



Pineapple breeding: development of new pineapple cultivars without leaf spines and resistant to fusariosis

Dayane Castro Silva · Willian Krause · Debora Sarana Ortolan Arantes ·
Angélica Padilha Freitas · Eileen Azevedo Santos · Dejánia Vieira de Araújo ·
Celice Alexandre Silva

Received: 28 April 2023 / Accepted: 3 June 2024 / Published online: 1 August 2024
© The Author(s), under exclusive licence to Springer Nature B.V. 2024

Abstract Almost all pineapple crops in Brazil are grown using the cultivar Perola. This scenario can be changed through the development of new cultivars with better fruit quality and resistance. The novel approach of the present study was to select pineapple clones that combine both resistance to fusariosis and characteristics related to plant and fruit quality as alternatives to the traditional cultivar Perola. Therefore, the objectives of this work were to estimate genetic parameters and select clones through the REML/BLUP methodology, based on morpho-agronomic characteristics and resistance to fusariosis. Thus, a selection index was used for quantitative characteristics and, later, for qualitative characteristics, such as fruit quality, presence or absence of leaf spines, and resistance to fusariosis. Significant

differences were found for most variables, denoting genetic variability among the evaluated clones. Fruit weight with and without crown and D-leaf length presented the highest heritability estimates (above 50%); however, fruit length, mean fruit diameter, soluble solids, titratable acidity, plant height, and number of active leaves presented the lowest heritability estimates due to greater residual variances. Characteristics related to plant and fruit development are strongly affected by the environment and may result in phenotypic changes. Dominance variance was higher than additive variance, which enables the obtaining of heterosis through vegetative propagation. Eleven out of the 20 superior selected clones presented absence of leaf spines and multiple crowns, higher fruit weight and soluble solids content, and desirable fruit shape

D. C. Silva
Graduate Program in Biotechnology and Biodiversity
of the Pro Central West Network, Center
for Agroenvironmental Research, Study, and Development,
Mato Grosso State University, Tangará da Serra, MT,
Brazil
e-mail: daykastro@gmail.com

W. Krause (✉) · E. A. Santos · D. V. de Araújo ·
C. A. Silva
Center for Agroenvironmental Research, Study,
and Development, Mato Grosso State University,
Tangará da Serra, MT, Brazil
e-mail: krause@unemat.br

E. A. Santos
e-mail: eileen.azevedo@unemat.br

D. V. de Araújo
e-mail: dejania@unemat.br

C. A. Silva
e-mail: celice@unemat.br

D. S. O. Arantes · A. P. Freitas
Master in Environment and Agricultural Production
Systems, Mato Grosso State University, Tangará da Serra,
MT, Brazil
e-mail: deboraortolanarantes@gmail.com

A. P. Freitas
e-mail: angelicafreitaas@hotmail.com

and pulp color; seven of them showed resistance to fusariosis, making them suitable for final testing for release as new cultivars.

Keywords *Ananas comosus* · Selection index · Genetic gain · Superior clones

Introduction

Pineapple (*Ananas comosus* (L.) Merril var. *comosus*) is one of the most important tropical fruits, whose trade has been growing in the main national and international markets; Costa Rica is the largest and Brazil is the fourth largest pineapple producing and exporting country (Altendorf 2019; FAO 2021). Pineapple has stood out among several fruit species grown in Brazil, reaching a total production of more than 2.3 mg and more than 63,000 hectares of planted area (FAO 2021), as the edaphoclimatic conditions in the country favor the development of this crop.

Smooth Cayenne is the most grown cultivar in the world. Its fruits have been used by fruit industries for canned pineapple because of its high yield, flavor, cylindrical fruit shape, and fiber content, which facilitate slicing and dicing (Sanewski et al. 2018). However, breeding programs have sought to develop new cultivars, as Josephine in Malaysia (Bartholomew et al. 2010); Aus Jubilee, Aus Carnival, and Aus Festival in Australia (Bartholomew et al. 2010; Sanewski 2014) and Tainung 17, Tainung 21, and Tainung 22 in Japan (Bartholomew et al. 2010; Tang et al. 2014; Kuan et al. 2018).

Perola is the most grown pineapple cultivar in Brazil. This variety has soft and juicy pulp with color varying from white–pale yellow, pleasant aroma, and soluble solids ranging from 13 to 16°Brix, which pleases consumers. However, it has spines on its leaves, which makes management and cultural practices difficult for growers. In addition, it is susceptible to fusariosis, the main disease of pineapple, making the crops vulnerable, as it attacks more than 85% of the pineapple planted area in the country (Matos 2018; Sanewski et al. 2018).

Therefore, pineapple breeding programs in Brazil have sought to obtain cultivars without leaf spines and with resistance to fusariosis. In this sense, the cultivars BRS Imperial (Cabral and Matos 2005), BRS Ajuba (Cabral and Matos 2008), and

BRS Vitoria (Ventura et al. 2009) of the Brazilian Agricultural Research Corporation (EMBRAPA), and IAC Fantastico (Usberti Filho et al. 1999) of the Agronomic Institute of Campinas (IAC) were released. These cultivars have fast growth, yellow fruit peels, cylindrical fruits, high sugar contents, low acid contents, slightly translucent pulps, pleasant flavor, and greater resistance to internal browning during transport and storage (Py et al. 1984; Coppens D'Eeckenbrugge et al. 2011; Paull et al. 2017). However, they have some limitations, such as small fruits, whitish pulps, and low adaptation to edaphoclimatic variations and different production systems.

Therefore, breeding programs in Brazil and around the world continue to search for varieties with better fruit quality and more adapted to different environments. Progeny test is one of the tools used to identify the best individuals. Progeny tests are important for breeders to estimate genetic parameters and select individuals when focusing on evaluating the magnitude and nature of the available genetic variance for quantifying and maximizing genetic gains, using appropriate selection procedures (Costa et al. 2006).

Selection based on the simultaneous selection index for several traits is essential for the improvement of fruit species, especially perennial ones, as it enables the addition of several information to the selection process, when focusing on choosing promising genotypes that combine several attributes of economic interest (Cruz et al. 2012). Concomitantly with the construction of indices, the use of variance components estimated by the restricted maximum likelihood method (REML) combined with genetic values predicted by the best linear unbiased predictor (BLUP) may result in the most accurate selection process. These estimates are essential for identifying the action of genes involved in the control of characteristics and enabling the prediction of genetic gains through selection. In addition, it allows breeders to plan strategies that best suit the breeding program (Resende 2002).

Mixed models have been widely used for improving several species, such as passion fruit (Assunção et al. 2015; Ferreira et al. 2016), elephant grass (Menezes et al. 2016), and conilon coffee (Carias et al. 2016). Abreu et al. (2017) estimated genetic parameters in Turiaçu pineapple clones and found a genetic variability in the population that was considered

adequate for the selection of the best clones for resistance to *Fusarium guttiforme* and fruit quality-related characteristics.

The novel approach of the present study was to select pineapple clones that combine both resistance to fusariosis and characteristics related to plant and fruit quality as alternatives to the traditional cultivar Perola. Therefore, the objectives of this work were to estimate genetic parameters and select clones through the REML/BLUP methodology, based on morpho-agronomic characteristics and resistance to fusariosis.

Material and methods

Pineapple population and experimental conditions

The experiment was conducted at the experimental area of the Mato Grosso State University (Unemat), in Tangara da Serra, Mato Grosso, Brazil (14° 39' S, 57° 25' W, and altitude of 321 m). The climate of the region is Aw, tropical, with a dry winter and two well-defined seasons: rainy summer and dry winter (Köppen 1936; Alvares et al. 2013); the mean annual rainfall depth is 1,800 mm, with the highest rainfall depths between November and March, and the mean temperature is approximately 25 °C (Martins et al. 2010).

The evaluated pineapple clones were developed through the pineapple breeding program of the Unemat, registered in Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado (SisGen) under the number ACABBB7. The clones were generated in May 2014 using crosses between the cultivars IAC Fantastico and Jupi; BRS Imperial and Pearl; BRS Imperial and Smooth Cayenne; and BRS Vitória and Smooth Cayenne (Table 1), performed in the morning, between 06:00 and 09:00 h. Emasculation of flowers of female parents was not needed due to the high incompatibility of the plants (Zhao and Qin 2018). Flowers were taken from male parents, using tweezers, for cross-pollination; they were placed in Petri dishes and the anthers were detached with the aid of metallic tweezers for the pollination of flowers of female parents. The tweezers were sterilized with 70% alcohol whenever the male and female parents were exchanged to avoid contamination. After pollination, the flowers

Table 1 Number of pineapple clones obtained in four crossings. Tangara da Serra, Mato Grosso, Brazil, 2020

Parents		Number of clones
Male (susceptible)	Female (resistant)	
Smooth cayenne	BRS imperial	24
Smooth cayenne	BRS vitória	8
Jupi	IAC fantastico	25
Perola	BRS imperial	34
Total		91

were covered with paper bags to prevent pollination by insects.

Fruits were harvested 60 days after crossing, and their seeds were collected, disinfected in 70% alcohol and sodium hypochlorite for 15 min, and placed on paper towels to dry. Transparent plastic boxes (Gerbox; 250 mL) with autoclaved sand were used for seed germination and stored in growth chamber at 24 °C, with a 12-h photoperiod and irrigation three times a day using sterile distilled water.

In December 2014, plantlets were transplanted into trays 60 days after germination and left in a greenhouse covered with 70% shade screen. In April 2015, seedlings were transplanted to beds in a greenhouse covered with 50% shade screen. The clones were multiplied by asexual propagation in the field for two generations. Ninety-one clones were evaluated in that experiment (Table 1).

Planting in the field was carried out in September 2018, using a randomized block design, with three replications, five plants per plot, and double rows with spacing of 1.20×0.4×0.4 m. Liming and soil fertilizer application at planting and as topdressing were carried out according to the soil analysis, following technical recommendations for the crop (Souza and Oliveira 2021).

Selection of clones through quantitative characteristics, using REML/BLUP

Characteristics related to plant and fruit were evaluated according to Queiroz et al. (2003). The plant-related characteristics evaluated were: plant height (PH cm), measured from the ground to the highest leaf at natural position of the plant; number of active leaves (NAL), by counting the number of

green and/or active leaves; and D-leaf length (DLL cm), measured from its insertion on the stem to the leaf tip. The latter two variables were measured at the plant flowering stage.

The fruit-related characteristics evaluated were: weight with and without crown (FWC and FWWC, respectively, g). weighted on a precision balance; length (FL cm), measured from the base to the apex of the fruit without crown, using a tape ruler; mean diameter (FMD mm), measured in the middle of the fruit, using a ruler; inflorescence axis diameter (FAD mm), the fruit was cut transversely in the middle and the maximum diameter was measured with a caliper; multiple crowns (presence or absence), considering two or more crowns per fruit; number of seedlings (NS), by counting the number of seedlings (suckers) per plant. The following chemical variables were also evaluated: soluble solids content (SS °Brix), pure fruit pulp was extracted and three drops were placed in a refractometer; the values were expressed as %; titratable acidity (TA), determined by titration with 0.1 N NaOH (AOAC 1995) and expressed as percentage of citric acids; and SS to TA ratio (SS/TA), determined by dividing SS by AT.

The prediction of genetic gains and estimation of variance components were carried out using the REML/BLUP procedure in the genetic statistical software Selegen (Resende 2016). The model of kindred clones was used in the matrix $Y = Xr + Za + Zd + Wp + e$, where Y is the data vector, r is the vector of replication effects (fixed) added to the overall mean, a is the vector of additive genetic effects (random), d is the vector of dominance genetic effects (random), p is the vector of plot effects, and e is the vector of errors or residuals (random); the uppercase letters represent the incidence matrices for the effects.

The structures of means and variances are given as follows:

$$E \begin{bmatrix} y \\ a \\ d \\ c \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}; \text{Var} \begin{bmatrix} y \\ a \\ d \\ c \\ e \end{bmatrix} = \begin{bmatrix} V & ZA\sigma_a^2 & ZD\sigma_d^2 & WI\sigma_c^2 & I\sigma_e^2 \\ A\sigma_a^2 Z' & A\sigma_a^2 & 0 & 0 & 0 \\ D\sigma_d^2 Z' & 0 & D\sigma_d^2 & 0 & 0 \\ I\sigma_c^2 W' & 0 & 0 & I\sigma_c^2 & 0 \\ I\sigma_e^2 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix}$$

where;

$$V = ZA\sigma_a^2 Z' + ZD\sigma_d^2 Z' + WI\sigma_c^2 W' + I\sigma_e^2$$

The mixed model equations are given as follows:

$$\begin{bmatrix} X'X & X'Z & X'Z & X'W \\ Z'X & Z'Z + A^{-1}\lambda_1 & Z'Z & Z'W \\ Z'X & Z'Z & Z'Z + D^{-1}\lambda_2 & Z'W \\ W'X & W'Z & W'Z & W'W + I\lambda_3 \end{bmatrix} \begin{bmatrix} b \\ \hat{a} \\ d \\ c \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ Z'y \\ W'y \end{bmatrix}$$

where;

$$\lambda_1 = \frac{\sigma_e^2}{\sigma_a^2} = \frac{1 - h_a^2 - c^2}{h^2};$$

$$\lambda_2 = \frac{\sigma_e^2}{\sigma_d^2} = \frac{1 - h_a^2 - c^2}{h_a^2 - h^2};$$

$$\lambda_3 = \frac{\sigma_e^2}{\sigma_c^2} = \frac{1 - h_a^2 - c^2}{c^2}$$

where σ_d^2 and h_a^2 are the genetic variance of dominance and heritability in the strict sense, respectively. D is the matrix of dominance genetic correlation among the individuals under evaluation. The presented system predicts the additive (\hat{a}) and dominance (\hat{d}) effects separately. The genotypic heritability values were classified according to Resende (2002).

The total genotypic values, given by $\hat{g} = \hat{a} + \hat{d}$ can be predicted directly by the following mixed model equations:

$$\begin{bmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z + G^{-1}\sigma_e^2 & Z'W \\ W'X & W'Z & W'W + I\lambda_3 \end{bmatrix} \begin{bmatrix} b \\ g \\ c \end{bmatrix} = \begin{bmatrix} Z'y \\ Z'y \\ W'y \end{bmatrix}$$

where $G = A\sigma_a^2 + D\sigma_d^2$.

According to the model, the REML estimators by the expectation–maximization (EM) algorithm (Dempster et al. 1977) to obtain estimates of variance components are:

$$\hat{\sigma}_e^2 = [y'y - \hat{b}'X'y - \hat{a}'Z'y - \hat{d}'Z'y - \hat{c}'W'y]/[N - r(x)]$$

$$\hat{\sigma}_c^2 = [\hat{c}'\hat{c} + \hat{\sigma}_e^2 tr C^{44}]/J_s$$

$$\hat{\sigma}_a^2 = [\hat{a}'A^{-1}\hat{a} + \hat{\sigma}_e^2 tr(A^{-1}C^{22})]/q$$

$$\hat{\sigma}_d^2 = [\hat{d}'D^{-1}\hat{d} + \hat{\sigma}_e^2 tr(D^{-1}C^{33})]/q$$

where; $\hat{\sigma}_{\text{and}}^2$: Residual variance. $\hat{\sigma}_c^2$: Environmental variance between plots. $\hat{\sigma}_{\text{the}}^2$: Additive genetic variance. $\hat{\sigma}_d^2$: Dominance genetic variance.

The additive index of Smith (1936) and Hazel (1943) was applied based on the predicted genotypic values. This index is based on y genotypic values and is given by:

$$I = \sum_{i=1}^n k_i y_i$$

where k weights are estimated, considering economic information, heritabilities, and genetic and phenotypic correlations. This index uses standardized genetic values, in which the relative economic importance or weights of the traits are provided (Viana and Resende 2014). Three weights were randomly evaluated. Regarding weight 1, the characteristics FWC, FWWC, and SS received weights of 100, 100, and 50, respectively, while the other characteristics received a weight of 1; weight 2 was 1 for all characteristics; and weight 3 consisted of using broad-sense heritability values of each characteristic obtained from the deviance analysis. The primary direction of the selection was established for the variables FWC, FWWC, FL, FMD, SS, SS/TA, NS, PH, DLL, and NAL, and the secondary for FAD and TA. Prediction of gains by selection were estimated using the Smith and Hazel selection index, based on a selection of 22%; 20 clones were selected, based on random weight 1, which provided more balanced gains.

Selection through qualitative characteristics

The qualitative characteristics evaluated in 20 selected clones were: presence or absence of leaf spines and multiple crowns. The clones were morphologically characterized by classifying them according to fruit color and shape. The fruits were evaluated when they were at the harvest stage. i.e., at physiological maturation. After harvesting, the external color of the fruit was classified as green, yellowish green, yellow, golden yellow, orange, light purple, or dark purple. The fruit shape was classified as cylindrical, oval, conical, trapezoidal with a wider base, or globose.

Clones showing presence of leaf spines and/or multiple crowns were excluded; thus, 11 clones were

selected and subjected to analysis of genetic resistance to fusariosis.

Phenotyping for resistance to fusariosis in the selected clones

Resistance to fusariosis (*Fusarium guttiforme*) was evaluated after selecting the 11 clones. Seedlings of 10–15 cm were used for inoculation with a solution with the fungus. The seedlings were collected four months after floral induction, inoculated, and planted in beds in a greenhouse covered with 50% shade screen at the experimental area of the Unemat. The isolates were purified through monospore culture and characterized through morphological analysis, according to Nirenberg and O'Donnell (1998), registered in SisGen under the number A365808.

The spore suspension used consisted of 10^5 conidia mL^{-1} of three isolates grown for 10 days in Petri dishes containing PDA medium and maintained at 25 °C with 12-h photoperiod. Twenty mL of sterile distilled water were added to the plate of the isolate 1 and scraped using a Drigalski spatula. The suspended material was filtered through sterile gauze and adjusted to the concentration of 10^5 conidia mL^{-1} after counting in a Neubauer hemocytometer under an optical microscope (Souto and Matos 1978). The same procedure was carried out for the other two isolates. Then, the three isolates were combined in a single container, forming a single suspension.

The methodology proposed by Souto and Matos (1978) was used for inoculation, consisting of making three to four holes in the stem of the seedlings with a perforating tool and submerging them for three minutes in the conidial suspension with mixture of isolates. The cultivars Perola (susceptible) and BRS Imperial (resistant) were used as controls. Soon after inoculation, the seedlings were planted in beds containing sterile substrate consisting of clay soil and washed sand in a ratio of 3:1 that favors the severity of the disease. The response of the plants to fusariosis was evaluated between 90 and 120 days after inoculation, after death of Perola and survival of BRS Imperial plants, which were used as susceptible and resistant controls, respectively (Matos et al. 2011).

The pathogen was identified at the end of the test through incubation of the plant material; the structures were identified in an optical microscope to confirm

the infection in the genotypes by the pathogen. A randomized block experimental design with three replications and five plants per plot was used, consisting of 13 genotypes (11 selected clones and two controls).

Results and Discussions

Estimate of genetic parameters in pineapple clones

Significant differences were found for all characteristics, except fruit inflorescence axis diameter, according to the chi-square test at 1% and 5% (Table 2). This difference denotes the existence of genetic variability among the clones and enables genetic gains through selection and, consequently, obtaining of pineapple clones with desirable fruit characteristics for fresh consumption and for industry.

Dominance variance was higher than additive variance for all evaluated characteristics. Additive variance occurs for any type of allelic interaction, whereas dominance variance only occurs when some degree of dominance is found. Dominance variance is not a problem for pineapple breeding programs focused on clone selection, as cloning enables to obtain all effects of an allele, such as dominance, additive, epistatic, and other effects (Cruz et al. 2012). Thus, a superior clone can transmit its entire genotype through vegetative propagation (Bernardo 2014). Estimates of coefficient of heritability denote good genetic control in the expression of characters and indicate great potential for selection. The h^2g values found for the characteristics evaluated in the present study varied from 0.03 ± 0.01 to 0.62 ± 0.06 , denoting a large amplitude (Table 2). Fruit weight with and without crown and D-leaf length presented high heritability (above 50%) (Table 2).

Fruit inflorescence axis diameter, soluble solids to titratable acidity ratio (SS/TA), and number of seedlings presented medium heritability (23%–49%). These results are favorable for selection of clones, which provide high gains for the following selection. The broad-sense heritability is an important parameter for vegetative propagation of crops such as pineapple and sugarcane, in which genetic variability is released only once and the genotype of a plant is fixed after crossing, with no chance of segregation in further stages (Zhou and Joshi 2012).

The other variables presented low heritability (below 20%) due to high residual variance (Table 3), which shows the great contribution of the environmental factor to the total variation among clones. Total soluble solids (SS), total titratable acidity (TA), and other characteristics related to pineapple development are strongly affected by the environment, which may result in phenotypic changes.

Values close to zero for these parameters denote that the genetic variation did not contribute to the determination of phenotypic variance; thus, these variables should not be considered useful for the selection of pineapple clones. Therefore, based on the results of dominance variance and genotypic heritability, the heterosis of clones was explored in the subsequent selection, using the Smith & Hazel selection index.

Simultaneous selection based on quantitative characteristics

The index of Hazel (1943) with random weight 1 resulted in higher genetic gains (in percentage) for several characteristics of interest (Table 3). The genetic gain is equivalent to the mean of predicted genetic effects vectors for the selected clones. Adding the overall mean to the genetic gain results to the improved population mean (Garcia and Nogueira 2005).

The selection provided gains above 20% for fruit weight (with and without crown), which is an important characteristic for pineapple crops, as the fruit is marketed mainly for fresh consumption and per unit. The mean fruit weight with crowns from the selected clones improved to 1647.45 g, classifying them in an extra category (≥ 1500 g) according to the European Union fruit classification criteria for exports (Radha and Mathew 2007). According to the Brazilian classification, these clones are classified as class 2 (1500–1800 g) (CEAGESP 2003).

The characteristic fruit inflorescence axis diameter had a genetic gain of approximately 6%, denoting a small increase in the improved mean. Commercially, fruits with a small inflorescence axis diameter are desirable as they directly impact pulp yield. However, this genetic gain was not expressive, as the improved mean of the clones was similar to that of the traditional cultivar Perola (2.4 cm) (Araújo et al. 2012).

Table 2 Likelihood ratio test values from the deviance analysis, estimates of genetic variance components by REML/BLUP, and percentage gains per selection by the Smith and Hazel index for fruit weight with crown (FWC g), fruit weight without crown (FWWC g), fruit length (FL cm), fruit mean diameter (FMD cm), fruit inflorescence axis diameter (FAD cm), soluble solids (SS) and titratable acidity by citric acids (TA) contents, SS to TA ratio (SS/TA), number of seedlings (NS), plant height (PH cm), D-leaf length (DLL cm), and number of active leaves (NAL) of 91 pineapple clones. Tangara da Serra, Mato Grosso, Brazil, 2020

Deviance and estimates of components	Characteristics											
	FWC	FWWC	FL	FMD	FAD	SS	TA	SS/TA	NS	PH	DLL	NAL
Likelihood ratio test	-36.89**	-79.77**	7.71**	2.42*	0.77 ^{ns}	37.59**	10.54**	53.62**	29.18**	3.45*	5.59*	26.12**
Additive genetic variance (σ_a^2)	3746.22	3479.42	0.82	0.10	0.01	0.11	0.00	0.63	0.24	8.79	5.86	23.30
Dominance genetic variance (σ_d^2)	135,277.73	138,538.95	11.87	0.73	0.14	2.00	0.02	14.82	3.16	158.82	125.56	49.83
Environmental variance among plots (σ_c^2)	15,124.79	12,955.13	2.43	0.36	0.02	0.68	0.02	5.84	1.26	18.89	7.07	22.88
Residual variance (σ_e^2)	87,201.78	74,952.94	90.05	21.44	0.14	8.01	0.63	34.88	9.92	904.26	110.47	417.96
Individual phenotypic variance (σ_p^2)	241,350.52	229,926.44	105.17	22.63	0.30	10.81	0.67	56.19	14.57	1090.77	248.97	513.98
Genotypic heritability (h_g^2)	0.58 ± 0.06	0.62 ± 0.06	0.12 ± 0.03	0.04 ± 0.02	0.49 ± 0.06	0.19 ± 0.03	0.03 ± 0.01	0.27 ± 0.04	0.23 ± 0.04	0.15 ± 0.04	0.53 ± 0.06	0.14 ± 0.03
Coefficient of determination of dominance effects (C_d^2)	0.56	0.60	0.11	0.03	0.46	0.18	0.03	0.26	0.22	0.14	0.50	0.10
Coefficient of determination of plot effects (C_p^2)	0.06	0.06	0.02	0.02	0.06	0.06	0.03	0.10	0.09	0.02	0.03	0.04
Overall mean	1369.61	1215.39	16.66	11.22	2.05	14.79	0.88	19.08	6.09	95.65	87.83	31.80

** and * significant at 1% (6.63) and 5% (3.84) error probability by the Chi-square test

Table 3 Selection gain for the characteristics: fruit weight with crown (FWC g), fruit weight without crown (FWWC g), fruit length (FL cm), fruit mean diameter (FMD cm), fruit inflorescence axis diameter (FAD cm), soluble solids (SS),

titratable acidity by citric acids (TA), SS to TA ratio (SS/TA), number of seedlings (NS), plant height (PH cm), D-leaf length (DLL cm) and number of active leaves (NAL) of 91 pineapple clones. Tangara da Serra, Mato Grosso, Brazil, 2020

Parameters	FWC	FWWC	FL	FMD	FAD	SS	AT	Ratio	NS	AP	DLL	NAL
Mean of selected clones	1848.65	1676.41	20.41	12.50	2.28	14.33	0.90	17.38	5.72	98.95	90.47	35.70
Overall mean	1369.61	1215.39	16.66	11.22	2.05	14.79	0.88	19.08	6.09	95.65	87.83	31.80
Selection differential	479.04	461.03	3.75	1.27	0.23	-0.46	0.02	-1.70	-0.37	3.30	2.64	3.90
Heritability	0.58	0.62	0.12	0.04	0.49	0.19	0.03	0.27	0.23	0.15	0.53	0.14
Selection gain	277.84	285.84	0.45	0.05	0.11	-0.09	0.00	-0.46	-0.09	0.49	1.40	0.55
Selection gain (%)	20.29	23.52	2.70	0.45	5.60	-0.60	0.07	-2.41	-1.40	0.52	1.59	1.72
Improved mean	1647.45	1501.22	17.11	11.27	2.17	14.70	0.88	18.62	6.00	96.14	89.23	32.35

The other characteristics (fruit length, fruit mean diameter, SS, TA, SS/TA, number of seedlings, plant height, D-leaf length, and number of active leaves) presented selection gains lower than 3%, with a low change in the improved mean.

The clones selected were Unemat 9, 10, 19, 21, 31, 41, 42, 71, 73, 74, 76, 82, 87, 88, 93, 103, 117, 122, 123, and 128.

Selection through qualitative characteristics

Nine clones (9, 41, 73.74, 76, 82, 87, 88, and 93) were discarded from the 20 selected genotypes due to presence of multiple crowns and/or leaf spines (Table 4).

Leaf spines and multiple crowns make the clone unsuitable for commercial release, as they are undesirable traits for growers and unappealing to consumers. Thus, nine clones were discarded because they presented some of these disadvantageous

Table 4 Qualitative characteristics of 20 clones selected by the Smith & Hazel index. Tangara da Serra, Mato Grosso, Brazil, 2020

Clone	Fruit shape	Pulp color	Multiple crowns	Leaf spines
Unemat 9	Trapezoidal	Off white	Absence	Presence
Unemat 10	Conical	Pale yellow	Absence	Absence
Unemat 19	Cylindrical	Off white	Absence	Absence
Unemat 21	Conical	Off white	Absence	Absence
Unemat 31	Conical	Off white	Absence	Absence
Unemat 41	Cylindrical	Yellow	Absence	Presence
Unemat 42	Cylindrical	Off white	Absence	Absence
Unemat 71	Cylindrical	Off white	Absence	Absence
Unemat 73	Oval	Off white	Absence	Presence
Unemat 74	Globose	Off white	Presence	Presence
Unemat 76	Trapezoidal	Off white	Absence	Presence
Unemat 82	Cylindrical	Off white	Presence	Presence
Unemat 87	Cylindrical	Pale yellow	Presence	Presence
Unemat 88	Trapezoidal	Pale yellow	Absence	Presence
Unemat 93	Conical	Pale yellow	Absence	Presence
Unemat 103	Cylindrical	Yellow	Absence	Absence
Unemat 117	Cylindrical	Yellow	Absence	Absence
Unemat 122	Conical	Pale yellow	Absence	Absence
Unemat 123	Conical	Pale yellow	Absence	Absence
Unemat 128	Cylindrical	Pale yellow	Absence	Absence

characteristics (Table 4). The presence of these characteristics in a cultivar makes cultural practices more expensive, which may make the fruit marketing unfeasible.

The presence of multiple crowns on the fruit can increase the fruit inflorescence axis and, consequently, flatten the upper part of the fruit, decreasing the market value of fruits for fresh consumption and canning. Multiple crowns due to fasciation can be hereditary, but they are also strongly affected by the environment and cultural operations. Soils with high fertility at the beginning of inflorescence result in fast plant growth and, after a prolonged dry period, can cause the development of multiple crowns (Collins 1960; Dalldorf 1975; Py et al. 1987; Sanewski et al. 2018). The fasciation of fruits and crowns is also connected to a high vigor of plants, which have a slow flowering; this is often reported for the pineapple cultivar Smooth Cayenne (White 1948; Collins 1960; Sanewski et al. 2018). Moreover, calcium deficiency, excessive nitrogen fertilizer application, and high temperatures during flower development may be associated to development of multiple crowns (Swete Kelly and Bartholomew 1993).

In addition to multiple crowns, the presence of spines on leaves makes cultural practices difficult for growers, thus, the absence of leaf spines is beneficial for crop management. The domestication of pineapple stimulated vegetative reproduction, reinforced self-incompatibility, and favored the development of varieties without or with few spines on leaves (Coppens D'Eeckenbrugge et al. 2011); thus, these varieties have been used in breeding programs, as the absence of leaf is desired by breeders and growers.

The 11 selected clones presented conical, trapezoidal, cylindrical, oval, or globose fruits. The pulp color varied from off-white to yellow (Table 4). The cylindrical shape of the fruit and the yellowish color of the pulp are among the most desirable characteristics for the domestic and foreign markets. Most markets prefer cylindrical pineapple fruits, with yellow pulp and peel, small crown, and pleasant flavor (Cabral and Junghans 2003).

In China, breeders are focused on developing cultivars with cylindrical fruits and sweeter flavor than existing varieties for the fresh fruit market, and cultivars with fruits suitable for canning, with larger,

cylindrical fruits, sweet flavor, and higher juice contents, for the industry market. In Brazil, breeders are focused on pineapple genotypes with cylindrical fruits, yellow and low-fibrous peels, high soluble solids content, moderate acidity, yellow pulps, and other characteristics for the fresh fruit market (Cabral et al. 1999; Cunha 2007).

Resistance to fusariosis in the selected clones

Seven out of the 11 selected clones were resistant to fusariosis (Table 5). The disease induced by the fungus *Fusarium guttiforme* is the most important and destructive for the pineapple crops, causing fruit losses of 30%–40%, seedling losses of up to 20%, and production losses of up to 100% (Ventura and Zambolim 2002; Matos et al. 2011).

Obtaining and growing resistant cultivars is one of the most cost-effective and efficient strategies against fusariosis. Growing resistant cultivars can result pineapple yield increases of 20%–30% in Brazil by avoiding losses caused by this disease. Moreover, production costs may decrease, as applications of fungicides for controlling the disease during the crop flowering will not be necessary, thus contributing to obtaining fruits free of fungicide residues and environmental preservation (Cabral and Coppens D'Eeckenbrugge 2002).

Table 5 Resistance to fusariosis in 11 pineapple clones and in pineapple cultivars used as susceptible and resistant controls. Tangara da Serra, Mato Grosso, Brazil, 2020

Clone	Resistance to Fusariosis
Unemat 10	Resistant
Unemat 19	Susceptible
Unemat 21	Resistant
Unemat 31	Resistant
Unemat 42	Resistant
Unemat 71	Resistant
Unemat 103	Resistant
Unemat 117	Susceptible
Unemat 122	Susceptible
Unemat 123	Resistant
Unemat 128	Susceptible
Perola	Susceptible
BRS imperial	Resistant

Absence of leaf spines and multiple crowns and resistance to fusariosis make a pineapple clone interesting and viable for breeders and growers; breeding programs can develop a more complete cultivar with better attributes than Perola, the traditional cultivar grown in Brazil for fresh consumption and industry processing.

Conclusions

Dominance variance was higher than additive variance for all evaluated pineapple characteristics, enabling the obtaining of heterosis, as the selected clones can transmit their entire genotype to subsequent generations through vegetative propagation.

Seven superior clones (Unemat 10, 21, 31, 42, 71, 103, and 123) were selected due to their higher fruit weights, soluble solids contents, and resistance to fusariosis, making them suitable for cultivation and use value testing.

Author Contributions WK participated in the development of hypotheses, experimental planning, and supervision of manuscript writing; DSOA and APF participated in experimental analyses; EAS, DVA and CAS participated in data analysis and interpretation of results; and DCS performed the experimental analyses, data preparation, statistical analysis, and manuscript writing.

Funding The authors declare that they did not receive any funds, grants, or other support during the preparation of this manuscript.

Declarations

Conflict of interests The authors declare that they have no relevant financial or non-financial interests to disclose.

References

- Abreu GB, Toledo MM, Cavallari MM, Araújo JRG, Rodrigues AAC, Melo LDL, Neves Júnior ACV (2017) Estimation of genetic parameters of Turiaçu pineapple clones and genetic correlation between traits. *Agric Sci* 8:1253–1262
- Altendorf S (2019) Major tropical fruits market review 2018. Food and Agriculture Organization (FAO). <http://www.fao.org/3/ca5692en/ca5692en.pdf>. Accessed 18 Jan 2022
- Alvares CA, Stape JL, Sentelhas PC, Gonçalves LM, Sparovek G (2013) Mapa de classificação climática de

- Köppen para o Brasil. *Meteorol Z* 22:711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- AOAC (1995) Official methods of analysis, 16th edn. Association of Official Analytical Chemists, Washington
- Araújo JRG, Aguiar Júnior RA, Chaves AMS, Reis FDO, Martins MR (2012) Abacaxi “Turiaçu”: cultivar tradicional nativa do Maranhão. *Rev Bras Frutic* 34:1270–1276
- Assunção MP, Krause W, Dallacort R, Santos PRJ, Neves LG (2015) Seleção individual de plantas de maracujazeiro azedo quanto à qualidade de frutos via REML/BLUP. *Revista Caatinga* 28:57–63
- Bartholomew DP, d’Eeckenbrugge GC, Chen C (2010) Register of new fruit and nut cultivars list, pineapple. *HortScience* 45:740–742
- Bernardo R (2014) Essentials of plant breeding. Stemma press, Wooldbury
- Cabral JRS, Junghans DT (2003) Variedades de abacaxi. Embrapa Mandioca e Fruticultura. <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/81569/1/Circular-Tecnica-63-Variedade-Abacaxi-Renato-Cabral-2003.pdf>. Accessed 23 Sep 2021
- Cabral JRS, Coppens D’eeckenbrugge G (2002) Abacaxizeiro. In: Bruckner CH (ed) Melhoramento de fruteiros tropicais. Editora UFV, Viçosa, pp 37–59
- Cabral JRS, Matos AP (2005) Imperial, nova cultivar de abacaxi. Cruz das Almas, Embrapa Mandioca e Fruticultura
- Cabral JRS, Matos AP (2008) BRS Ajubá, nova cultivar de abacaxi. Cruz das Almas, Embrapa Mandioca e Fruticultura
- Cabral JRS, Souza JDS, Ferreira FR (1999) Variabilidade genética e melhoramento do abacaxi. Embrapa Recursos Genéticos e Biotecnologia. <http://www.cpatsa.embrapa.br/catalogo/livroorg/abacaxi.pdf>. Accessed 23 Sep 2021
- Carias CMDOM, Gravina GDA, Ferrão MAG, Fonseca AFAD, Ferrão RG, Vivas M, Viana AP (2016) Predição de ganhos genéticos via modelos mistos em progênies de café conilon. *Coffee Sci* 11:39–45
- Collins JL (1960) The Pineapple: Botany, cultivation and utilization. Interscience Publishers Inc, New York
- CEAGESP. Companhia de entrepostos e armazéns gerais de São Paulo (2003) Normas de classificação do abacaxi. Ceagesp. <https://ceagesp.gov.br/wp-content/uploads/2015/07/abacaxi.pdf>. Accessed 10 Sep 2021
- Coppens D’eeckenbrugge G, Sanewski GM, Smith MK, Duval MF, Leal F (2011) Ananas. In: Kole C (ed) Wild crop relatives: genomic and breeding resources tropical and subtropical fruits. Springer, Berlin, pp 21–41
- Costa RB, Resende MDV, Gonçalves PDS, Rego F, Contini A, Roa R (2006) Genetic evaluation of *Hevea brasiliensis* [(Willd ex Adr. de Juss.) Müell. Arg.] for juvenile vigour using the REML/BLUP method. *Florest Ambient* 12:08–14
- Cruz CD, Regazzi AJ, Carneiro PCS (2012) Métodos biométricos aplicados ao melhoramento genético. Editora UFV, Viçosa
- Cunha GAP (2007) Equipe técnica de abacaxi comemora 30 anos de atividades e realizações. Embrapa Mandioca e Fruticultura Tropical. <https://www.embrapa.br/busca-de-publicacoes/-/publicacao/654393/equipe-tecnica-de-abaca>

- [xi-comemora-30-anos-de-atividades-e-realizacoes](#). Accessed 15 Apr 2022
- Dalldorf ER (1975) Plant selection: multiple tops in ‘smooth cayenne’ pineapples. Pineapple Series, Pretoria
- Dempster AP, Laird NM, Rubin DB (1977) Maximum likelihood from incomplete data via the EM algorithm. *J R Stat Soc* 39:1–38
- FAO – Food and Agriculture Organization (2021) Crops and livestock products. FAO. <https://www.fao.org/faostat/en/#data/QCL>. Accessed 12 Feb 2023
- Ferreira RT, Viana AP, Silva FHDE, Santos EA, Santo JO (2016) Seleção recorrente intrapopulacional em maracujazeiro-azedo via modelos mistos. *Rev Bras Frutic* 38:158–166
- Garcia CH, Nogueira MCS (2005) Utilização da metodologia REML/BLUP na seleção de clones de eucalipto. *Scientia Forestalis* 68:107–112
- Hazel HN (1943) The genetic basis for constructing selection indexes. *Genetics* 28:476–490
- Köppen W (1936) Das geographische System der Klimate. In: Köppen W, Geiger R (eds) *Handbuch der Klimatologie*—Verlag von Gebrüder Borntraeger, Berlin
- Kuan CS, Lee TC, Tsai MH, Tsai HW, e Tang, CH, (2018) A New Pineapple Cultivar *Ananas comosus* (L.) Merr. (‘Tai-nung No. 22’). *HortScience* 53:578–581
- Martins JA, Dallacort R, Inoue MH, Santi A, Kölling EM, Colleti AJ (2010) Probabilidade de precipitação para a microrregião de Tangará da Serra, Estado do Mato Grosso. *Pesquisa Agropecuária Trop* 40:291–296. <https://doi.org/10.5216/pat.v40i3.6365>
- Matos AP, Junghans DT, Spironello A (2011) Variedades de abacaxi resistentes à fusariose. Embrapa Mandioca e Fruticultura, Cruz das Almas
- Matos AP (2018) Plano estratégico para a cultura do abacaxi 2017–2021. Embrapa Mandioca e Fruticultura. <https://ainfo.cnptia.embrapa.br/digital/bitstream/item/187804/1/SerieDocumentos225-189-17-MarcioCanto-AINFO.pdf>. Accessed 12 Aug 2018
- Menezes BRDS, Daher RF, Gravina GDA, Silva VB et al (2016) Seleção de genótipos de capim-elefante (*Pennisetum purpureum*) utilizando a metodologia Reml/Blup. *Revista de Ciências Agrárias* 39:360–365
- Nirenberg HI, O’Donnell K (1998) New *Fusarium* species and combinations within the *Giberella fujikuroi* species complex. *Mycologia* 90:434–458
- Paull RE, Bartholomew DP, Chen CC (2017) Pineapple breeding and production practices. In: Lobo MG, Paull RE (eds) *Handbook of pineapple technology: production, postharvest science, processing and nutrition*. John Wiley & Sons, Chichester, pp 16–38
- Py C, Lacoëuilhe JJE, Teisson C (1984) *L’ananas Sa Culture, ses produits*. Editions G. P, Maisonneuve, Paris
- Py C, Lacoëuilhe JJE, Teisson C (1987) *The Pineapple. Cultivation and uses*. Editions G. P, Maisonneuve, Paris
- Queiroz CRP, Lorenzoni MM, Ferreira FR, Cabral JRS (2003) Catálogo de caracterização e avaliação de germoplasma de abacaxi. Embrapa Recursos Genéticos e Biotecnologia. <https://www.embrapa.br/busca-de-publicacoes/-/publicacao/184676/catalogo-de-caracterizacao-e-avaliacao-de-germoplasma-de-abacaxi>. Accessed 18 Oct 2018
- Radha T, Mathew L (2007) Tropical fruits. In: Peter KV (ed) *Fruit crops*. New India Publishing Agency, New Delhi, pp 91–115
- Resende MDV (2002) Genética biométrica e estatística no melhoramento de plantas perenes. Embrapa Florestas, Brasília
- Resende MDV (2016) Software selegen-REM/BLUP: a useful tool for plant breeding. *Crop Breed Appl Biotechnol* 16:330–339
- Sanewski G (2014) Aus-Festival. *Plant Var J* 27:275–278
- Sanewski GM, d’Eeckenbrugge GC, Junghans DT (2018) Varieties and breeding. In: Sanewski GM, Bartholomew DP, Paull RE (eds) *The pineapple: botany, production and uses*, 2nd edn. CABI, Boston, MA, pp 42–84
- Smith HF (1936) A discriminant function for plant selection. *Ann Eugen* 7:240–250
- Souto GF, Matos AP (1978) Método para avaliar resistência a *Fusarium moniliforme* var. *subglutinans* em abacaxi. *Rev Bras Frutic* 1:23–30
- Souza LFS, Oliveira AMG (2021) Calagem e adubação para o abacaxizeiro. In: Borges AL (ed) *Recomendações de calagem e adubação para abacaxi, acerola, banana, citros, mamão, mandioca, manga e maracujá*. Editora técnica, Brasília, pp 95–122
- Swete Kelly D, Bartholomew DP (1993) Other disorders. In: Broadley RH, Wassman RCI, Sinclair E (eds) *Pineapple pests and disorders*. Queensland Department of Primary Industries, Brisbane, pp 43–52
- Tang C, Tsai MH, Tsai HW, Kusan CS (2014) A new variety of pineapple (*Ananas comosus* (L.) Merr.) ‘TN21 Golden.’ *J Taiwan Agr Res* 63:167–177
- Usberti Filho JA, Siqueira WJ, Spironello A, Tanaka MAS, Sigris JMM, Martins ALM, Bortoletto N, Tshako AT, Gushiken A (1999) IAC Gomo-de-mel. Instituto Agrônomo de Campinas, Campinas
- Ventura JA, Zambolin L (2002) Controle das doenças do abacaxizeiro. In: Zambolin L, Vale FXR, Monteiro AJA, Costa H (eds) *Controle de doenças de plantas fruteiras*. Editora UFV, Viçosa, pp 445–487
- Ventura JA, Cabral JRS, Matos AP (2009) ‘Vitória’: new pineapple cultivar resistant to fusariosis. *Acta Hort* 822:51–55
- Viana AP, Resende MDV (2014) Genética quantitativa no melhoramento de fruteiras. Interciência, Rio de Janeiro
- White OE (1948) Fasciation the Botanical Review 14:319–358
- Zhao H, Qin Y (2018) Genetic Diversity of Pineapple. In: Ming R (ed) *Genetics and genomics of pineapple*. Springer, Cham, pp 51–59
- Zhou M, Joshi S (2012) Trends in broad sense heritability and implications for sugarcane breeding in South Africa. *Sugar Tech* 14:40–46

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.