ARTICLE

Inbreeding and founder cultivars contributions in low chill requirement peaches and nectarines

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Abstract: *The pedigree analysis from genealogical data can estimate the inbreeding from identity-by-descent, being a powerful tool for germplasm characterization. The aim of this study was to evaluate the genetic diversity of peach and nectarine cultivars from the Agronomic Institute Prunus germplasm. This assessment was based on inbreeding and coancestry coefficients, considering two cases according to the origin of pollen donor in open pollinations: case I as self-pollinated, and case II as outcrossing. This study provided information regarding the founder cultivars. The historical investigation of the genealogy of 84 cultivars returned up to eight generations. Thirty-one founder cultivars were identified. The inbreeding coefficient of 40 (case I) and 14 (case II) for the cultivars were higher than expected, evidencing some degree of inbreeding. However, the averages for the coancestry coefficients were low (case I: 0.144; case II: 0.087), indicating genetic variability among the cultivars, which may be used in breeding programs.*

Keywords: *Pedigree, coancestry coefficient, degree of relationship, kinship analysis, mating system*

INTRODUCTION

The presence of genetic variability is a key point to determine the capability of the population to be genetically improved (Toro et al. 2014, Antonios et al. 2021). New approaches for estimating the genetic parameters used in breeding programs have favored the inclusion of historical development of cultivars' parents, e.g., inbreeding coefficient (Antonios et al. 2021). The pedigree matrix, for providing kinship and additive genetic relationship, are widely used in breeding programs (VanRaden 1992, Toro et al. 2014, Goudet et al. 2018, Antonios et al. 2021), as well in association studies (Sinnwell et al. 2014, Antonios et al. 2021). The knowledge of the genealogy among cultivars is fundamental for studies of genetic prediction, parental selection, and the cultivar protection process (Fresnedo-Ramírez et al. 2015, Antonios et al. 2021).

The inbreeding (F) and the coancestry coefficients (θ) are the probability of two alleles taken randomly from the same or different individuals, respectively, being identical by descendent (IBD), e.g., inherited from a common ancestor (Sinnwell et al. 2014, Toro et al. 2014, Goudet et al. 2018, Arellano-Suarez et al. 2020, Antonios et al. 2021). For instance, the expected kinship, i.e., the relationship between members of the same family, is 0.500 for an individual with itself (or self-pollinated), 0.250 between full-sibs and 0.125 between

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half-sibs, being diploid species and with no inbreeding accumulated in past generations (Scorza et al. 1985, Fehr 1987, Lansari et al. 1994). Considering population with random mating, the average ⍰ of a progeny is equal to the F of its parents (VanRaden 1992, Legarra 2016, Goudet et al. 2018). Thus, the F of two cultivars could be estimated as θ of their progeny (Goudet et al. 2018).

The inbreeding and the coancestry coefficients can be estimated from the genealogy of the individuals, by pedigree information (VanRaden 1992, Toro et al. 2014, Goudet et al. 2018, Antonios et al. 2021). Despite the advances in molecular marker techniques, pedigree analysis remains recommended, mostly when the IBD coefficients involve more than two individuals at a time (Cussens and Sheehan 2016). Different from the molecular markers, pedigree analysis is able to identify individuals that may have two alleles identical by descendent. The inbreeding and the coancestry coefficients have been applied in human genetic analysis and in germplasm studies for breeding programs of plants and animals (VanRaden 1992, Muniz et al. 2001, Goudet et al. 2018, Antonios et al. 2021), as an indicator of genetic variability (Toro et al. 2014). Besides its use for conservation genetics, these parameters can be used to estimate quantitative parameters with accuracy and as a tool for parental selection intending to avoid the inbreeding depression (VanRaden 1992, Toro et al. 2014, Whitehead et al. 2018, Antonios et al. 2021).

Peach (*Prunus persica* (L.) Batsch) and nectarine (*P. persica* var. *nucipersica* Dippel), despite having hermaphrodite flowers, are considered as autogamous species (Scorza et al. 1985, Bassi and Monet 2008). However, these species can reach between 10 and 90% of cross-pollination in open pollination, depending on the cultivar (Hansche 1990, Bassi and Monet 2008). This suggests a low genetic variability of peach and nectarine germplasm, although some studies have shown the opposite (Font i Forcada et al. 2014, Kwon et al. 2015, Thurow et al. 2017). The loss of genetic variability has a negative impact on the development of breeding programs as it may increase the vulnerability against biotic and abiotic factors (Raseira and Franzon 2014, Khadivi-Khub et al. 2016, He and Li 2020). In addition, as consequence of the high inbreeding coefficients, the inbreeding depression may negatively impact economically important traits (Antonios et al. 2021).

The Agronomic Institute (IAC) of São Paulo State, Brazil, was responsible for the research that promoted the initial adaptation of stone fruits in Brazilian subtropical climate. In 1950, the IAC started the breeding program of stone fruits, aiming at the selection of cultivars with low chill requirement (between 50 and 250 Chill hours) and with good fruit quality, primarily for fresh market peaches and nectarines (Sobierajski and Blain 2022). Therefore, the estimate of the inbreeding coefficient of cultivars of the IAC-Prunus germplasm can contribute to genetic conservation and selection of the parents involved in the crossings. This is essential to the development of new cultivars. Thus, the present study aimed to estimate the inbreeding and coancestry coefficients and founders' contributions of peach and nectarine cultivars of the IAC-Prunus germplasm using pedigree information.

MATERIAL AND METHODS

The IAC-Prunus germplasm belongs to the IAC and is the basis of breeding program for peaches and nectarines of low chilling requirement (Sobierajski and Blain 2022). It is situated in Jundiaí, State of São Paulo, Brazil (lat 23° 06' 52 S, long 46° 56' 03" W, alt 740 m asl). The climate is monsoon-influenced humid subtropical climate (Cwa), according to Köppen's classification system (Alvares et al. 2013). Currently, 84 cultivars have been conserved in the IAC-Prunus germplasm (Table 1), and their pedigree was collected from breeding reports and scientific publications.

We rebuilt the genealogical tree of each of the 84 cultivars as follows: when we identified the parents of a particular cultivar, we attempted to identify the parents of these parents, i.e., the grandparents of this particular cultivar. We repeated this procedure over the generations until no information was available. Thus, the variables required (id, momid and dadid) were inserted using the cultivars' names. The resulting genealogical tree (referred as to the input file) contained 148 individuals. No information about the level of self-incompatibility of the cultivars in the input file was found. Thus, we considered two cases. Case I: the offspring from open pollination were assumed as self-pollinated. Case II: the offspring from open pollination were assumed as outcrossing to unknown pollen donor.

The input file was used to estimate the inbreeding and coancestry coefficients as quantitative indicators of genetic diversity. The inbreeding (F) and coancestry (Θ) coefficients are given by the equations 01 and 02, according to Wright (1922), and described by Gauvin et al. (2015) and Goudet et al. (2018).

Table 1. List of peach (*Prunus persica*) and nectarine (*P. persica* var. *nucipersica*) cultivars from IAC-Prunus germplasm

Cultivars			
'IAC Alô Doçura'	'IAC Delicioso Precoce'	'IAC 6982-29'	'IAC Padrão'
'IAC Arlequim'	'Diamante'	'IAC 91-2'	'IAC Pérola de Mairinque'
'IAC Aurojima'	'IAC Doçura'	'IAC N 5483-19'	'IAC Petisco'
'IAC Aurora-1'	'IAC Doçura-2'	'IAC N 680-167'	'IAC Petisco-2'
'IAC Aurora-2'	'IAC Doçura-3'	'IAC Jóia-1'	'IAC Precoce de Itupeva'
'IAC Big Aurora'	'IAC Doçura-4'	'IAC Jóia-2'	'Precocinho'
'IAC Biuti'	'IAC Douradão'	'IAC Jóia-3'	'Premier'
'IAC Bolão'	'IAC Dourado-1'	'IAC Jóia-4'	'IAC Régis'
'IAC Branca de Guapiara'	'IAC Dourado-2'	'IAC Jóia-5'	'Rei da Conserva'
'IAC Campinas-1'	'IAC Douragreen'	'IAC Josefina'	'IAC Relíquia'
'IAC Canário'	'Eldorado'	'IAC Karina'	'IAC Rosalina'
'IAC Catita'	'Flordaprince'	'Maravilha'	'IAC Setembrino'
'IAC Catuiba'	'IAC 1153-5'	'Marli'	'IAC Sol do Vale'
'IAC Centenária'	'IAC 280-28'	'IAC Momo'	'IAC Somel'
'IAC Centenário'	'IAC 282-24'	'IAC Natal'	'Sunred'
'IAC Colibri'	'IAC 2982-24'	'IAC Néctar'	'Sunripe'
'IAC Colombina'	'IAC 2982-32'	'Okinawa'	'IAC Supermel'
'Coral'	'IAC 371-2'	'IAC Ouromel'	'IAC Talismã'
'IAC Cristal'	'IAC 651'	'IAC Ouromel-2'	'IAC Tropical-1'
'IAC Cristalino'	'IAC 680-177'	'IAC Ouromel-3'	'IAC Tropical-2'
'IAC Delícia'	'IAC 680-178'	'IAC Ouromel-4'	'IAC Tutu'

$$F = \frac{1 + F_A}{2} \qquad (01)$$

Where: F_A, inbreeding coefficient of the common ancestor. If the ancestor A is not inbred, the F_A is 0; If the common ancestor is inbred himself, the F_A must be estimated from his pedigree (Wright 1922).

$$\Theta_{xy} = \sum (1+ FA) \, \frac{1}{2}^{g_{ax} + g_{ay} + 1} \qquad (02)$$

Where: g_{ax} and g_{ay}, number of generations between the cultivars x and y, and the common ancestor a; F_A, inbreeding coefficient of the common ancestor.

These parameters were calculated using the R-software environment (R Core Team 2019), from the function 'kinship' counted in 'kinship2' package (Sinnwell et al. 2022), which uses linear mixed and mixed-effects Cox models of family data (Zhao 2006). As result, the package supplies a kinship matrix containing the inbreeding and coancestry coefficients of all individuals included into the input file. It is worth mentioning that 'kinship2' package algorithm assumes the founder cultivars as no inbreeding (Sinnwell et al. 2014, Sinnwell et al. 2022). The estimated inbreeding and coancestry coefficients were plotted in a heat map obtained by 'RColorBrewer' package (Neuwirth 2022), from R software (R Core Team 2019).

The genetic contribution (GC) of the founder cultivars was obtained according to Gauvin et al. (2015), in equation 03:

$$GC_{(s,a)} = \sum \frac{1}{2}^{g_p} \qquad (03)$$

Where: g_p, generations between the ancestor (a) and the cultivar (s) through all possible paths (p).

The genetic contribution of the founders was calculated using the R-software environment (R Core Team 2019), and the functions 'gen.genealogy' and 'gen.founder', counted in 'GENLIB' package (Gauvin et al. 2015, Houde et al. 2022). The 'GENLIB' package estimates the parameters based on the kinship and provides functions for genealogical analysis, including relatedness, inbreeding and genetic contribution of founders (Gauvin et al. 2015). The 'GENLIB' package was developed for human genealogical studies, which biologically do not admit self-fertilization. Therefore, only case II was considered in this part of the study.

RESULTS AND DISCUSSION

The pedigree data considered in this study was analyzed, reconstructing a genealogical depth of eight generations. Thirty-one cultivars were identified as founders of the IAC-Prunus germplasm (Table 2). The founder cultivars 'Waldo' and 'Rei da Conserva' had the highest genetic contribution (14.24 and 13.64%, respectively), along with 'Panamint' (7.97%), Lake City (5.83%) and 'Pérola de Itaquera' (5.37%). The genetic contribution of the remaining founders ranged from 1.23% to 4.45%. The genetic contribution of a founder cultivar represents how much the genome of this ancestor contributes to genetic constitution of its descendants, i.e., of the IAC-Prunus germplasm (Gauvin et al. 2015). The cultivars 'Okinawa' and 'Rei da Conserva' were identified as founders and cultivars of the IAC-Prunus germplasm simultaneously. The founder 'Waldo' participates in the genome of 47 cultivars of the IAC-Prunus germplasm, while the founder 'Rei da Conserva' participates in the genome of 43 (Figure 1). Regarding the other cultivars, they ranged from one ('Campinas-1' and 'Cristalino') to nine ('IAC 282-24') founders identified. The majority of the cultivars of IAC-Prunus germplasm (38.09%) have five founders identified (Figure 1).

Table 2. Founder cultivars and their genetic contributions (GC%) to IAC-Prunus germplasm. Jundiaí, SP, Brazil

Cultivar Founder	**GC** (%)	**Cultivar Founder**	**GC** (%)
'15 de novembro'	1.23	'NJN21'	4.29
'Abóbora'	1.23	'Okinawa'	4.29
'Aldrighi'	1.23	'Panamint'	7.97
'Amsdem'	1.23	'Peento'	1.84
'Cardeal'	1.23	'Perola de Itaquera'	5.37
'Delicioso'	1.23	'Precoce Rosado de Tatui'	1.84
'Fla 3-4N'	1.84	'Prelúdio'	1.23
'FlordaWon'	1.23	'Rei da Conserva'	13.64
'Gaudério'	1.23	'Rubi'	1.23
'Halford 2'	1.84	'Serrano'	1.23
'Hawaiian'	3.53	'Southland'	3.53
'Highland'	2.15	'Suber'	4.45
'IAC 159-4-A1'	1.23	'Sunlite'	1.84
'Interludio'	1.23	'Tos China'	4.29
'Lake City'	5.83	'Waldo'	14.24
'Merril Princess'	1.23		

Lansari et al. (1994) investigated the genetic relationship among almond cultivars. They found several rates of genetic contribution across germplasm from different countries. The first two almond cultivars from each country with the highest genetic contribution accounted for more than 50% of the total rate (Lansari et al. 1994). In a germplasm from the United States, these authors identified nine cultivars as founders, but just two ('Nonpareil' and 'Mission') were responsible for 37.9 and 30.2% of genetic contribution, respectively (Lansari et al. 1994). Also, according to Lansari et al. (1994) the high genetic contribution rates from a few founders suggested the intensive use of those founders and their progeny in breeding programs, which led to lack of genetic variability in almond cultivars (Lansari et al. 1994). Considering the investigation about peach and nectarine founder cultivars, the high number of founders and the diverse geographic origin of the cultivars resulted in a relatively high genetic variability for the IAC-Prunus germplasm. Furthermore, although peach is an autogamous species, the occurrence of homozygote lines is not expected. Worldwide, breeders use the hybridization between two desirable cultivars to establish progenies F_1 with high genetic variability (Raseira and Nakasu 2001).

The inbreeding coefficients of the IAC-Prunus germplasm were higher than expected in no inbreeding mating system in 40 cultivars for Case I and 14 cultivars for Case II. This led to F values higher than 0.50 (Table 3; Figure 2A and 2B). The results comparing the pollen origin in the open pollination mating system showed that 27 cultivars had higher F values in case I than in case II. Apart from the 'FlordaPrince', all other 26 cultivars could be considered as no inbreeding in case II. In fact, the F value for 'FlordaPrince' showed no difference between the two cases (Case I: 0.55; Case II: 0.54). Figure 3A shows the pedigree of 'FlordaPrince', highlighting that the inbreeding of this cultivar results from the cross between the progenies from 'Southland' and 'Hawaiian', which originated the 'Fla 9-10' and 'Fla 2-7' cultivars. This result suggests that the 'FlordaPrince' inbreeding is due to the cross between individuals closely related and not by unknown about the mating system.

The F coefficient is directly affected by the mating system and may be overestimated if the correct cross rates are not used (Arellano-Suarez et al. 2020). For instance, the values of this coefficient for the nectarines 'IAC Josefina' and 'IAC Karina' showed high numerical difference between case I (F = 0.88) and case II (F = 0.50). Figures 3B and 3C show the pedigree of 'IAC Josefina' and 'IAC Karina', respectively. It is possible to observe the high similarity between these two nectarine pedigrees, and the F measured in case I was probably overestimated because of the assumption of open pollination as self-pollination. Generally, the cultivars that showed high F values have to be used with caution in parental crosses in order to avoid the reduction of fitness due to the inbreeding depression (Charlesworth 2006).

The average values for the coancestry coefficients among the cultivars from IAC-Prunus germplasm remained low (Case I: $\theta_{xy} = 0.144$; Case II: $\theta_{xy} = 0.087$). Considering case I, 46.04% of the progenies showed no kinship ($\theta_{xy} = 0$), while in case II this rate was 51.35% (Figure 2A and 2B, respectively). The low coancestry coefficients indicate small probability

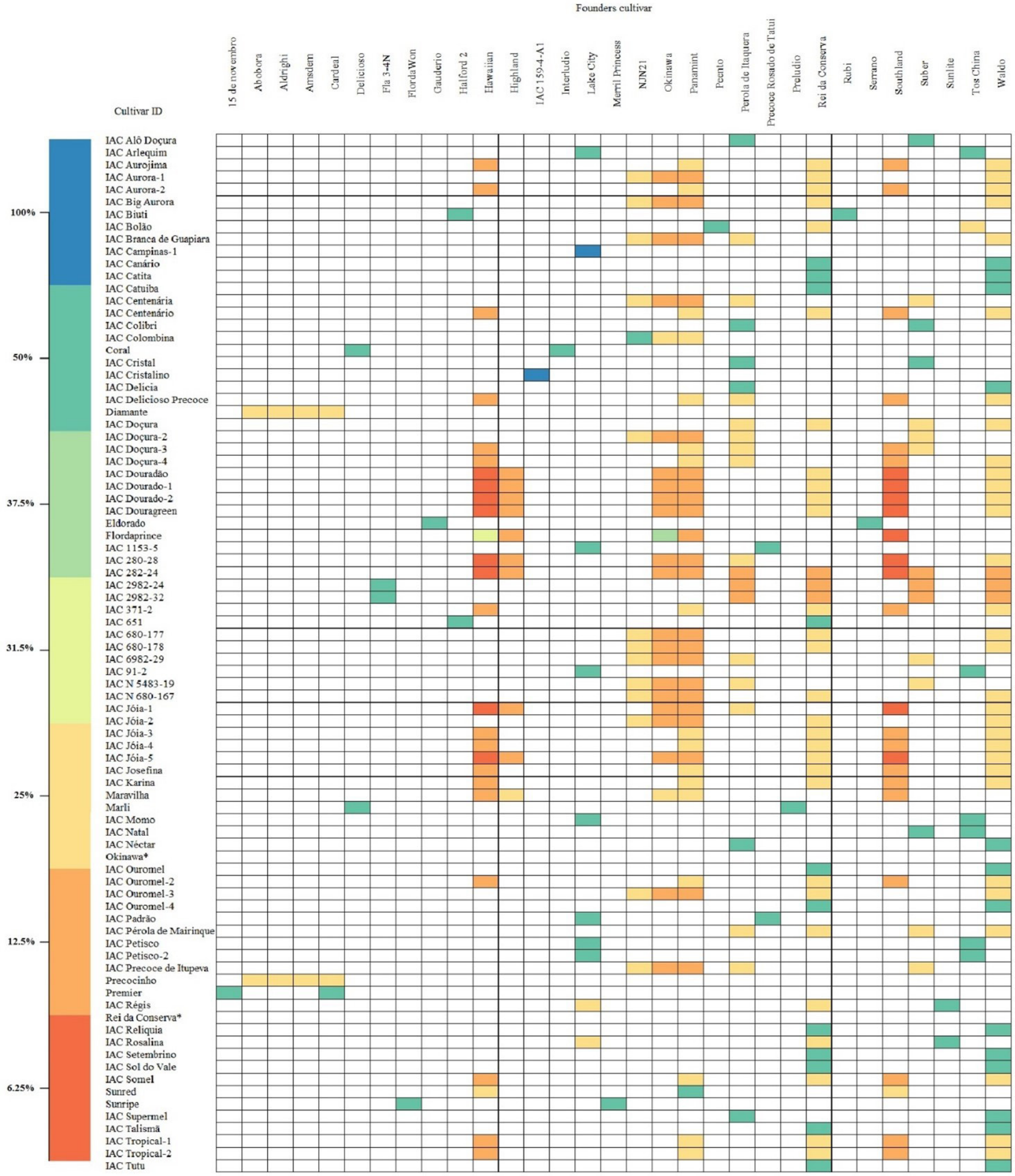

Figure 1. Genetic contribution (%) of the founders to the genome of 84 cultivars from IAC-Prunus germplasm. *Cultivars simultaneously listed as founder and current germplasm. The color gradient represents the increase of genetic contribution percentage: orange, lowest values; blue, highest values.

of two alleles being identical by descendent, when sampled randomly from independent individuals. This may reduce the probability of increase of homozygosity and the expression of recessive alleles (Charlesworth 2006).

The data showed that, under case I, 5.05% of the progenies were classified as half-sibs, 4.59% as full-sibs, and 1.29% as self-pollinated. The progeny from the cross between the cultivars ‘IAC Centenário’ x ‘IAC Karina’ (blue dot outside diagonal in Figure 2A) showed the highest coancestry value (θ_{xy} = 0.750). This may be explained by the fact that ‘IAC Karina’ cultivar was originated from open-pollination of ‘IAC Centenário’, whose parentage proves to be from open-

Table 3. Inbreeding coefficient (F) of cultivars from IAC-Prunus germplasm, considering the cultivars from open pollination as self-pollinated (Case I) and as outcrossing to unknow pollen donor (Case II)

Cultivar	**F**		**Cultivar**	**F**	
	Case I	**Case II**		**Case I**	**Case II**
‘IAC Alô Doçura’	0.75	0.75	‘IAC Delicioso Precoce’	0.50	0.50
‘IAC Arlequim’	0.50	0.50	‘Diamante’	0.50	0.50
‘IAC Aurojima’	0.75	0.50	‘IAC Doçura’	0.50	0.50
‘IAC Aurora-1’	0.75	0.50	‘IAC Doçura-2’	0.50	0.50
‘IAC Aurora-2’	0.75	0.50	‘IAC Doçura-3’	0.50	0.50
‘IAC Big Aurora’	0.75	0.50	‘IAC Doçura-4’	0.50	0.50
‘IAC Biuti’	0.50	0.50	‘IAC Douradão’	0.75	0.50
‘IAC Bolão’	0.50	0.50	‘IAC Dourado-1’	0.50	0.50
‘IAC Branca de Guapiara’	0.75	0.75	‘IAC Dourado-2’	0.50	0.50
‘IAC Campinas 1’	0.75	0.75	‘IAC Douragreen’	0.75	0.50
‘IAC Canário’	0.75	0.75	‘Eldorado’	0.50	0.50
‘IAC Catita’	0.75	0.75	‘Flordaprince’	0.55	0.54
‘IAC Catuiba’	0.75	0.75	‘IAC 1153-5’	0.50	0.50
‘IAC Centenária’	0.75	0.50	‘IAC 280-28’	0.75	0.50
‘IAC Centenário’	0.75	0.50	‘IAC 282-24’	0.50	0.50
‘IAC Colibri’	0.75	0.75	‘IAC 2982-24’	0.50	0.50
‘IAC Colombina’	0.50	0.50	‘IAC 2982-32’	0.50	0.50
‘Coral’	0.75	0.50	‘IAC 371-2’	0.50	0.50
‘IAC Cristal’	0.50	0.50	‘IAC 651’	0.50	0.50
‘IAC Cristalino’	0.75	0.75	‘IAC 680-177’	0.75	0.50
‘IAC Delícia’	0.50	0.50	‘IAC 680-178’	0.75	0.50
‘IAC 6982-29’	0.75	0.50	‘IAC Ouromel-4’	0.50	0.50
‘IAC 91-2’	0.50	0.50	‘IAC Padrão’	0.50	0.50
‘IAC N 5483-19’	0.75	0.50	‘IAC Pérola de Mairinque’	0.50	0.50
‘IAC N 680-167’	0.75	0.50	‘IAC Petisco’	0.50	0.50
‘IAC Jóia-1’	0.50	0.50	‘IAC Petisco-2’	0.50	0.50
‘IAC Jóia-2’	0.50	0.50	‘IAC Precoce de Itupeva’	0.75	0.75
‘IAC Jóia-3’	0.50	0.50	‘Premier’	0.75	0.50
‘IAC Jóia-4’	0.50	0.50	‘IAC Régis’	0.75	0.50
‘IAC Jóia-5’	0.50	0.50	‘IAC Rei da Conserva’	0.50	0.50
‘IAC Josefina’	0.88	0.50	‘IAC Relíquia’	0.50	0.50
‘IAC Karina’	0.88	0.50	‘IAC Rosalina’	0.75	0.50
‘Maravilha’	0.50	0.50	‘IAC Setembrino’	0.75	0.75
‘Marli’	0.50	0.50	‘IAC Sol do Vale’	0.75	0.75
‘IAC Momo’	0.50	0.50	‘IAC Somel’	0.75	0.50
‘IAC Natal’	0.75	0.50	‘Sunred’	0.75	0.50
‘IAC Néctar’	0.50	0.50	‘Sunripe’	0.50	0.50
‘Okinawa’	0.50	0.50	‘IAC Supermel’	0.75	0.75
‘IAC Ouromel’	0.75	0.75	‘IAC Talismã’	0.50	0.50
‘Precocinho’	0.75	0.50	‘IAC Tropical 1’	0.75	0.50
‘IAC Ouromel-2’	0.50	0.50	‘IAC Tropical 2’	0.75	0.50
‘IAC Ouromel-3’	0.50	0.50	‘IAC Tutu’	0.50	0.50

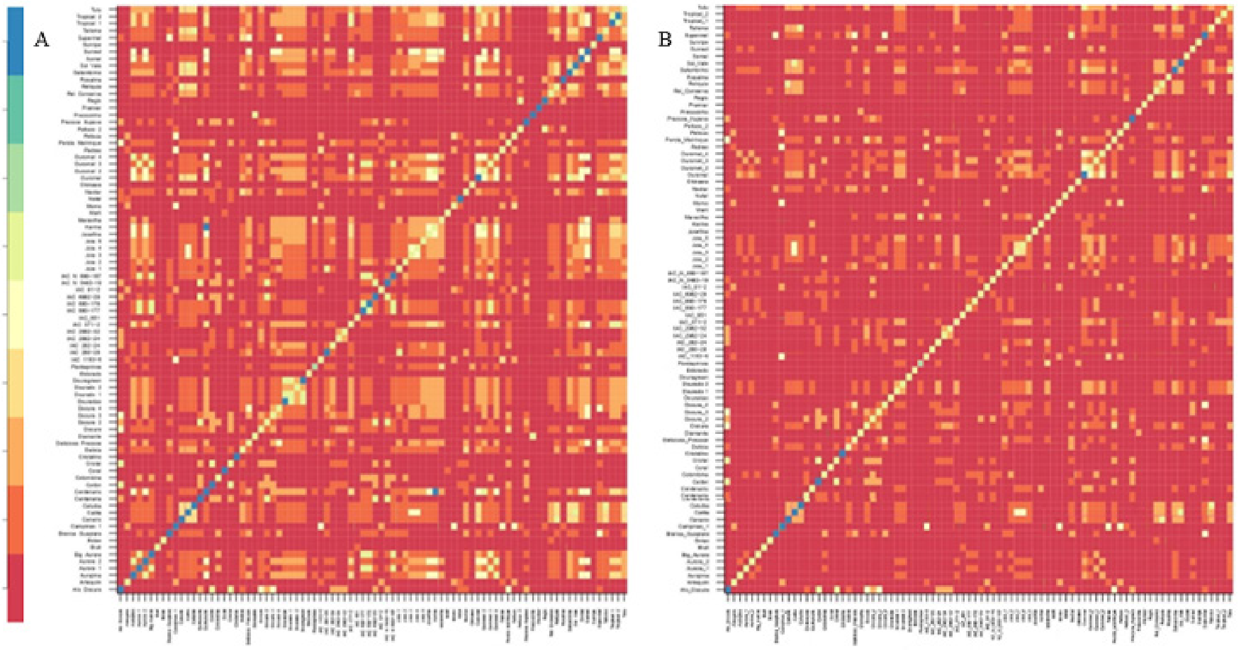

Figure 2. Inbreeding (values in the ascending diagonal line - F) and coancestry coefficients (values out of the ascending diagonal line - θ) of 84 cultivars from IAC-Prunus germplasm, according to pedigree information: (A) considering the cultivars from open pollination as self-pollinated (Case I), and (B) considering the cultivars from open pollination as outcrossing to unknow pollen donor (Case II). The color gradient represents the increase of coefficients values: red, lowest values; blue, highest values.

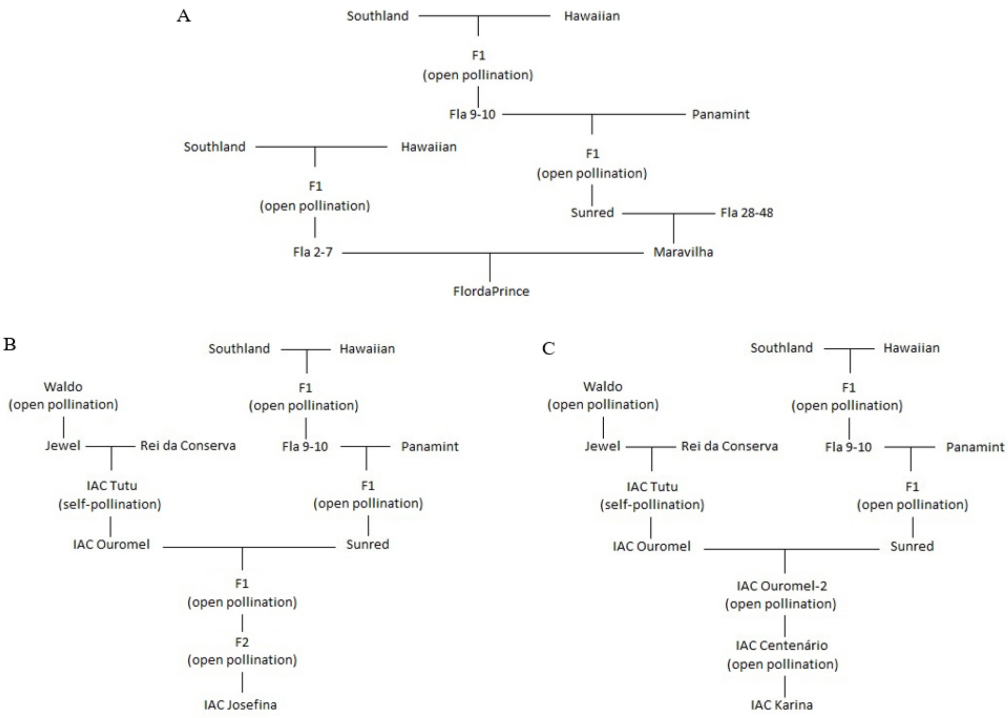

Figure 3. Pedigree of 'FlordaPrince' (A), 'IAC Josefina' (B) and 'IAC Karina' (C) cultivars.

pollination of ‘IAC Ouromel-2’ (Figure 3C). Regarding case II, the rates of progenies with coancestry coefficient equal to 0.500 fall to 0.29%, while the rate of full-sibs (4.10%) remains similar to that in case I. The percentage of half-sib progenies increased to 8.63%.

The comparison between cases I and II emphasizes the importance of the correct mating system notation used in the hybridizations to estimate the inbreeding and coancestry coefficients, since these parameters are involved into other genetics parameters, such as heritability. For instance, narrow-sense heritability is the ratio between additive and phenotypic variance, and the additive variance tends to be low in high inbreeding coefficient, mainly in small populations (Reis et al. 2009).

Monet and Bassi (2008) presented a list of qualitative traits and their inheritance. However, the most significant economic traits in peaches and nectarines are polygenic with quantitative inheritance (Monet and Bassi 2008), turning the estimate of heritability into a key issue for advances in breeding programs. Some quantitative traits showed low to medium heritability, such as: soluble solids (h^2: 0.01), firmness (h^2: 0.13), acidity (h^2: 0.19), fruit length (h^2: 0.31) (Hansche et al. 1972) and fruit weight (h^2: 0.32) (Raseira and Franzon 2014). Nunes et al. (2008) investigated the influence of pedigree matrix inclusion in the selection, testing by simulated data and different heritability. These authors found more accurate estimate from the model that includes parentage among progenies than from models without this information. These results indicate that genealogy should be taken into account, especially when the estimate of heritability is low to medium, i.e., $h^2 < 0.50$ (Nunes et al. 2008). Thus, considering the peach and nectarine heritability cited above, the use of kinship coefficients in breeding program may lead to more accurate estimates of the parameters involved in genetic selection, even overcoming the challenge of selecting genetically divergent parents, but with favorable agronomic characteristics.

CONCLUSION

The large number of founder cultivars identified in the IAC-Prunus germplasm (31 cultivars) provided the genetic diversity of this germplasm.

The inbreeding from identity by descent was more frequent in case I (40 cultivars) than in case II (14 cultivars). This highlights the importance of the correct identification of mating system in the open pollinations for accurate estimation of genetic parameters.

The genetic variability among cultivars from the IAC-Prunus germplasm, measured by the coancestry coefficients, allows the use of these cultivars as genetically divergent parents. However, the use of related cultivars in the crosses must be avoided.

The matrix of kinship produced by the pedigree analyses is a tool that can provide accurate estimates of peach and nectarine heritability. This statement particularly holds for heritability with low to medium magnitude.

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