to 14.01% (Table 1).

Similarly, the number of seeds deriving from cross-pollination per week (Nseed), were significant among the parent clones. Two groups were identified according to Dunnett's test. Group G1 composed of only female clone 410-200-15 with performances below those of the controls HA10 and HA25. Groups G2 consisted of three parent clones, RE43, 410-106-33, and 103-104-6, with the two controls, HA10 and HA25, and recorded number of seeds deriving from cross-pollination per week similar to those of the above-mentioned controls.

Using the Newman-Keuls test, in the latest group, the female clone, RE43, with low production of seeds per week, was different from parent clone 103-104-6 with high production of seeds per week. Overall, the female clones 410-200-15 and RE43 were inter-sterile, whereas clone 103-104-6 was inter-fertile. Furthermore, the untransformed averages stretched out from 1.600 to 1185.800. Likewise, the variability around the mean fluctuated from 11.22 to 18.96% (Table 1).

Concerning the seeds obtained per hybridised flower (Seedflow), significant differences were noted among female clones (Table 1). Indeed, three groups were recorded for both Dunnett and Newman-Keuls tests. The first group consisted of the only female clone, 410-200-15 for which seed production potential per hybridised flower per week was below that of the controls HA10 and HA25. The second group, was composed of parent clones RE43, 410-106-33 and the controls HA10 and HA25 for which seed production per hybridised flower per week was similar to that of the controls. Thus, they were characterised by intermediate production of seeds. The third group, comprised of the only female clone, 103-104-6. Its performance in relation to seed production per hybridised flower per week was above that of the controls, HA10 and HA25. Therefore, it is distinguished from the two previous groups by having high production level of seeds per hybrid. Moreover, the untransformed means spread out from 0.015 to 18.404. Likewise, the gaps among mean and individual measures oscillated from 10.70 to 19.56%.

For ripe fruit weight, significant differences occured among the four female clones (Table 1). Two classes were identified using Dunnett's test. Class C1 comprised the parent clones RE43, 103-104-6, 410-200-15 as well as the control clones HA10 and HA25. This class recorded performances similar to those of the above-mentioned controls. Class C2 comprised the only parent clone 410-106-33 with performances

TABLE 1. Classification of bloomed flowers, seeds deriving from self-pollinations, seeds obtained per self-pollinated flower, and ripe fruit weight as a function of female clones

Dependent variable	Femaclone*	According to Dunnett	Transformed average* (According to Newman-Keuls)	CV (%)**	Untransformed average*** (According to Newman-Keuls)
Blooflow	RE43	Similar to controls	7.900a	14.01	62.410
	103-104-6		8.084a	13.69	65.351
	410-200-15		8.949a	12.37	80.085
	HA10		9.929a	11.15	98.585
	410-106-33		10.075a	10.99	101.506
	HA25		12.501a	8.86	156.275
Nseed	410-200-15	Below controls	-	11.22	1.600
	RE43	Similar to controls	-	17.32	106.800a
	410-106-33		-	17.98	668.800ab
	HA25		-	14.23	759.200ab
	HA10		-	18.96	760.800ab
	103-104-6		-	15.50	1185.800b
Seedflow	410-200-15	Below controls	0.123	19.56	0.015
	RE43	Similar to controls	1.241a	16.36	1.540
	HA25		2.023a	18.25	4.093
	HA10		2.413a	19.02	5.823
	410-106-33		2.472a	18.57	6.111
	103-104-6	Above controls	4.290	10.70	18.404
Weigfruit	RE43	Similar to controls	-	15.54	533.040a
	103-104-6		-	17.20	881.400ab
	HA10		-	15.04	1008.400ab
	HA25		-	14.95	1014.080ab
	410-200-15		-	10.36	1463.600b
	410-106-33	Above controls	-	8.51	1781.000

Dependent variables*: Nseed: seeds number coming from cross-pollination per week. Seedflow: number seeds obtained per hybridised flower per week. Weigfruit: weight of ripe fruit. Blooflow: Bloomed flowers number per week. Femaclone: Clone used as female parent. Transformed average*: Obtained average applying $\surd x$ transformation. CV (%)**: Coefficient of variation. Untransformed average***: Obtained average squaring the transformed average, mainly the variables Blooflow and Seedflow. Data in the same column not followed by the same letter are significantly different after the Newman-keuls and Student t tests at the $P<0.05$ level

above the controls HA10 and HA25. When the Newman-Keuls test was applied to class C1, the female clone RE43 produced light fruits compared to 410-106-33 clone which produced heavy fruits. The untransformed means stretched out from 533.040 to 1781.000. In the same way, the variability around the mean ranged from 8.51 to 17.20%.

Inter-fertility variability among female parent clones with all descriptors. Kaiser's criterion showed that factorial axes F1 and F2 recorded eigenvalues greater than 1 (F1 eigenvalue = 1.933; F2 eigenvalue = 1.206; F3 eigenvalue = 0.841; F4 eigenvalue = 0.020). According to angle criterion, the frequencies histogram of factorial axis F3 eigenvalue recorded brutal fall of the latter. In

Figure 1, the point corresponding to factorial axis F3 is the inflection point. Above this point, is not informative. Consequently, before this point, F1 and F2 preceding it contained essential information. Overall, axes F1 and F2 were retained for the rest of the study. These two factorial axes described 78.46% of the total variation. Factorial axis F1 explained 49.26% of the total variation. The number of seeds deriving from cross-pollinations per week (Nbseed) and the number of seeds obtained per self-pollinated flower per week (Seedflow) were well represented (Table 2). This axis represented the ability of tested parents to produce seeds. Factorial axis F2 accounted for 30.17% of the residual variation unexplained by the factorial axis F1. This axis described the rhythm of flowers issue. Therefore, it represented the potential of tested parents to yield flowers. Thus, factorial axes F1 and F2 were chosen for the rest of the study (Fig. 1).

Descriptors were chosen based on the representation quality, QLT_{kl} in abbreviate. The Blooflow, Nbseed and Seedflow were well represented on the 1-2 plane (QLT_{kl}(1-2) of Blooflow = 0.910; QLT_{kl}(1-2) of Nbseed = 0.990; QLT_{kl}(1-2) of Seedflow = 0.959). In addition, Nbseed and Seedflow were positively and significantly correlated (r Nbseed / Seedflow = + 0.910*). Between the two, the best represented, namely the Nbseed was chosen for the rest of the study. The other was dropped. Overall, the Blooflow and Nbseed were used in the rest of the study (Fig. 2; Table 2).

The projection of six female parent clones on the plane 1-2 of the factorial map with all the four variables, allowed the observation of some distinctly a priori clustered groups. These were: (i) G1, composed of clones 410-106-33, 103-104-6 including control HA10, (ii) G2 consisting of

TABLE 2. Square cosine of the four studied descriptors on the two factorial axes retained as well as their representation quality on the plane1-2

Descriptors	Axes		QLT_{kl}
	F1	F2	1 - 2
Blooflow	0.188	0.722	0.910
Nbseed	0.963	0.027	0.990
Seedflow	0.930	0.029	0.959
Weigfruit	0.027	0.469	0.496

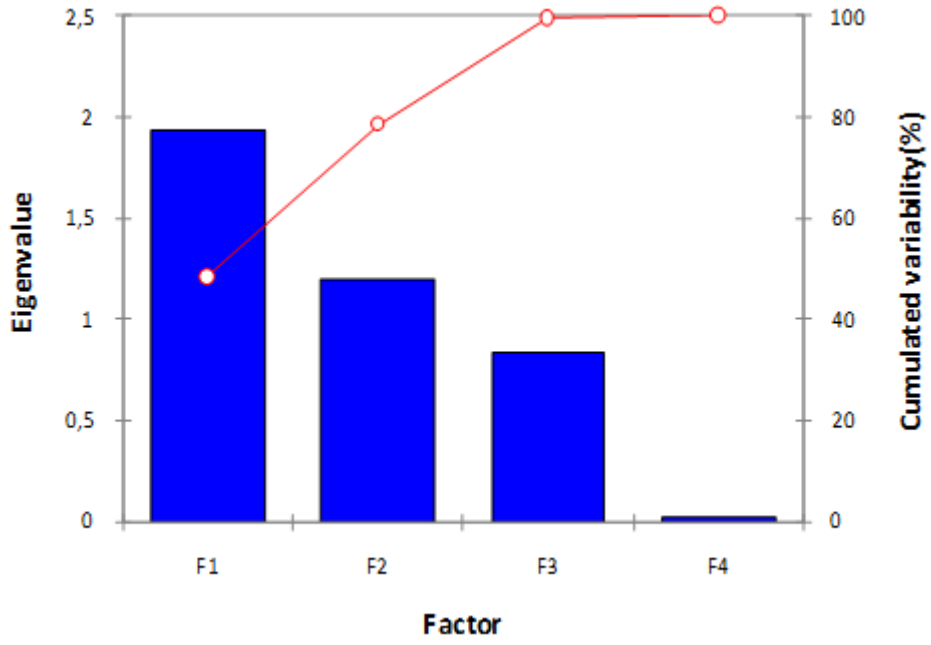

Figure 1. Scree plot of the eigenvalues of the Principal Component Analysis showing the first angle or inflection point (point here representes the eigenvalue of F3).

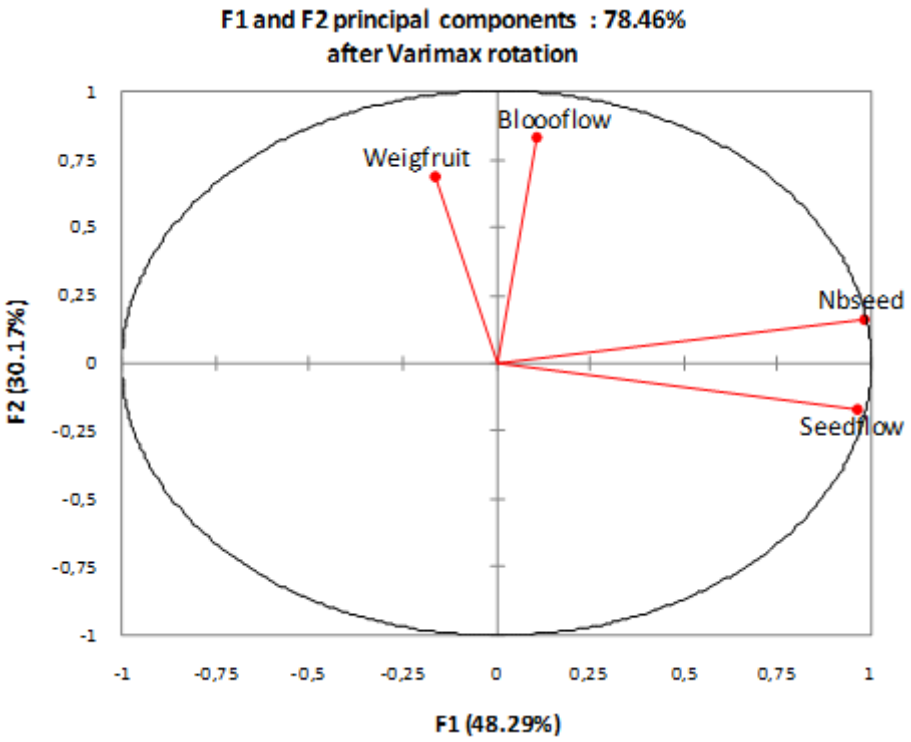

Figure 2. Quality of representation of the four variables used on the planes 1-2 and 1-3 of circle of correlation of the Principal Component Analysis.

clones RE43 and 410-200-15 and (iii) G3, comprised the only clone HA25. Axis F2 separate G2 group from G1 and G3 groups. Group G2, both characterised by low bloomed flowers per week (Blooflow) and number of seeds deriving from cross-pollinations per week (Nbseed; Fig. 3).

Clustering of parent clones. The HCA performed with Seedflow and Blooflow, the two most relevant descriptors, provided three a posteriori groups confirming the three a priori groups previously identified. Group G1 comprised of clones 410-106-33, 103-104-6 and the control HA10. It was characterised by few bloomed flowers per week, and high number of seeds deriving from cross-pollinations per week. Group G2, consisted of clones RE43 and 410-200-15, both characterised a few low bloomed flowers per week and number of seeds deriving from cross-pollinations per week. G3 group, consisted of the only control clone HA25, and stood out from the two aforementioned clones by high number of bloomed flowers per week and seeds deriving from cross-pollinations per week (Fig. 4; Table 3).

Genetic distance showed that G1 and G3 groups could be related and could belong to the same group. Finally, two big groups would exist from the six clones studied. The former, comprising of parent clones 410-106-33, 103-104-6, HA10, and HA10, both characterised by greater number of bloomed flowers per week and seeds deriving from cross-pollinations per week (Blooflow = 136.06; Nbseed = 815.50). The latter, consisting of RE43 and 410-200-15, both stood out from the previous four by low bloomed flowers per week and seeds deriving from cross-pollinations per week (Blooflow = 71.80; Nbseed = 54.20; Table 4).

Relatedness among identified groups. Groups G1 and G3 would be morphologically related. Overall, two big groups could be identified from the six clone parents typed with two of the four descriptors used: (i) $G1_{1\text{-}3}$ and (ii) $G2_2$. $G2_2$ group, composed of RE43 and 410-200-15

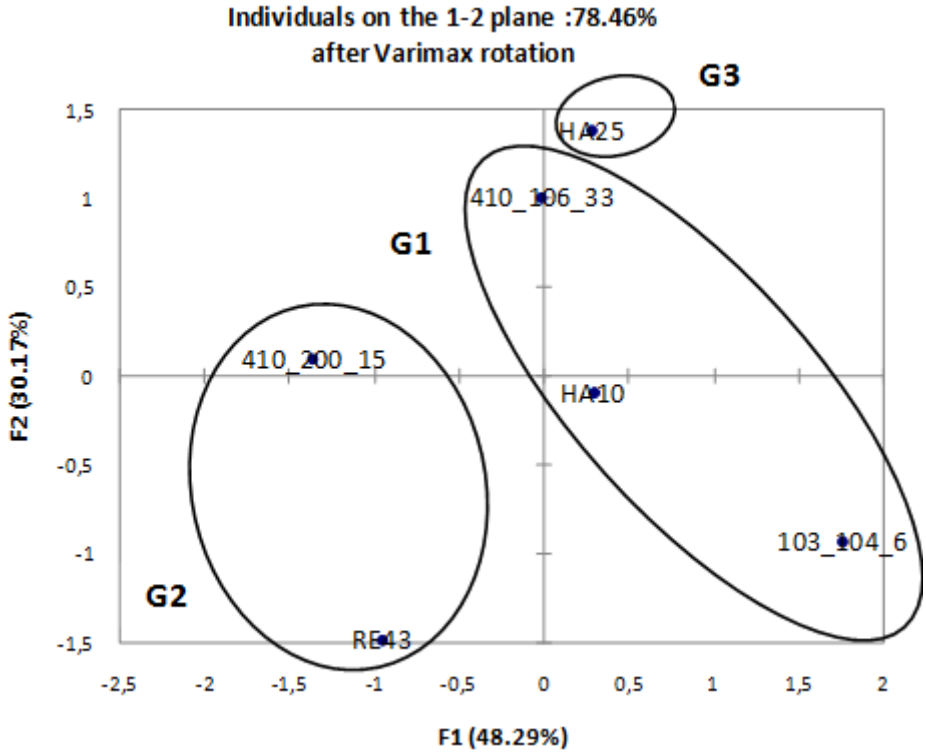

Figure 3. Images of individuals projected on the 1-2 plane of factorial maps of the Principal Component Analysis.

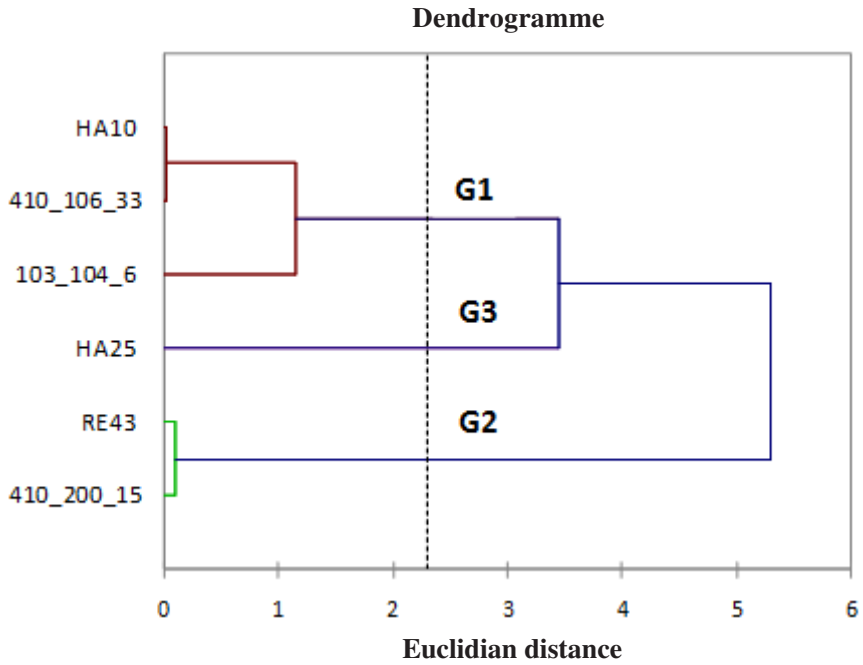

Figure 4. Hierarchical tree showing the structuring of the parent clones using the euclidian distance from the Hierarchical Cluster Analysis.

TABLE 3. Hierarchical classification of the parent clones by means of the identified relevant variables

Classe	Blooflow	Nbseed
G1	88.933	871.800
G2	71.800	54.200
G3	183.200	759.200
Mean	114.644	561.733

Descriptor* : G1: Group composed of clones 410-106-33, 103-104-6 and control HA10. G2: Group composed of clones RE43 and 410-200-15. G3: Group comprised control clone HA25

TABLE 4. Relatedness among groups by means of the euclidian distance proceeding from the Cluster Hierarchical Analysis

	G1	G2	G3
G1	0	1.867	**1.592**
G2	1.867	0	2.445
G3	**1.592**	2.445	0

The bold numeral **(1.592)** illustrated the most related groups represented by G1 and G3.

produced the lowest seeds number deriving from cross-pollinations per week (Table 4).

DISCUSSION

Considering the analysis by descriptor, the four parent clones produced similar blooming flowers number per week (Blooflow; Table 1). This might find an explanation through the gradual blooming according to a gradient ranging from bottom to top. The number of bloomed flowers seems to be the same in all tested parent clones. This could be a characteristic of the species, because each bloomed flower only lives one day regardless species.

The female clone, 410-200-15, and to a certain extent RE43, 410-106-33 and the controls HA10 and HA25, were inter-sterile and lowly inter-fertile, respectively (Table 1). Varieties RE43 and HA10 belong to Queen Victoria and Smooth Cayenne variety, respectively. They were classified in a group presenting some traits of domestication in Cardin (1990). They produced a few seeds by cross-pollinations.

The genitor clone 410-106-33, and to a certain extent 410-200-15, produced the heaviest fruits (Table 1). They seemed to express a metabolism more active in the stocking and mobilisation of nutrients from stem toward the fruit in formation. Their mean weight was 1781,000 and 1463,600 g, respectively; and was similar to those of the hybrids C2, C6, C7, C10, C11, C15 and C19 described in Atse and Coppens d'Eeckenbrugge (1997). The order of magnitude of their weights classifies them in grade A (1.5 to 2.3 kg) and B (1.1 to 1.5 kg) of fruits intended for export.

With the typological analyses, female clones 410-200-15 and RE43 showed low production potential of seeds by cross-pollinations. The former is a hybrid, while the latter is a commercial type (Fournier, 2011). Parent clone 410-200-15 comes from ♀ HA10 x ♂ Perolera crossing. Therefore, its female parent is Smooth Cayenne HA10. It was characterised as inter-sterile in Cardin (1990). Such an inter-sterility highlights the non-compatibility between the clone 410-200-15 and five other parent clones with which it was crossed. Incompatibility is under gametophytic control (Brewbaker and Gorrez, 1967).

Authors such as Majumber *et al*. (1964), Brewbaker and Gorrez (1967) and Coppens d'Eeckenbrugge *et al*. (1997) postulated a single-gene control. Others (Hayman, 1956); Cardin, 1990; Issali *et al*., 1998) postulated the assumption of a control of at least two-gene at the S and Z loci. The latter hypothesis appears to us as the most plausible. Indeed, to determine the incompatibility genotype, the differential compatibility needs to be known (Chan, 1986). This consists of analysing a direct cross and its reciprocal. For this purpose, these crosses must give similar results.

Considering back cross ♀ HA10 x ♂ 410-200-15, the result showed that it was fertile; whereas its reciprocal was sterile (Data not shown). Here, the female clone HA10 would be homozygous.

In contrast, the back cross ♀HA10 x ♂410-106-33 and its reciprocal are fertile; thus the female genitor HA10 would be heterozygous. The same individual cannot be both homozygous and heterozygous. Therefore, incompatibility in pineapple would be controlled by at least two loci. In Gramineae, two loci control the expression

of sexual incompatibility (Lundquist, 1969). In flower, sexual incompatibility is based on the recognition between proteins of pollen and those of stigma or style. Incompatibility is the rule in Monocotyledons (Brian, 1974). It favours outbreeding, but avoids the inbreeding depression. Overall, the female clone 410-200-15 can be cultivated in several-mixed cropping for on-farm trials; however, clone 410-106-33 is self-compatible (Issali, 1998). It should be subjected to some successive back crosses using HA10 as genitor donor. This would allow the introgression of incompatibility alleles located at the S and Z loci, before release. In the same way, the genitor clone 103-104-6, which was proven to be both self and inter-compatible, should be involved in the same back crosses process to reduce its very high compatibility. Overall, the four female clones assessed in this study were not all inter-fertile.

Groups G1, composed of clones 410-106-33, 103-104-6 and HA10; while G3, comprised of the only control clone HA25 which belong to the same morphological entity. We clustered them in a big group $G1_{1-3}$. The female genitors HA10 and HA25 are two varieties of group Smooth Cayenne, originated from Venezuela (Morton, 1987). Nevertheless, the clones Smooth Cayenne and Queen Victoria RE43 were considered as varieties, and not as different cultivars (Coppens d'Eeckenbrugge *et al*., 1997).

They derive from accumulation of minor somatic mutations. The female genitor 103-104-6 comes from cross♀ Perolera x♂ Perolera; the latter which originated from Venezuela and Columbia (Morton, 1987). This genitor is one of the types of cultivar Smooth Cayenne (Morton, 1987). The crosses ♀103-104-6 x ♂HA10 and ♀103-104-6 x ♂ HA25 produced 1083 and 477 seeds, respectively. Different populations of pineapple are not reproductively isolated, consequently they belong to the same species complex (Coppens d'Eeckenbrugge *et al*., 1997).

ACKNOWLEDGEMENT

We are thankful to both Drs. Essi Kouman KOBENAN and Martin KEHE for manuscript review and work facilities at the Anguededou Station, respectively.

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