Selection for papaya resistance to multiple diseases in a base population of recurrent selection

Ramon de Moraes · Marcelo Vivas · Derivaldo Pureza da Cruz · Renato Santa-Catarina · Rafael Nunes de Almeida · Yure Pequeno de Souza · Rogério Figueiredo Daher · Alexandre Pio Viana · Messias Gonzaga Pereira

Abstract Papaya has a narrow genetic base concerning disease resistance, with few genetically distinct cultivars for planting in the world. Losses in crop production caused by fungal and viral diseases, added to the absence of resistant cultivars available to producers, have reduced the competitiveness of crops. Therefore, this study aimed to select promising individuals for resistance to phoma spot and black spot based on direct or combined genetic gains in the base population of the recurrent papaya selection. The population used in this study originated from the crossing of dioecious, female individuals and holders of a gene pool for resistance to phoma spot and black spot. These were crossed with elite individuals with a gene pool for production traits and fruit quality. The experiment was carried out without an experimental design, containing one plant per plot. Three measurements were taken on 255 individuals for five traits of disease resistance, being: four associated with black spot (incidence and severity on the leaf and fruit) and one associated with phoma spot (severity on the leaf). With the observations obtained, the REML/BLUP procedure was performed to estimate the temporary and permanent environmental effects. Such values were used to know the genetic parameters of the population and to elaborate a combined selection index, as well as to compare the gains with the direct selection. The results indicate environmental variance was relatively high with low repeatability for the traits. Both selection strategies provide gains in reducing the diseases studied. Combined selection is recommended as it provides greater expected gain than direct selection. However, direct selection can be considered for the development of lines per se, as it offers the opportunity to already select superior individuals during the process of breeding the recurrent population or, to be part of the recombination phase.

Keywords Asperisporium caricae · Stagonosporopsis caricae · Direct selection · Combined selection · Selection index

Introduction

Papaya (Carica papaya L.) is considered one of the most cultivated and consumed fruit trees in the
subtropical and tropical regions of the globe (Serrano and Cattaneo 2010; Carvalho et al. 2020). The expansion of new cultivation areas faces challenges such as crop susceptibility to diseases of a viral, fungal, and bacterial nature. Among the main fungal diseases that affect papaya at various stages of its development, the phoma spot (Stagonosporopsis caricae (Sydow., P. Sydow)) stands out, which has the potential to reduce the leaf area and is considered the second major disease of post-harvest fruits; and, the black spot (Asperisporium caricae (Speg.) Maubl.) that by reducing the photosynthetic area of the leaves and commercially depreciating the fruits, can cause severe losses of production (Rezende and Fancelli 2016).

The appearance of the first symptoms of phoma spot and black spot recommend the beginning of disease control in the field (Rezende et al. 2016). However, for the time being, for S. caricae there is no product available capable of efficiently controlling this disease, for this purpose, integrated disease management has been used, for example: avoiding injury to plant and fruit tissues. To the black spot control, sprays are made from restricted organic chemical groups such as dithiocarbamates and triazoles, or inorganic as copper oxychloride and cuprous oxide (Agrofit 2020). The majority use of sprays of these chemical groups can result in 'selection pressure' resulting in isolates of phytopathogens resistant to fungicides, which would further aggravate the crop’s phytosanitary barriers (Lucas et al. 2015; Dorigan et al. 2019).

Thus, the genetic resistance to diseases, the adaptation and the rusticity of papaya appear as sustainable alternatives for the control of this phytosanitary problem (Oliveira et al. 2010). Different experimental techniques, genetic designs and sophisticated tools are being explored by breeding programs to expand the genetic base and/or explore the existing variability in the genus Carica (Serrano and Cattaneo 2010; Moreira et al. 2018; Pereira et al. 2019a).

There is no commercial record of a genotype that has or is widely resistant to S. caricae and A. caricae. The main cause is the narrow genetic base concerning disease resistance. To circumvent this problem, dioecious papaya has been explored for having a broad genetic basis and rusticity, which may confer resistance to phoma spot and black spot (Vivas et al. 2010a; 2012; 2013b; 2014 b; Moraes et al. 2019). It is believed that the correct characterization of the gene pool for phytosanitary resistance traits belonging to dioecious plants, can contribute to the genetic improvement of the species.

Based on this premise, a base population can be developed using the dioecious plants with genes for diseases and elite parents with genes for fruit yield and quality. This population, plant breeding methodologies can be applied, such as the recurrent selection and the segregating individuals can be evaluated using the precise analysis, such as the mixed model methodology (Moreira et al. 2019; Santa -Catarina et al. 2020a, b).

In early stages of recurrent papaya selection, a favorable strategy is to find plants that stand out for having the greatest number of desirable genes and thus create a population of superior plants. Another strategy that recurrent selection in papaya allows is to find plants that stand out individually, as they can be explored as a gene source for each specific characteristic and be used later in different stages of the breeding program and within other methods such as backcrossing or strategy such as hybridization.

Given the above, it is assumed that the identification and selection of papaya genotypes resistant to black spot and phoma spot may be affected by different selection strategies. In this context, the present study was carried out to study the effect of direct and combined selection, and, consequently, selecting genotypes resistant to black spot and phoma spot from the base population of the S0 recurrent family selection program (UCP-C0). For this, genetic parameters, repeatability coefficient, and genetic selection gains in different alternatives for breeding purposes were estimated.

Materials and methods

Obtaining the study population

The material studied came from the base population of the recurrent papaya selection program called UCP-C0 (UENF Caliman Population Cycle 0) (Santa-Catarina et al. 2020a). To obtain the UCP-C0, five half-sib progenies were used as female parents, considered to be resistant to black spot and phoma spot diseases: STA-22 (3), STA-05 (5), STA -17 (6), STA-02 (6), and STA-04 (5), (Vivas et al. 2012, 2013a, 2014). Five
andromonoecious progenies (hermaphrodites) were used as pollen donors for being parents of hybrids already registered with MAPA—Ministry of Agriculture, Livestock and Supply, named: SS-72/12, JS-12, Sekati, UC-36/7, and UC-41/7 (Pereira et al. 2019a, b, c).

To pollinate female plants, a mixture of pollen from andromonoecious plants was prepared from flowers near the anthesis phase. Fifty flowers of hermaphroditic plants were collected from each elite parent to compose the “mix”, totaling 250 flowers. The pollen was removed from the flowers and placed in a 2 ml Eppendorf tube to prepare the mixture and form the pollen mix. After obtaining the pollen mix, the flower buds of the female plants were pollinated using a brush. After pollination, the flowers were protected with a paper bag 13.5 cm wide × 19.5 cm long to ensure control of the crossing. As only female plants from the dioecious population were used and received pollen from hermaphroditic plants, at this moment, there was sexual conversion through the replacement of the Y chromosome (male) by the sex chromosome Yh (hermaphrodite) (Ming et al. 2007).

In the end, pollinated fruits were collected, and from these fruits, equal amounts of seeds were collected, only then were they grouped to form the base papaya population UCP-C0. In the greenhouse, the grouped seeds were sown, and, after germination, the seedlings were acclimatized for approximately 30 days. After acclimatization, the seedlings were transplanted in the experimental area.

Experimental conditions

The seedlings were transplanted to the experimental area, with 1.5 m × 3.6 m spacing, using three seedlings per hole. The transplant took place in September 2016. The sexing of the plants occurred approximately 90 days after the transplant, where the female plants were eliminated, leaving only one hermaphrodite plant per hole, which was considered the measurement plot. The evaluations took place in June, September, and December 2017. Crop management was carried out according to the recommendation for crop and guided by the company CALIMAN agricultural SA.

The experimental area was located at coordinates 19°23’S, 40°04’W, and 33 m altitude above sea level, in Linhares, ES, in the Santa Terezinha farm, in the Caliman Agricola SA company. During the experiment, there was a rainfall volume of 1366 mm and the daily averages of wind speed, air temperature, and relative air humidity of 2.94 m.s⁻¹, 24.4 °C, 73.15% respectively, data obtained by the weather station of Linhares—ES, INMET (Fig. 1). The region’s climate is classified as Awi-type (humid tropical), with rainy summer and dry winter (Alvares et al. 2013).

It is noteworthy that it was not possible to use the experimental design for the evaluation since each plant corresponds to a different individual. Thus, each plant was evaluated individually.
Traits evaluated

The traits evaluated were: Incidence of black spot on the leaf (IBSLF), calculated by the ratio between the number of leaves with symptoms of black spot and the total number of leaves of the plant, according to the formula: \[ \text{IBSLF} = \left( \frac{\text{No. of leaves with black spot}}{\text{Total number of leaves}} \right) \times 100. \] Incidence of black spot on fruit (IBSFT), calculated by the ratio between the number of fruits with symptoms of black spot and the total number of fruits of the plant, according to the formula: \[ \text{IBSFT} = \left( \frac{\text{No. of fruits with black spot}}{\text{Total number of fruits}} \right) \times 100. \] The severity of phoma spot on the leaf (SPSLF): observed on the leaf posterior to the leaf whose petiole held the first newly opened inflorescence. The severity of black spot on the leaf (SBSLF): observed on the leaf whose petiole held the first newly opened inflorescence; Severity of black spot on fruit (SBSFT): observed in stage 0 fruits (harvest point).

The values of black spot severity on the leaf were estimated with the aid of a diagrammatic scale adopted by Vivas et al. (2011) with the injured area values of 0.2; 1.6; 3.5; 5.4; 7.6 and 12.8%. The severity of black spot on the fruit was estimated with the fruits at stage 0 of maturation, with the aid of a diagrammatic scale proposed by Vivas et al. (2010b), with percentages of 0.1, 0.3, 0.6, 1.2, 2.5, 5.0, 10.0, and 20.0%. The phoma spot severity values were estimated using a diagrammatic scale described by Terra et al. (2008), with the injured area values of 1.2, 4, 8, 16, and 32%.

Data analysis—methodology of mixed models

The following components of variance (individual REML) and genetic parameters associated with repeatability were estimated: \( \sigma^2_{\text{ip}} \): permanent phenotypic variation between plants (genotypic variation + permanent environmental variation between measurements); \( \sigma^2_{\text{et}} \): temporary environmental variation; \( \sigma^2_{\text{ri}} \): individual phenotypic variation (\( \sigma^2_{\text{ip}} + \sigma^2_{\text{et}} \)); \( r \): individual repeatability (\( \frac{\sigma^2_{\text{ri}}}{\sigma^2_{\text{ri}} + \sigma^2_{\text{et}}} \)); \( rm \): repeatability of the mean of \( m \) repeated measurements (\( \sqrt{rm} \)); and \( OM \): general mean of the experiment. To estimate the Blup’s, and, the LRT statistical test (Likelihood Ratio Test) was used to test the significance of the effects via chi square. The following model was used: \[ Y = Xm + Wp + e. \] Where: \( y \) is the observation vector; \( m \) is the measurement effect vector (assumed to be fixed) added to the overall average; \( p \) is the plant’s permanent effect vector (genotypic effects + permanent and temporary environmental effects supposed at random); and \( e \) the residual (random) vector (Resende 2016). This is the basic model of repeatability used for experiments without experimental design. The application of the model is justified since in the UCP-C0, each plant is a different individual, and it is not possible to use an experimental design.

Two different selection strategies were used to check whether there was an increase in genetic gain. The genotypic values obtained by the REML/BLUP procedure for each trait were used to rank the individuals. On the basis of these values, the first one strategie was used to selection of the 30 best individuals for each trait was made. For the second strategie, a simultaneous selection of traits was used via the combined selection index (ISC).

Selection criteria adopted

Direct selection

In the direct selection, 30 superior individuals (11.7%) (with lower values) were classified (supplementary table), and the selection gain was estimated by \( GS = (Ds \times rm) \), where \( Ds \) is the selection differential express by \( Ds = (X_s - X_0) \), which was calculated through the difference between the mean of the population \( X_0 \) estimated through the general mean of the experiment and the average value of the selected individuals \( X_s \), and, \( rm \): average repeatability, which provides the upper limit of the heritability coefficients (Viana and Resende 2014).

To assist the visualization of individuals in the direct selection, the Venn diagram was used as a tool for grouping the genotypes. The top 30 individuals for each of the evaluated traits were plotted on the Venn diagram with the aid of the “vennDiagram” package available in the statistical software R.
Simultaneous selection based on the selection index

To select the individuals simultaneously considering several traits in combination, a combined selection (ISC) is used. The combined selection was carried out using the index that associates weights with standardized averages of the selected traits. The index can be estimated using the following equation: \( R_n = \frac{1}{F_{pi}} \). Where, \( F_{pi} \) is the standardized permanent phenotypic value of trait \( i \), and \( p \) is the economic weight attributed to trait \( i \).

The weights assigned to the five traits were: SPSLF (200), SBSFT (200), SBSLF (100), IBSFT (200), and IBSLF (100). These weights were established based on the importance of the genetic resistance of each trait, according to the knowledge of the breeders of the UENF/CALIMAN papaya breeding program. As in the studied population, each plant is a different individual, higher weights (200) were attributed to the most important characteristics related to the phytosanitary quality of the fruit (SBSFT, IBSFT), and the weight (200) for the SPSLF trait was by trial and error aiming to maximize the gains for all traits.

To build the index, Selegen REML/BLUP and Microsoft Office Excel 2016 software were used.

For each trait, the permanent phenotypic values were obtained for each individual, and these were standardized using the following equations: \( F_{pi} = \left( \frac{X_i - \overline{X}}{\sigma} \right) \), where \( F_{pi} \) is the standardized phenotypic value; \( X_i \) is the value for the individual; \( \overline{X} \) is the general average of all individuals; \( \sigma \) is the standard deviation of the distribution. After standardization, the permanent phenotypic values were multiplied by the weights taken from the index mentioned above. The individuals with the lowest total sum of all characteristics (final ISC value) were the highest.

Results

Components of variance and genetic parameters

The chi-square test demonstrated significant differences in the effects of genotypes, thus evidencing the existence of significant differences between individuals. Thus, the existence of genetic variability among individuals allows the selection of superior genotypes based on these evaluated traits (Table 1).

The temporary environmental variance (\( \sigma_{et}^2 \)) represented the highest percentage of the individual phenotypic variance (\( \sigma_i^2 \)) for all traits analyzed (Table 2). These values indicate that the environmental variance for these traits was relatively high, compared with the genotypic variance between plants. Such a fact may have occurred due to the complexity in the interaction involved between plant x pathogen x environment and the nature of the trait.

It was observed that in the region of the experiment, an atypical climatic condition occurred with a concentration of rain in short periods, with an accumulated volume of approximately 1366 mm (August/2016 ~ December/2017). Also, the maximum relative humidity in this period did not exceed 81%. A low wind speed (< 3.0 m s\(^{-1}\)) was also observed during the experiment (Fig. 1). The atypicality of climatic conditions may have influenced the genetic response of individuals.

The repeatability coefficient based on the mean (rm) of three measures and the mean accuracy showed an intermediate magnitude (\( r > 0.3 \)) for the trait IBSLF, and the other traits had a low magnitude (Table 2). For the average accuracy parameter, there was a variation from 0.19 (SBSFT) to 0.61 (IBSLF). In general, the use of selection procedures based on mixed models is justified, because even with low repeatability characteristics, favorable genetic gains were predicted, and the genotypes have the potential.
for selection (Tables 1 and 2). The low repeatability indicates the strategy of selection gain in the medium to long term (Viana and Resende 2014).

**Table 2** Estimates of variance components and genetic parameters associated with the repeatability of the traits obtained through the REML procedure, evaluated in 255 papaya plants

| Traits   | $\sigma^2_{fp}$ | $\sigma^2_{et}$ | $\sigma^2_f$ | rm  | Acm | OM  |
|----------|-----------------|-----------------|--------------|-----|-----|-----|
| SPSLF    | 0.67            | 7.81            | 8.48         | 0.20| 0.45| 2.21|
| SBSFT    | 0.56            | 44.44           | 45.00        | 0.04| 0.19| 1.18|
| SBSLF    | 23.46           | 1076.98         | 1100.44      | 0.06| 0.25| 3.29|
| IBSFT    | 85.51           | 1056.02         | 1141.52      | 0.19| 0.44| 41.90|
| IBSLF    | 1065.57         | 5251.86         | 6317.43      | 0.38| 0.61| 87.47|

$\sigma^2_{fp}$: Permanent phenotypic variance between plants (genotypic variance + environmental variance), permanent between measures. $\sigma^2_{et}$: Temporary environmental variance. $\sigma^2_f$: Individual phenotypic variance. rm: repeatability of the mean of m repeated measurements. Acm: accuracy of the mean of repeated m measurements. MG: Overall mean of the experiment. SPSLF: Severity of phoma-spot on the leaf. SBSFT: Severity of black spot on the fruit. SBSLF: Severity of black spot on the leaf. IBSFT: Incidence of black spot on the fruit. IBSLF: Incidence of black spot on the leaf.

**Table 3** Estimate of the original averages of the UCP0 population (Xo), means of the selected individuals (Xs), rm: representing the maximum of heritability, Selection deviation (Ds), Selection gain in terms of percentage (Gs%). Selection truncated for the trait (*).

| Traits   | Xo   | SBSFT | SBSLF | IBSFT | IBSLF |
|----------|------|-------|-------|-------|-------|
| rm (h²)  | 2.21 | 1.18  | 3.29  | 41.91 | 87.47 |
| Truncated selection (p = 0.1) |
| Xs       | 1.89 | 1.17  | 3.13  | 41.60 | 86.45 |
| Ds       | -0.32| -0.01 | -0.16 | -0.31 | -1.03 |
| Gs%      | -2.90| -0.05 | -0.30 | -0.14 | -0.45 |

**Table 3** Estimate of the original averages of the UCP0 population (Xo), means of the selected individuals (Xs), rm: representing the maximum of heritability, Selection deviation (Ds), Selection gain in terms of percentage (Gs%). Selection truncated for the trait (*).

| Traits   | Xs   | SBSFT | SBSLF | IBSFT | IBSLF |
|----------|------|-------|-------|-------|-------|
| rm (h²)  | 2.23 | 1.14  | 3.30  | 43.48 | 103.13|
| Xs       | 2.03 | 1.18  | 3.09  | 41.55 | 87.19 |
| Ds       | -0.24| 0.00  | -0.20 | -0.28 | 1.67  |
| Gs%      | -1.66| -0.04 | -0.36 | -0.16 | -0.12 |

**Selection by index**

| Traits   | Xs   | SBSFT | SBSLF | IBSFT | IBSLF |
|----------|------|-------|-------|-------|-------|
| rm (h²)  | 2.16 | 1.15  | 3.11  | 39.07 | 84.40 |
| Xs       | 2.35 | 1.25  | 3.76  | 42.42 | 77.99 |
| Ds       | 0.14 | 0.07  | 0.47  | 0.52  | -9.48 |
| Gs%      | 1.25 | 0.24  | 0.86  | 0.24  | -4.12 |

Selection practiced in favor. SPSLF: Severity of phoma-spot on the leaf. SBSFT: Severity of black spot on the fruit. SBSLF: Severity of black spot on the leaf. IBSFT: Incidence of black spot on the fruit. IBSLF: Incidence of black spot on the leaf.

They had these traits in common (SBSFT $\cap$ IBSFT $\cap$ IPSLF), these genotypes present a greater level of...
resistance to the black spot on fruits and low incidence of black spot on leaves, standing out as promising holders of alleles of resistance to black spots. They are indicated in the use of advance of generation and/or crossing to explore the combinatorial capacity and heterosis.

When practicing selection for the SPSLF trait, a genotype (UCPC015-152) had the SBSFT trait in common, \( \text{SPSLF} \cap \text{SBSFT} \); two genotypes (UCPC015-047 and UCPC015-049), had the IBSFT trait in common, \( \text{SPSLF} \cap \text{IBSFT} \); seven other genotypes (UCPC015-023, UCPC015-035, UCPC015-124, UCPC015-148, UCPC015-149, UCPC015-162 and UCPC015-163), had the SBSLF trait in common, \( \text{SPSLF} \cap \text{SBSLF} \); two genotypes (UCPC015-172 and UCPC015-062), had the IBSLF trait in common, \( \text{SBSLF} \cap \text{IBSLF} \).

When practicing the selection for the SBSFT trait, six genotypes (UCPC015-115, UCPC015-117, UCPC015-128, UCPC015-144, UCPC015-147, UCPC015-167), had the IBSFT trait in common, \( \text{SBSFT} \cap \text{IBSFT} \); a genotype (UCPC015-055), had the IBSLF trait in common, \( \text{SBSFT} \cap \text{IBSLF} \).

For the selection based on the SBSLF trait, two genotypes (UCPC015-164 and UCPC015-197), had the IBSFT trait in common, \( \text{SBSLF} \cap \text{IBSFT} \).

And finally, when practicing selection for the IBSFT trait, three genotypes (UCPC015-087, UCPC015-091 and UCPC015-166), had the IBSLF trait in common, \( \text{IBSFT} \cap \text{IBSLF} \).

Individuals highlighted in direct selection should be considered alongside the recurrent selection methodology as a source of individual resistance genes. It is possible to indicate these genotypes for a generational advance. In this way, the lines extracted by the generation advance can be used in combinatorial analysis consecutively.

**Combined selection**

The Selection considering the index (ISC), presented favorable gains for all evaluated characteristics (Table 3). The gains obtained by the ISC were greater than or equal to the indirect gains observed by the direct selection. This fact indicates that there is no loss in gain when practicing selection using the ISC. Also, there was a 93.3% coincidence between individuals selected by ISC and those selected by direct selection.

It is observed that the ISC, indicates the selection of five of the six genotypes highlighted in the triple intercession in the Venn diagram, the exception was for the “UCPC015-167” genotype. A situation that indicates a good accuracy obtained by the index.

The permanent phenotypic values were below the average for the genotypes selected by the index. The UCPC015-115 genotype stood out from the others for having the lowest permanent phenotypic value of 33.71 for IBSFT, while the population average was 41.91. This genotype also stands out for SBSLF, where there is one of the lowest responses to the development of the disease concerning the other genotypes. The material UCPC015-116 was able to provide lower permanent phenotypic value for IBSLF (78.17) while the general average was 87.47. The excellent response of the genotype also occurred in the SBSFT trait with a permanent phenotypic value of 1.14.

Individuals highlighted in the combined selection should be considered in the recurrent selection in the recombination phase. These genotypes will contribute to the accumulation of favorable genes in the population. The gains predicted by the index were higher than the gains predicted in direct selection (Table 3).
Discussion

Conducting individual genotype assessment contributes to accurate estimates of permanent phenotypic effects. Individual assessment contributes to the high significance of the LRT test ($x^2$). Therefore, every effect extracted from the estimate is inherent to the interaction of the plant with the environment and not between the average of individuals with the environment.

The variance of the temporary environmental effect ($\sigma^2_{et}$) showed a higher percentage of individual phenotypic variance ($\sigma^2_{f}$) for all traits. According to Viana and Resende (2014), $\sigma^2_{et}$ is responsible for the temporary variation associated with the momentary environmental effects manifested in each measurement, such as climatic fluctuations of the years and their interactions with the effects verified in the plant. The year 2016 was considered irregular contrasting with the historical series reported by Alvares et al. (2013), for the State of Espirito Santo, with a long period of drought (Fig. 1), which may have modified the responses regarding resistance to the diseases under study or reduced the potential of the inoculum (Moreira et al. 2020).

Climatic factors influence the response in plant development. These environmental conditions counteract the severity and incidence of diseases that affect the crop, especially those of a fungal nature (Oliveira et al. 2011; Moreira et al. 2020). Also, the severity and incidence values were low in general, pointing out that the climatic factors may not have contributed so favorably to the occurrence of diseases (Fig. 1). Temperatures between 27 and 23 °C plus high rainfall and strong winds favor the occurrence of black spot. In contrast, the phoma spot occurs with greater intensity in regions with high relative humidity and when rains occur which facilitate the penetration of the fungus (Oliveira et al. 2011; Moreira et al. 2020).

Repeatability estimates are an important parameter in choosing a genotype, according to what is reported by Cruz et al. (2014), as they can predict the stability of the response of a trait. Therefore, repeatability measures the average correlation between two or more measurements from the same individual. Repeatability is influenced by its nature and the environmental conditions to which the population is subjected (Cruz et al. 2014). Regarding the repeatability of the characteristics evaluated in this work, they were considered of low repeatability, according to Resende (2002). This fact indicates that a single measurement of character in the individual does not represent his real capacity and, therefore, more than one measurement is necessary to decide on his use.

As it is a disease trait, it is expected that low repeatability occurs, of which, the environment exerts a great influence on the host, on the pathogen, and the interaction of pathogen x host. Studies by Liberato et al. (2004) found similar results for traits of resistance to anthracnose in papaya fruit.

In terms of selection, favorable results were found to reduce the magnitude of all traits if analyzed simultaneously by the combined selection via index (ISC) or if analyzed individually by direct selection (DS) for the traits SPSLF, SBSLF, and IBSFT. The possibility of selecting 30 superior genotypes shows that the initial population of recurrent selection has the potential to advance the stages using the recurrent selection (RS) method and/or the development of new papaya lines. In this case, different strategies can be adopted by breeders based on the objective to be achieved. The classification of genotypes based on the ISC is considered satisfactory, since, in terms of genetic gain, the lowest averages for different diseases were achieved based on the genotypes classified by the index.

ISC is more appropriate in the situation where the objective is to develop a population per se, in which individuals are selected from the combination of all the traits being studied, in which the selected individuals have the desired traits, both in terms of resistance the disease in the plant, and in terms of disease resistance in the fruits.

When it comes to the fact that individuals who are directly superior in terms of a particular trait are left out of the combined selection, it must be considered that these individuals are sources of favorable alleles and can be used during the recombination phase of superior individuals (Santa-Catarina et al. 2020a).

The DS of the SBSFT, IBSFT, and IBSLF traits indicated the individual “UCPC015-167”, which did not occur in the ISC, however, in the case of RS, it should be selected as a source of resistance to severity and incidence in the fruit and still incidence on the leaf for black spot. Thus, in the recombination stage of the S1 families, it is indicated to select 30 superior individuals, considering both DS and ISC.
In recent studies for agronomic traits of interest such as production and fruit quality carried out by Santa-Catarina et al. (2020a), the selection of 30 individuals in the UCPC0 population was indicated, from these, the DS or ISC also indicated 19 proposed here. Highlighting the genotype “UCPC015-166”, which in the classification by Santa-Catarina et al. (2020a) ranked second and which was also classified by the ISC proposed in this study. The genotypes: “UCPC015-148”, “UCPC015-152”, “UCPC015-159”, “UCPC015-162”, “UCPC015-167”, and “UCPC015-178” form a group of individuals from the Formosa standard; the “UCPC015-144” and “UCPC015-197” genotypes form a small group from the standard Solo. The genotypes above have favorable alleles for multiple diseases and agronomic traits of production and quality, being recommended the selection of genotypes not only for the recombination stage but also for advancing generation.

Conclusion

The combined selection proved to be consistent for providing better selection gains and precision in the selection process.

Thirty individuals were indicated for selection through the combined selection index, pointing out in these genotypes a high genetic potential for the line development per se and/or hybrids with resistance to black spot and phoma-spot.

The genotypes: “UCPC015-052”, “UCPC015-166”, “UCPC015-064”, “UCPC015-202”, “UCPC015-061”, “UCPC015-108”, “UCPC015-144”, “UCPC015-240”, “UCPC015-041”, “UCPC015-003”, “UCPC015-189”, “UCPC015-186”, “UCPC015-152”, “UCPC015-148”, “UCPC015-197”, “UCPC015-167”, “UCPC015-178”, “UCPC015-162”, “UCPC015-159”, combine attributes of resistance to black spot and/or phoma spot, implying that the composition of the base population is satisfactory for the purpose for which it was created.

Acknowledgements The authors are grateful for funding from Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro, Conselho Nacional de Desenvolvimento Científico e Tecnológico, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

References

AGROFIT (2020) Sistema de Agrotóxicos Fitossanitários. http://www.agricultura.gov.br/assuntos/insumos-agropecuarios/insumos-agricolas/agrotoxicos/agrofit. (Acesso em 10 fevereiro 2021)

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen’s climate classification map for Brazil. Meteorol Zt. https://doi.org/10.1127/0941-2948/2013/0507

Carvalho C, Kist BB, Beling RR (2020) Anuário Brasileiro de Fruticultura 2020. Editora Gazeta, Santa Cruz do Sul, p 77

Cruz CD, Regazzi AJ, Carneiro PCS (2014) Métodos biométricos aplicados ao melhoramento genético, vol 2. UFV, Imprensa Universitária, Viçosa

Dorigan AF, Carvalho GD, Poloni NM, Negrisoli MM, Maciel JLN, Ceresini PC (2019) Resistance to triazole fungicides in Pyricularia species is associated with invasive plants from wheat fields in Brazil. Acta Sci Agron. https://doi.org/10.4025/actasciagron.v41i1.39332

Liberato JR, Cruz CD, Tatagiba JS, Zambolim L (2004) Minimum number of assessment times to compare chemical control treatments for papaya fruit anthracnose. Fitopatol Bras. https://doi.org/10.1590/S0100-41582004000600011

Lucas JA, Hawkins NJ, Fraaije BA (2015) The evolution of fungicide resistance. Adv Appl Microbiol. https://doi.org/10.1016/bs.aambs.2014.09.001

Ming R, Yu Q, Moore PH (2007) Sex determination in papaya. Semin Cell Dev Biol. https://doi.org/10.1016/j.scbdb.2006.11.013

Moraes R, Vivas M, Vivas JMS, Daher RF, Gravina GA, Francelino HO, Pereira MG (2019) Genetic parameters and performance of papaya genotypes to black spot resistance (’Asperisporium caricae’). Aust J Crop Sci. https://doi.org/10.21475/aajs.19.13.05.p1097

Moreira SO, Kuhlcamp KT, Barros FLDS, Zucoloto M, Moitinho ACR (2018) Intrapopulation recurrent selection by mixed models in papaya of the formosa group. Rev Bras Frutic. https://doi.org/10.1590/0100-29452018870

Moreira NF, Pereira TNS, Catarina RS, Cortes DFM, Vettorazzi JCF, Ramos HCC, Pereira MG (2019) Quantification of floral abnormalities in a population generated from sexual polymorphism aiming at recurrent selection in papaya. Bragantia. https://doi.org/10.1590/1516-4499.20180197

Moreira TR, Silva SF, Gandine SMS, Souza KB, Senhorelo AP, Heitor FD, Billo D (2020) Thermal favorability for the Oidium caricae and Asperisporium caricae in areas of edaphoclimatic aptitude for the Carica papaya. J Therm Biol. https://doi.org/10.1016/j.jtherbio.2020.102648

Oliveira EJ, Amorim VBO, Matos ELS, Costa JL, Castellen MS, Pádua JG, Dantas JLL (2010) Polymorphism of...
microsatellite markers in papaya (Carica papaya L.). Plant Mol Biol Rep. https://doi.org/10.1007/s11105-010-0180-6
Oliveira AAR, Santos Filho HP, Andrade E C, Meissner Filho PE (2011) Impacto potencial das mudanças climáticas sobre as doenças do mamoeiro no Brasil. Embrapa Mandioca e Fruticultura-Capítulo em livro científico (ALICE)
Pereira MG, Luz LND, Catarina RS, Ramos HCC, Pereira TNS, Barros GDB, Azevedo AON (2019b) UC10: a new early Formosa papaya cultivar. Crop Breed Appl Biotechnol. https://doi.org/10.1590/1984-70332019v19n1c18
Pereira MG, Luz LND, Catarina RS, Ramos HCC, Pereira TNS, Barros GDB, Silveira SFD (2019c) ‘UC14’: a new papaya cultivar with intermediate fruit size. Crop Breed Appl Biotechnol. https://doi.org/10.1590/1984-70332019v19n2c31
Pereira MG, Poltronieri TPS, Pereira TNS, Catarina RS, Vettorazzi JCF, Cortes DFM (2019a) Twenty-two-year papaya breeding program: from breeding strategy establishment to cultivar development. Funct Plant Breed J. https://doi.org/10.35418/2526-4117/v1n2a
Resende MDV (2016) Software Selegen-REML/BLUP: a useful tool for plant breeding. Crop Breed Appl Biotechnol. https://doi.org/10.1590/1984-70332016v16n4a49
Resende MDV (2002) Genética biométrica e estatística no melhoramento de plantas perenes. Embrapa Informação Tecnológica, Colombo: Embrapa Florestas
Rezende JAM, Fancelli MI (2016) Doenças do mamoeiro (Carica papaya L.). Kimati H, Amorim L, Bergamim Filho A Santa-Catarina R, Pereira MG, Vettorazzi JCF, Cortes DFM, Poltronieri TPS, Azevedo AON, Viana AP (2020a) Papaya (Carica papaya L.) S1 family recurrent selection: opportunities and selection alternatives from the base population. Sci Horticul. https://doi.org/10.1016/j.scienta.2019.108848
Santa-Catarina R, Vettorazzi JCF, Cortes DFM, Santana JGS, Poltronieri TPS, Miranda DP, Pereira MG (2020b) Phenotypic characterization of recurrent selection S1 Papaya (Carica papaya L.) families by multivariate approach. Euphytica. https://doi.org/10.1007/s10681-020-02655-1
Serrano LAL, Cattaneo LF (2010) O cultivo do mamoeiro no Brasil. Rev Bras Fruticul. https://doi.org/10.1590/S0100-29452010000300001
Terra CEPS, Vivas M, Melo CS, Silveira SF, Pereira MG (2008) Elaboração e validação de escala diagramática para avaliação da severidade da podridão preta (Phoma caricae papayae) em folhas de mamoeiro (Carica papaya). In: XX Congresso Brasileiro de Fruticultura. Anais, Vitória ES
Viana AP (2014) Genética quantitativa no melhoramento de frutais. Interse, Venezuela
Vivas M, Silveira SFD, Terra CEPS, Pereira MG (2010a) Reação de germoplasma e híbridos de mamoeiro à mancha-de-phoma (Phoma caricae-papayae) em condições de campo. Trop Plant Pathol. https://doi.org/10.1590/S1982-56762010000500009
Vivas M, Terra CEPS, Silveira SFD, Fontes RV, Pereira MG (2010b) Escala diagramática para avaliação da severidade da pinta-preta em frutos de mamoeiro. Summa Phytopathol. https://doi.org/10.1590/S0100-54052010000200010
Vivas M, Silveira SFD, Terra CEPS, Pereira MG (2011) Testers for combining ability and selection of papaya hybrids resistant to fungal diseases. Crop Breed Appl Biotechnol. https://doi.org/10.1590/S1984-70332011000100005
Vivas M, Silveira SFD, Vivas JMS, Pereira MG (2012) Patometria, parâmetros genéticos e reação de progênies de mamoeiro à pinta-preta. Bragantia. https://doi.org/10.1590/S0006-87052012005000021
Vivas M, Silveira SFD, Amaral Junior ATD, Cardoso DL, Pereira MG (2013a) Herança da resistência do mamoeiro a doenças fúngicas com base em análise dialéctica de Hayman. Bragantia. https://doi.org/10.1590/brag.2013.047
Vivas M, Silveira SFD, Vivas JMS, Pereira MG (2013b) Previsão de ganhos genéticos e seleção de progênies de mamoeiro para resistência à pinta-preta. Trop Plant Pathol. https://doi.org/10.1590/S1982-56762013000200008
Vivas M, Silveira SFD, Vivas JMS, Viana AP, Amaral Junior ATD, Pereira MG (2014) Seleção de progênies femininas de mamoeiro para resistência a mancha-de-phoma via modelos mistos. Bragantia. https://doi.org/10.1590/1678-4499.216
Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.