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Novel approaches for selection of *Coffea canephora* by correlation analysis

H.D. Vieira[1], A. Ferreira[2], F.L. Partelli[2] and A.P. Viana[3]

[1] Universidade Estadual do Norte Fluminense Darcy Ribeiro, Laboratório de Fitotecnia, Campos dos Goytacazes, RJ, Brasil
[2] Universidade Federal do Espírito Santo, Campus São Mateus, São Mateus, ES, Brasil
3 Universidade Estadual do Norte Fluminense Darcy Ribeiro, Laboratório de Melhoramento Genético Vegetal, Campos dos Goytacazes, RJ, Brasil

Corresponding author: A.P. Viana
E-mail: pirapora@uenf.br

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ABSTRACT. The objective of this study was to investigate, using path analysis, the genotypic correlations of primary and secondary production components as well as their decomposition into direct and indirect effects on the yield of coffee crops subjected to programed cycle pruning (PCP). Twenty-two Conilon coffe genotypes belonging to the breeding program developed by Incaper were subjected to PCP and 17 morpho-agronomic traits were measured in new branches. The traits plagiotropic branch length and number of plagiotropic *leaves* were discarded to eliminate collinearity problems. Path analysis was efficient in identifying the traits with greatest influence on yield. The most important traits linked to yield were number of orthotropic branches and orthotropic branch dry matter, while the secondary traits were orthotropic branch diameter, orthotropic internode length, and length of the plagiotropic branch internode. To increase coffee crop yield, producers should select genotypes that produce an intermediate number of orthotropic branches, which have a higher dry matter yield. Subsequently, they should select genotypes with larger orthotropic branch diameters, and among these, those which have shorter orthotropic and plagiotropic internode lengths.

Key words: Coffee; Genotypes; Programed cycle pruning; Growth variables

INTRODUCTION

The genus *Coffea* comprises at least 124 species, according to Davis et al. (2011). *Coffea arabica* and *Coffea canephora* are the most widely used species for commercial production, accounting for approximately 58 and 42%, respectively, of the 8.8 million tons produced in 2016 in the world (ICO, 2018).

Coffea canephora, also known as Conilon coffee, is a self-sterile diploid plant that is allogamous due to gametophytic self-incompatibility. Vegetatively propagated plants retain the traits inherited from the mother plant, which ensures uniform development of the crop, greater productivity, better fruit quality, and the possibility of producing varieties with a differentiated maturation cycle (Partelli et al., 2014a). The use of new technologies such as programed cycle pruning, coupled with others previously applied in Conilon coffee, have considerably increased the yield of coffee crops (Verdim Filho et al., 2014; Covre et al., 2015; Martins et al., 2017).

Differences in morpho-physiology and productivity between Conilon coffee clones indicate the existence of genetic variability (Fonseca et al., 2006, Dalcomo et al., 2015) in the production phase, in the fruit maturation time, as well as in leaf patterns (Gomes et al., 2016) and in nutrient absorption and allocation across materials (Partelli et al., 2014b; Marré et al., 2015).

Studies on the growth and development of Conilon coffee have identified superior genotypes for number of leaves, plant height, rate of plagiotropic branch production, root, stem, and shoot dry matter, and nutrient accumulation (Covre et al., 2013; Marré et al., 2015). Some experiments with coffee have also shown variations between clones regarding their nutrient utilization efficiency (Tomaz et al., 2009).

To better understand the association between traits, Wright (1921) proposed 'path analysis, a methodology that allows for unfolding genotypic correlations into direct and indirect effects of the explanatory variables on a main trait by standardizing variables and regression equations. As such, the technique provides a measure of the influence of each cause and its effect.

When the selection process involves many traits, some of the independent variables may show a certain degree of interrelationship, characterizing multicollinearity (Ferreira et al., 2005). Some of the effects of elevated multicollinearity are unstable regression coefficient estimates, overestimated direct effects of explanatory variables on the main variables, and simple correlation coefficient estimates above unity, which may lead to wrong results and misinterpretations (Cruz et al., 2004). Path analysis has been widely used in the breeding of several crops. However, no studies of this nature have been found involving Conilon coffee crops under programed cycle pruning.

Producers seek superior genotypes and increased sustainability. Therefore, studies focusing on the evaluation of genotypes that identify superior individuals in various management and environmental conditions, mainly under programed cycle pruning, are important to increase yields and consequently the profitability and sustainability of coffee growing.

Given the above-described scenario and the lack of research involving the growth of new branches of Conilon coffee after pruning, we examined the viability of using path analysis to evaluate the genotypic correlations of primary and secondary production components and their direct and indirect effects on the yield of Conilon coffee genotypes after programed cycle pruning.

MATERIAL AND METHODS

The study was conducted in Cachoeiro do Itapemirim, ES, Brazil. The crop was planted in June 2005, in a randomized block design with 55 treatments (genotypes of *C. canephora* var. Conilon) and four replicates. Each plot consisted of a five-plant row with 3.0 × 1.2 m spacing, where the second and fourth plants were considered the usable plot.

The study involved 51 genotypes originating from a phenotypic selection of mother plants from farms in the Castelo region in southern Espírito Santo state, Brazil (herein called "Castelo Evaluation Group"), three genotypes belonging to cultivar Incaper 8142 (Conilon Vitória), and one seed-propagated cultivar (Emcaper 8151 - Robusta Tropical).

After the fourth harvest (September 2010), all plants were subjected to programed cycle pruning (PCP) (Verdim Filho et al., 2014), after which five orthotropic stems were maintained. Plagiotropic branches on those stems that had produced grains in over 50% of their rosettes were removed.

Of all genotypes, the following 22 were selected for the study: the 18 most promising clones belonging to the Castelo Evaluation Group (AC02, AC03, AC12, AC13, AC22, AC24, AC26, AC27, AC28, AC29, AC30, AC35, AC36, AC37, AC39, AC40, AC43, and AC46), three genotypes belonging to cultivar Conilon Vitória (12V - early; 02V - medium; and 13V - late), and cultivar Robusta Tropical. In the selection of clones from the Castelo Evaluation Group, the most productive of the four harvests (2007, 2008, 2009, and 2010) were chosen, provided that they had good vigor, tolerance to rust, and grains with a good size and uniform maturation.

The following traits were evaluated in the branches produced after PCP, in the 2010/2011 crop year: 1) number of orthotropic branches produced per plant (NOB), obtained from a monthly and cumulative count of the new branches produced (length equal to or greater than 10 cm), maintaining five new branches in each plant to originate the new crown and removing the others; 2) dry matter of eliminated orthotropic branches (ODM), obtained from a monthly and cumulative count after oven-drying at 65ºC for 72 h; 3) length of new orthotropic branches (OBL), obtained as the distance between the insertions of the five new branches and with old ones and their apical meristems (cm); 4) diameter of new orthotropic branches (OBD), determined by taking a standardized measurement in the central region of the second internode of each of the five branches (mm); 5) number of orthotropic branch nodes (NON), determined from a direct count on each of the five new branches; 6) average orthotropic internode length (OIL), determined as the ratio between the length of new orthotropic branches (OBL) and their respective number of nodes (NON); 7) number of new plagiotropic branches produced (NPB), obtained from a direct count on each of the five new orthotropic branches; 8) average plagiotropic branch length (PBL), measured on two selected branches per plant, one on each side of the planting row, obtained as the distance between the insertion of these branches on the orthotropic branches and their apical meristem; 9) number of plagiotropic nodes (NPN), obtained from a direct count on the selected branches; 10) number of leaves produced from plagiotropic branches (NLP), obtained from a monthly and cumulative count on the branches mentioned in item 8; 11) plagiotropic internode length (PIL), obtained as the ratio between branch length (PBL) and number of nodes (NPN) of the selected plagiotropic branches (cm); 12) largest crown-base diameter (CBD), measured in the transverse direction of the planting row, whose limit is the projection of the longest branches (cm); 13) percentage of flowering rosettes on plagiotropic branches (%FR), obtained as the ratio between number of rosettes that produced flowers and the number of plagiotropic nodes (NPN), counted directly on the selected branches; 14) number of flowers produced by rosettes (FP/RF), obtained from a direct and cumulative count, at each flowering event, on the selected branches; 15) number of remaining fruits per rosette (RF/FR), obtained from a direct count, 30 days after the last flowering event, on the selected branches; 16) flower development rate (%DEV), determined as the ratio between the number of flowers produced per rosette (FP/FR) and the number of remaining fruits per rosette (RF/FR), on the selected branches, 30 days after the last flowering event; 17) number of remaining fruits per branch (RF/BR), determined as the product between number of remaining fruits per rosette (RF/FR) and the number of rosettes that produced flowers per branch; and 18) yield of processed grains (YLD), obtained after harvesting and processing the fruits that were present on the two orthotropic branches that were not eliminated during programed cycle pruning (number of 60 kg bags ha^{-1}).

Growth traits were evaluated monthly until September 2011. However, for the analyses, accumulated values were used for the traits NOB, ODM, OBL, OBD, NON, NPB, PBL, NPN, NLP, and CBD; and mean values were used for OIL and PIL. The yield-related traits %FR and FP/FR were analyzed after each major flowering event, which occurred on 08/24, 09/07, 09/17, 10/05, and 10/29/2011, and the accumulated values were used in the analyses. The traits FP/FR, %DEV, and RF/FR were evaluated 30 days after the last major flowering event, on 11/29/2011. Fruits were harvested per clone, according to the maturation time, starting in May and ending in August 2011. The ripe coffee harvested from each plot was weighed and samples were sent for drying, processing, calculation of yield, and transformation into 60-kg bags ha^{-1}.

The matrix of genetic correlations between the evaluated morpho-agronomic traits was constructed using GENES computer software (Cruz, 2013). In the case of evidence of collinearity between traits (elevated degree of interrelationship), a multicollinearity diagnostic was performed, involving an analysis of the eigenvalues of the genetic correlation matrix, in order to identify the nature of the existing linear dependence between the traits and detect which contribute to the appearance of multicollinearity. When necessary, some of the traits were discarded; among those considered redundant, we opted for maintaining those which provided a greater contribution to the explanation of yield.

Next, a two-chain path analysis was carried out with the yield obtained from the 2011 harvest (YLD) as the main dependent variable; NOB, ODM, OBL, %FR, RF/FR, and RF/BR as the primary explanatory variables; and PBL, CBD, OBD, NON, NPB, NPN, NLP, OIL, PIL, FP/FR, and %DEV as the second explanatory variables. The unfolding of genetic correlations between the primary and secondary explanatory variables into direct and indirect effects on the *yield* trait was used to explain the obtained results.

RESULTS

The separation of the measured traits into primary and secondary for the coffee-growing activity in the first year after pruning took into consideration agronomic criteria and trends observed in the field. The traits percentage of flowering rosettes (%FR), number of fruits per flowering rosette (RF/FR), and number of fruits per branch (RF/BR) were included in the first group, as they were measured in a period during which the systems of internal (autonomous) and external (environment-sensitive) control had already manifested and had been defined as a great part of the success or lack thereof in coffee crop yield. Plant height, which in our study is represented by the length of orthotropic branches (OBL), was included in the main group, because it was mentioned as one of the phenotypic traits most highly correlated with yield in *C. canephora* (Fonseca et al., 2007), as in *C. arabica* (Martinez et al., 2007).

The ability to produce new branches (NOB) is also related to yield in the coffee crop (Fonseca et al., 2007), and because these new branches grow concomitantly with the flowering and development of the grains produced on the branches that were not eliminated during the pruning cycle, we chose to include the NOB trait. Further, in view of the discovery that the number of these new produced branches (NOB) is not directly proportional to the dry matter produced (ODM), the latter trait was also included in the primary group for the yield of Conilon coffee after pruning.

An analysis of the matrix of genetic correlations between the measured variables (Table 1) revealed that several traits were strongly linked. Correlations greater than 0.80 were found between NOB and ODM , CBD and OBL, PBL and OBD, PBL and OBL, PBL and CBD, NPN and NLP, and RF/FR and RF/BR.

TABLE 1. Estimation of genotypic correlation coefficients among 17 agronomic and morphological characters evaluated in *Coffea canephora*, after programed cycle pruning.

	ODM	OBL	PBL	CBD	OBD	NON	NPB	NPN	NLP	OIL	PIL	%FR	FP/FR	FR/RF	%DEV	FR/BR
NOB	0.83	-0.22	-0.25	-0.04	-0.11	0.66	0.26	0.14	0.13	-0.47	-0.39	-0.32	-0.42	-0.28	0.02	-0.24
ODM		-0.04	0.05	0.20	0.17	0.57	0.28	0.15	0.18	-0.34	-0.06	0.02	-0.24	-0.20	-0.06	-0.11
OBL			0.85	0.81	0.70	-0.11	0.28	0.29	0.25	0.77	0.74	0.43	0.18	0.18	0.02	0.29
PBL				0.88	0.80	-0.06	0.27	0.53	0.48	0.63	0.68	0.48	0.06	-0.01	-0.10	0.22
CBD					0.80	0.09	0.32	0.43	0.37	0.55	0.63	0.35	-0.02	-0.05	-0.06	0.15
OBD						0.06	0.55	0.39	0.36	0.45	0.59	0.57	0.19	0.17	0.07	0.35
NON							0.48	0.37	0.43	-0.68	-0.37	0.00	-0.34	-0.14	0.20	0.08
NPB								0.55	0.63	-0.16	-0.15	0.10	-0.18	-0.04	0.15	0.18
NPN									0.97	-0.01	-0.25	0.10	-0.32	-0.23	0.01	0.13
NLP										-0.12	-0.28	0.13	-0.30	-0.18	0.07	0.19
OIL											0.73	0.26	0.30	0.18	-0.12	0.11
PIL												0.49	0.37	0.21	-0.13	0.17
%FR													0.63	0.62	0.30	0.74
FP/FR														0.77	0.10	0.67
RF/BR															0.70	0.92
%DEV																0.70

OIL - average orthotropic internode length. PIL - plagiotropic internode length. OBL - length of new orthotropic branches. PBL - average plagiotropic branch length .CBD - largest crown-base diameter. OBD - diameter of new orthotropic branches. FP/FR - number of flowers produced per rosette. FR/BR - number of remaining fruits per branch. RF/FR - number of remaining fruits per rosette. ODM - dry matter of eliminated orthotropic branches. NLP - number of leaves produced from plagiotropic branches.NON - number of orthotropic branch nodes .NPN - number of plagiotropic branch nodes .NOB - number of orthotropic branches. NPB - number of new plagiotropic branches produced. PCP - programed cycle pruning. YLD - yield of processed grains. %FR - percentage of flowering rosettes on plagiotropic branches. %DEV – development.

Although some values led to the suspicion of collinearity in the group of traits considered primary for yield (NOB, ODM, OBL, %FR, RF/FR, and RF/BR), the diagnostic showed that the traits exhibited weak collinearity, with a condition number (CN) equal to 48.95 and a matrix determinant of 0.0088, which does not generate difficulties for path analysis. For the group considered secondary (PBL, CBD, OBD, NON, NPB, NPN, NLP, OIL, PIL, FP/FR, and %DEV), the diagnostic revealed strong collinearity, with an NC of 2,663.5 and a matrix determinant of 0.0 (zero). According to Cruz et al. (2004), in these cases, measures should be adopted to overcome their adverse effects, one of the most widely employed of which is the elimination of some problem variables from the regression model.

After the traits PBL and NLP were excluded, the multicollinearity diagnostic receded from the *severe* to the *weak* category, with a matrix determinant of 0.0084 and CN equal to 47.34, no longer posing difficulties for path analysis. The PBL variable was chosen to be discarded due to the number of times it appeared (three times), indicating suspicion of collinearity. The NLP trait, which has a high correlation (0.97) with NPN, was discarded due to redundancy of results. Despite their discard, the performance of these two traits can be inferred by using estimates obtained though interrelated traits, which were maintained in the path analysis. Afterwards, the correlation coefficients between selected variables were decomposed into their diverse effects.

In the path analysis, the traits selected as primary showed a genotypic determination coefficient (R^2) for the coffee yield of 0.7555, which was much higher than the residual effect (0.4945), indicating that their choice was efficient to explain the yield of the 22 coffee genotypes in the 2011 crop (Table 2). Traits with high positive correlations with the basic variables and with a direct effect in a positive direction indicate cause-effect; i.e., the auxiliary trait is the main factor causing alterations in the basic variable (Silva et al., 2010). This suggests that although the correlation is an association between two variables in a given experimental condition, its decomposition is dependent on the set of traits evaluated, and the management conditions in this study affect these associations. For the NOB trait, the finding of an elevated value with a negative sign (–0.951) implies correlation of traits in the opposite direction, where an increase in one corresponds to a reduction in the other. The opposite phenomenon occurs for the ODM trait, in which a high positive value (1.000) supports the hypothesis of a true association with YLD. Elevated correlations, negative for NOB and positive for ODM, also explain the finding of negative genetic correlations between the two traits. For the management and selection of the genotypes that most contributed to the measure evaluated (pruning management), it is important to identify traits highly correlated with the basic variable, these being those with the greatest direct effect in the direction favorable to the management situation presented, so that the inferences point to the selection of genotypes with greater productive potential when subjected to programed cycle pruning.

The much lower total phenotypic correlation coefficients for both NOB (–0.179), and ODM (0.230) indicate that the selection pressure intensified on one of the traits might not provide satisfactory genetic gains in YLD, since this genetic correlation is caused mainly by indirect effects. The direct negative effects of NOB on YLD are indirectly reduced via the ODM contribution (0.879), and the positive effects of ODM on YLD are indirectly reduced via NOB (–0.785).

TABLE 2. Estimates of the direct and indirect effects of the primary explanatory variables on the basic productivity variable of *Coffea canephora* (YLD) after programed cycle pruning.

	NOB	ODM	OBL	%DEV	RF/FR	FR/BR
Direct whit YLD	-0.951	1.000	-0.269	0.213	0.155	0.244
Indirect via NOB		-0.785	0.204	0.302	0.268	0.229
via ODM	0.879		-0.042	0.019	-0.214	-0.119
via OBL	0.058	0.011		-0.115	-0.047	-0.079
via %DEV	-0.068	0.004	0.092		0.133	0.158
via RF/FR	-0.044	-0.031	0.027	0.096		0.142
via FR/BR	-0.059	-0.028	0.072	0.180	0.223	
Total	-0.179	0.230	0.085	0.695	0.517	0.574
R²	0.759					
Residual effect	0.491					

NOB - number of orthotropic branches .OBL - length of new orthotropic branches. FR/BR - number of remaining fruits per branch. RF/FR - number of remaining fruits per rosette. ODM - dry matter of eliminated orthotropic branches. YLD - yield of processed grains. %DEV - development.

Thus, indirect selection through the NOB variable will only be efficient in increasing YLD if the indirect effects are concomitantly considered via ODM. Consequently, to obtain a greater increase in YLD, a selective and restricted scheme should be implemented to take advantage of the direct and desirable effects of the ODM trait on yield (YLD) while eliminating the indirect and undesirable effects of the NOB variable. In other words, among the individuals producing a moderate number of orthotropic branches after pruning, those with more vigorous branches and with a higher dry matter yield should be selected. Additionally, the fact that we are evaluating several quantitative traits that are under the control of several genes with various interactions and under environmental influence may generate a number of alterations in the population. In this case, path analysis highlights the true cause-effect relationships, which helps to interpret these results and properly directs the selection of new genotypes under differentiated conditions that respond to new management settings.

The traits OBL, %FR, RF/FR, and RF/BR had low correlations (–0.269, 0.213, 0.155, and 0.244, respectively) with the basic variable YLD, demonstrating a lack of a cause-effect relationship. Therefore, they are not indicated for direct selection. Because they also showed low values of indirect contributions (highest value equal to 0.302), the above-mentioned traits are also not indicated for indirect selection aiming at increases in YLD.

The OBL variable showed a practically null correlation (0.085) and a low-magnitude negative direct effect (–0.269) on the basic trait YLD. The hypothesis of replacing this trait with another of greater contribution was tested (data not shown); however, in its absence, path analysis displayed genotypic determination coefficients (R^2) much lower than the residual effect, in addition to very elevated estimates for direct and indirect effects (much higher than 1 and much lower than –1). This demonstrates that orthotropic branch length works as a point of balance between the other traits taken as primary.

In the traits selected as secondary, path analysis showed a genotypic determination coefficient of 0.6429, which is higher than the residual effect (0.5976). This indicates that the yields of the 22 coffee genotypes in the 2011 harvest are more closely related to the afore-mentioned traits than to uncontrolled environmental factors (Table 3).

The highest direct and true associations with the yield of the coffee genotypes were obtained via OBD (0.678) and PIL (0.521) rather than via OIL (–0.870). The fact that the total phenotypic correlation coefficients were much lower, (OBD = 0.391, PIL = 0.275, and

OIL = –0.036) indicates that selection pressure intensified directly on those traits may not lead to satisfactory genetic gains in YLD, since the elevated genetic correlation values are mainly a consequence of indirect effects.

TABLE 3. Estimates of the direct and indirect effects of the secondary explanatory variables on the basic variable. Productivity of *Coffea canephora* (YLD). After programed cycle pruning.

	CBD	OBD	NON	NPB	NPN	OIL	PIL	FP/FR	%DEV
Direct whit YLD	-0.280	0.678	-0.226	-0.351	0.350	-0.870	0.521	0.403	0.230
Indirect via CBD		-0.223	-0.026	-0.089	-0.121	-0.153	-0.177	0.006	0.016
via OBD	0.541		0.042	0.370	0.266	0.307	0.397	0.129	0.047
via NON	-0.021	-0.014		-0.107	-0.084	0.152	0.084	0.076	-0.046
via NPB	-0.112	-0.192	-0.167		-0.193	0.057	0.051	0.064	-0.051
via NPN	0.152	0.137	0.131	0.193		-0.004	-0.088	-0.110	0.004
via OIL	-0.476	-0.394	0.587	0.141	0.010		-0.632	-0.265	0.103
via PIL	0.329	0.305	-0.194	-0.076	-0.131	0.379		0.193	-0.069
via FP/FR	-0.008	0.077	-0.136	-0.074	-0.127	0.123	0.149		0.042
via %DEV	-0.013	0.016	0.046	0.034	0.003	-0.027	-0.031	0.024	
Total	0.113	0.391	0.058	0.041	-0.029	-0.036	0.275	0.520	0.276
R^2	0.643								
Residual effect	0.598								

OIL - average orthotropic internode length. PIL - plagiotropic internode length. CBD - largest crown-base diameter. OBD - diameter of new orthotropic branches. FP/FR - number of flowers produced per rosette. NON - number of orthotropic branch nodes .NPN - number of plagiotropic branch nodes. NPB - number of new plagiotropic branches produced. YLD - yield of processed grains. %DEV - development.

In the OBD trait, the reduction of the phenotypic correlation coefficient from 0.678 (direct) to 0.391 (total) can be explained by the indirect and negative effects of OIL on YLD (–0.394). The decline in PIL from 0.521 to 0.275 can also be attributed to the indirect effects of the OIL trait, which in this case were negative (–0.632). Further, OIL also had its direct and negative influence on YLD reduced from –0.870 to –0.036, through indirect and positive contributions from the traits PIL (0.379) and OBD (0.307).

Therefore, to obtain a higher increase in YLD based only on the secondary traits of greater direct contribution (OBD, OIL, and PIL), a selective and restricted scheme should be applied by selecting the individuals with the lowest OIL among those with orthotropic branches of largest diameter after programed cycle pruning, followed by those with the lowest PIL. Another interesting situation is that in which the auxiliary variable shows low association with the main trait, but its direct effect has a high magnitude. This suggests that the auxiliary variable should not be discarded in indirect selections, since simultaneous selection practices can be adopted with satisfactory gains for many variables.

The phenotypic correlation coefficient for number of flowers per flowering rosette (FP/FR) rose from 0.403 (direct) to 0.530 (total), showing that intensified selection directly on this trait can provide satisfactory genetic gains in YLD, since the direct gain, which is already acceptable, is intensified by the positive values obtained in the balance of indirect effects.

In the comparison of the estimates of direct and indirect effects of the nine secondary variables on the six primary variables (Table 4), path analysis revealed higher genotypic determination coefficients than the residual effects for the primary traits NOB, OBL, %FR, RF/FR, and RF/BR, indicating that the values obtained in the measurements of the coffee genotypes are more closely related to secondary traits than to uncontrolled environmental factors. This was not true for the ODM trait, whose R^2 was only 0.422 and the effect of the residual variable was 0.760, indicating that the secondary explanatory variables used do not explain most of the variation in the primary variable ODM.

TABLE 4. Estimates of the direct and indirect effects of the nine secondary variables on the six primary variables of *Coffea canephora* genotypes after programed cycle pruning.

Effect	**NOB**	**ODM**	**OBL**	**%FR**	**FP/FR**	**FR/BR**
Trait DPR						
Direct	0.026	0.143	0.001	-0.368	-0.058	-0.029
Indirect via OBD	0.261	0.260	-0.331	0.261	-0.104	-0.137
via NON	0.096	0.051	0.044	0.006	0.001	0.001
via NPB	-0.037	-0.031	0.121	-0.060	0.024	0.024
via NPN	-0.255	-0.107	0.109	0.247	0.020	0.206
via OIL	0.362	-0.074	0.479	-0.197	0.024	-0.098
via PIL	-0.507	-0.059	0.391	0.490	0.094	0.233
via FP/FR	0.005	0.002	-0.001	-0.010	-0.014	-0.014
via %DEV	0.011	0.011	-0.004	-0.015	-0.037	-0.037
TOTAL	-0.039	0.197	0.809	0.353	-0.049	0.149
Trait ODB						
Direct	0.327	0.326	-0.415	0.328	-0.130	-0.172
Indirect via DOR	0.021	0.114	0.001	-0.294	-0.046	-0.023
via NON	0.064	0.034	0.029	0.004	0.001	0.000
via NPB	-0.064	-0.053	0.208	-0.103	0.042	0.042
via NPN	-0.230	-0.096	0.099	0.223	0.018	0.186
via OIL	0.300	-0.062	0.398	-0.164	0.020	-0.081
via PIL	-0.470	-0.055	0.363	0.455	0.087	0.216
via FP/FR	-0.044	-0.023	0.013	0.099	0.132	0.137
via %DEV	-0.013	-0.013	0.005	0.019	0.045	0.045
TOTAL	-0.109	0.173	0.700	0.566	0.168	0.350
Trait NON						
Direct	1.022	0.545	0.468	0.059	0.010	0.007
Indirect via CDB	0.002	0.013	0.000	-0.035	-0.005	0.003
via OBD	0.021	0.020	-0.026	0.021	-0.008	-0.011
via NPB	-0.055	-0.046	0.181	-0.090	0.037	0.036
via NPN	-0.219	-0.092	0.094	0.212	0.017	0.177
via OIL	-0.447	0.092	-0.592	0.244	-0.029	0.121
via PIL	0.298	0.035	-0.230	-0.289	-0.055	-0.137
via FP/FR	0.078	0.040	-0.023	-0.176	-0.234	-0.242
via %DEV	-0.038	-0.038	0.015	0.054	0.131	0.131
TOTAL	0.662	0.570	-0.113	0.001	-0.138	0.079
Trait NPB						
Direct	-0.116	-0.096	0.380	-0.189	0.077	0.076
Indirect via CDB	0.008	0.046	0.000	-0.117	-0.018	-0.009
via ODB	0.179	0.178	-0.226	0.179	-0.071	-0.094
via NON	0.487	0.260	0.223	0.028	0.005	0.003
via NPN	-0.323	-0.135	0.139	0.313	0.025	0.260
via OIL	-0.107	0.022	-0.142	0.058	-0.007	0.029
via PIL	0.117	0.014	-0.090	-0.113	-0.022	-0.054
via FP/FR	0.042	0.022	-0.012	-0.095	-0.126	-0.131
via %DEV	-0.028	-0.028	0.011	0.040	0.095	0.095
TOTAL	0.259	0.281	0.282	0.103	-0.043	0.177
Trait NPN						
Direct	-0.588	-0.246	0.252	0.568	0.046	0.473
Indirect via CDB	0.011	0.062	0.001	-0.160	-0.025	-0.012
via ODB	0.128	0.128	-0.163	0.128	-0.051	-0.067
via NPB	0.382	0.204	0.175	0.022	0.004	0.003
via NRP	-0.064	-0.053	0.209	-0.104	0.042	0.042
via OIL	-0.007	0.002	-0.010	0.004	-0.001	0.002
via PIL	0.202	0.024	-0.156	-0.196	-0.038	-0.093
via FP/FR	0.072	0.037	-0.021	-0.164	-0.218	-0.225
via %DEV	-0.002	-0.002	0.001	0.003	0.007	0.007
TOTAL	0.135	0.155	0.287	0.102	-0.233	0.129
Trait CEO						
Direct	0.661	-0.136	0.877	-0.361	0.043	-0.179
Indirect via CDB	0.014	0.078	0.001	-0.201	-0.032	-0.016
via OBD	0.148	0.148	-0.188	0.149	-0.059	-0.078
via NON	-0.690	-0.368	-0.316	-0.040	-0.007	-0.005
via NPB	0.019	0.016	-0.061	0.031	-0.012	-0.012
via NPN	0.007	0.003	-0.003	-0.006	-0.001	-0.005
via PIL	-0.583	-0.068	0.450	0.564	0.108	0.268
via FP/FR	-0.070	-0.036	0.021	0.158	0.211	0.218
via %DEV	0.022	0.022	-0.009	-0.032	-0.077	-0.077
Effect	**NOB**	**ODM**	**OBL**	**%FR**	**FP/FR**	**FR/BR**
TOTAL	-0.471	-0.341	0.771	0.261	0.175	0.115
Trait PIL						
Direct	-0.802	-0.093	0.619	0.776	0.149	0.369

Effect	NOB	ODM	OBL	%FR	FP/FR	FR/BR
Indirect via CDB	0.017	0.091	0.001	-0.233	-0.037	-0.018
via ODB	0.192	0.191	-0.243	0.192	-0.076	-0.101
via NON	-0.380	-0.203	-0.174	-0.022	-0.004	-0.003
via NPB	0.017	0.014	-0.055	0.028	-0.011	-0.011
via NPN	0.148	0.062	-0.064	-0.143	-0.012	-0.119
via OIL	0.481	-0.099	0.637	-0.262	0.032	-0.130
via FP/FR	-0.085	-0.044	0.025	0.192	0.256	0.265
via %DEV	0.025	0.025	-0.010	-0.036	-0.086	-0.086
TOTAL	-0.388	-0.056	0.736	0.492	0.211	0.165
Trait FP/FR						
Direct	-0.229	-0.118	0.067	0.519	0.692	0.715
Indirect via CDB	-0.001	-0.003	0.000	0.007	0.001	0.001
via ODB	0.063	0.062	-0.079	0.063	-0.025	-0.033
via NON	-0.346	-0.185	-0.158	-0.020	-0.004	-0.002
via NPB	0.021	0.018	-0.070	0.035	-0.014	-0.014
via NPN	0.185	0.077	-0.079	-0.179	-0.015	-0.149
via OIL	0.202	-0.041	0.267	-0.110	0.013	-0.055
via PIL	-0.297	-0.035	0.229	0.287	0.055	0.137
via %DEV	-0.020	-0.020	0.008	0.028	0.068	0.068
TOTAL	-0.422	-0.244	0.185	0.630	0.772	0.667
Trait %DEV						
Direct	-0.190	-0.188	0.075	0.270	0.648	0.649
Indirect via CDB	-0.002	-0.008	0.000	0.021	0.003	0.002
via ODB	0.023	0.023	-0.029	0.023	-0.009	-0.012
via NON	0.206	0.110	0.094	0.012	0.002	0.001
via NPB	-0.017	-0.014	0.056	-0.028	0.011	0.011
via NPN	-0.006	-0.003	0.003	0.006	0.001	0.005
via OIL	-0.078	0.016	-0.104	0.043	-0.005	0.021
via PIL	0.107	0.012	-0.082	-0.103	-0.020	-0.049
via FP/FR	-0.024	-0.012	0.007	0.055	0.073	0.075
TOTAL	0.019	-0.064	0.020	0.298	0.703	0.704
R^2	0.623	0.422	0.982	0.789	0.994	0.985
Residual effect	0.614	0.760	0.133	0.460	0.077	0.122

OIL - average orthotropic internode length. PIL - plagiotropic internode length. OBL - length of new orthotropic branches. PBL - average plagiotropic branch length .CBD - largest crown-base diameter. OBD - diameter of new orthotropic branches. FP/FR - number of flowers produced per rosette. FR/BR - number of remaining fruits per branch. RF/FR - number of remaining fruits per rosette. ODM - dry matter of eliminated orthotropic branches. NLP - number of leaves produced from plagiotropic branches.NON - number of orthotropic branch nodes .NPN - number of plagiotropic branch nodes .NOB - number of orthotropic branches.NPB - number of new plagiotropic branches produced. YLD - yield of processed grains. %FR - percentage of flowering rosettes on plagiotropic branches. %DEV - development.

The highest total phenotypic correlations between the secondary and primary traits were found for CBD with OBL (0.809); OBD with OBL (0.700) and with %FR (0.566); NON with NOB (0.662) and ODM (0.570); OIL with NOB (–0.471) and OBL (0.771); and PIL with OBL (0.736) and %FR (0.492). As expected, the number of flowers per flowering rosette (FP/FR) had high correlation coefficients of 0.63 with %FR, 0.772 with RF/FR, and 0.667 with RF/BR. The variables NPB and NPN, in turn, showed low correlation values with the primary traits.

Analysis of the direct and indirect effects of the nine secondary variables (PBL, CBD, OBD, NON, NPB, NPN, NLP, OIL, PIL, FP/FR, and %DEV) on the six primary variables (NOB, ODM, OBL, %FR, RF/FR, and RF/BR) and the main variable YLD (Table 5) showed that the largest total effects on yield occurred on the traits FP/FR (0.520) and OBD (0.391), indicating that these two should be considered when unrestricted selections are made.

TABLE 5. Estimates of the direct and indirect effects of the nine secondary variables on the six primary variables and the main productivity variable of *Coffea canephora* coffee genotypes, after programed cycle pruning.

Effect		NOB	ODM	OBL	%FR	RF/FR	FR/BR	Residual Effect	Ef.total YLD
Trait	CBD								
Direct		-0.025	0.152	0.000	-0.079	-0.009	-0.007	-0.312	-0.280
Indirect	via ODB	-0.247	0.275	0.089	0.056	-0.016	-0.033	0.417	0.541
	via NON	-0.091	0.054	-0.012	0.001	0.000	0.000	0.026	-0.021
	via NPB	0.035	-0.032	-0.032	-0.013	0.004	0.006	-0.078	-0.112
	via NPN	0.241	-0.113	-0.029	0.053	0.003	0.050	-0.053	0.152
	via OIL	-0.342	-0.079	-0.129	-0.042	0.004	-0.024	0.136	-0.476
	via PIL	0.479	-0.062	-0.105	0.105	0.015	0.057	-0.159	0.329
	via FP/FR	-0.004	0.003	0.000	-0.002	-0.002	-0.004	0.001	-0.008
	via %DEV	-0.010	0.011	0.001	-0.003	-0.006	-0.009	0.003	-0.013
TOTAL		0.037	0.208	-0.217	0.075	-0.008	0.036	-0.019	0.113
Trait	OBD								
Direct		-0.310	0.345	0.111	0.070	-0.020	-0.042	0.524	0.678
Indirect	via CDB	-0.020	0.121	0.000	-0.063	-0.007	-0.006	-0.249	-0.223
	via NON	-0.061	0.036	-0.008	0.001	0.000	0.000	0.017	-0.014
	via NPB	0.060	-0.056	-0.056	-0.022	0.007	0.010	-0.135	-0.192
	via NPN	0.218	-0.102	-0.027	0.048	0.003	0.045	-0.048	0.137
	via OIL	-0.284	-0.065	-0.107	-0.035	0.003	-0.020	0.113	-0.394
	via PIL	0.445	-0.058	-0.097	0.097	0.014	0.053	-0.147	0.305
	via FP/FR	0.041	-0.024	-0.004	0.021	0.021	0.033	-0.012	0.077
	via %DEV	0.013	-0.014	-0.001	0.004	0.007	0.011	-0.003	0.016
TOTAL		0.103	0.184	-0.188	0.121	0.026	0.085	0.060	0.391
Trait	NNO								
Direct		-0.967	0.577	-0.126	0.013	0.002	0.002	0.274	-0.226
Indirect	via CDB	-0.002	0.014	0.000	-0.007	-0.001	-0.001	-0.029	-0.026
	via ODB	-0.019	0.022	0.007	0.004	-0.001	-0.003	0.033	0.042
	via NPB	0.052	-0.049	-0.049	-0.019	0.006	0.009	-0.118	-0.167
	via NPN	0.208	-0.097	-0.025	0.045	0.003	0.043	-0.045	0.131
	via OIL	0.422	0.097	0.159	0.052	-0.005	0.030	-0.168	0.587
	via PIL	-0.282	0.037	0.062	-0.062	-0.009	-0.034	0.093	-0.194
	via FP/FR	-0.073	0.042	0.006	-0.038	-0.036	-0.059	0.021	-0.136
	via %DEV	0.036	-0.040	-0.004	0.012	0.020	0.032	-0.009	0.046
TOTAL		-0.626	0.603	0.030	0.000	-0.021	0.019	0.052	0.058
Trait	NPB								
Direct		0.110	-0.102	-0.102	-0.040	0.012	0.019	-0.247	-0.351
Indirect	via CDB	-0.008	0.048	0.000	-0.025	-0.003	-0.002	-0.099	-0.089
	via ODB	-0.169	0.188	0.061	0.038	-0.011	-0.023	0.286	0.370
	via NPB	-0.460	0.275	-0.060	0.006	0.001	0.001	0.130	-0.107
	via NPN	0.306	-0.143	-0.037	0.067	0.004	0.064	-0.067	0.193
	via OIL	0.101	0.023	0.038	0.012	-0.001	0.007	-0.040	0.141
	via PIL	-0.110	0.014	0.024	-0.024	-0.003	-0.013	0.037	-0.076
	via FP/FR	-0.040	0.023	0.003	-0.020	-0.020	-0.032	0.012	-0.074
	via %DEV	0.026	-0.029	-0.003	0.008	0.015	0.023	-0.007	0.034
TOTAL		-0.244	0.298	-0.076	0.022	-0.007	0.043	0.005	0.041
Trait	NPN								
Direct		0.556	-0.260	-0.068	0.121	0.007	0.115	-0.121	0.350
Indirect	via CDB	-0.011	0.066	0.000	-0.034	-0.004	-0.003	-0.135	-0.121
	via ODB	-0.121	0.135	0.044	0.027	-0.008	-0.016	0.205	0.266
	via NPB	-0.361	0.216	-0.047	0.005	0.001	0.001	0.102	-0.084
	via NPN	0.060	-0.056	-0.056	-0.022	0.007	0.010	-0.136	-0.193
	via OIL	0.007	0.002	0.003	0.001	0.000	0.001	-0.003	0.010
	via PIL	-0.191	0.025	0.042	-0.042	-0.006	-0.023	0.063	-0.131
	via FP/FR	-0.068	0.039	0.006	-0.035	-0.034	-0.055	0.020	-0.127
	via %DEV	0.002	-0.002	0.000	0.001	0.001	0.002	-0.001	0.003
TOTAL		-0.128	0.164	-0.077	0.022	-0.036	0.031	-0.005	-0.029
Trait	OIL								
Direct		-0.625	-0.144	-0.236	-0.077	0.007	-0.044	0.248	-0.870
Indirect	via CDB	-0.014	0.083	0.000	-0.043	-0.005	-0.004	-0.170	-0.153
	via ODB	-0.140	0.156	0.051	0.032	-0.009	-0.019	0.237	0.307
	via NON	0.653	-0.390	0.085	-0.009	-0.001	-0.001	-0.185	0.152
	via NPB	-0.018	0.017	0.017	0.007	-0.002	-0.003	0.040	0.057
	via NPN	-0.006	0.003	0.001	-0.001	0.000	-0.001	0.001	-0.004
	via PIL	0.551	-0.072	-0.121	0.120	0.017	0.065	-0.183	0.379
	via FP/FR	0.066	-0.038	-0.006	0.034	0.033	0.053	-0.019	0.123
	via %DEV	-0.021	0.024	0.002	-0.007	-0.012	-0.019	0.006	-0.027
TOTAL		0.446	-0.361	-0.207	0.056	0.027	0.028	-0.025	-0.036
Trait	PIL								
Direct		0.758	-0.099	-0.166	0.166	0.023	0.090	-0.251	0.521

Effect		NOB	ODM	OBL	%FR	RF/FR	FR/BR	Residual Effect	Ef.total YLD
Indirect	via CDB	-0.016	0.096	0.000	-0.050	-0.006	-0.004	-0.197	-0.177
	via ODB	-0.182	0.202	0.065	0.041	-0.012	-0.025	0.307	0.397
	via NON	0.360	-0.215	0.047	-0.005	-0.001	-0.001	-0.102	0.084
	via NPB	-0.016	0.015	0.015	0.006	-0.002	-0.003	0.036	0.051
	via NPN	-0.140	0.066	0.017	-0.031	-0.002	-0.029	0.031	-0.088
	via OIL	-0.455	-0.104	-0.171	-0.056	0.005	-0.032	0.180	-0.632
	via FP/FR	0.080	-0.046	-0.007	0.041	0.040	0.065	-0.023	0.149
	via %DEV	-0.024	0.027	0.003	-0.008	-0.013	-0.021	0.006	-0.031
TOTAL		0.367	-0.059	-0.198	0.105	0.033	0.040	-0.013	0.275
Trait	FP/FR								
Direct		0.217	-0.125	-0.018	0.111	0.107	0.174	-0.063	0.403
Indirect	via CDB	0.001	-0.003	0.000	0.002	0.000	0.000	0.006	0.006
	via ODB	-0.059	0.066	0.021	0.013	-0.004	-0.008	0.100	0.129
	via NON	0.328	-0.196	0.043	-0.004	-0.001	-0.001	-0.093	0.076
	via NPB	-0.020	0.019	0.019	0.007	-0.002	-0.003	0.045	0.064
	via NPN	-0.175	0.082	0.021	-0.038	-0.002	-0.036	0.038	-0.110
	via OIL	-0.191	-0.044	-0.072	-0.024	0.002	-0.013	0.076	-0.265
	via PIL	0.281	-0.037	-0.062	0.061	0.009	0.033	-0.093	0.193
	via %DEV	0.019	-0.021	-0.002	0.006	0.011	0.017	-0.005	0.024
TOTAL		0.399	-0.258	-0.050	0.134	0.120	0.163	0.012	0.520
Trait	%DEV								
Direct		0.179	-0.199	-0.020	0.058	0.101	0.158	-0.046	0.230
Indirect	via CDB	0.001	-0.009	0.000	0.004	0.001	0.000	0.018	0.016
	via ODB	-0.022	0.024	0.008	0.005	-0.001	-0.003	0.037	0.047
	via NON	-0.195	0.116	-0.025	0.003	0.000	0.000	0.055	-0.046
	via NPB	0.016	-0.015	-0.015	-0.006	0.002	0.003	-0.036	-0.051
	via NPN	0.006	-0.003	-0.001	0.001	0.000	0.001	-0.001	0.004
	via OIL	0.074	0.017	0.028	0.009	-0.001	0.005	-0.029	0.103
	via PIL	-0.101	0.013	0.022	-0.022	-0.003	-0.012	0.033	-0.069
	via FP/FR	0.023	-0.013	-0.002	0.012	0.011	0.018	-0.007	0.042
TOTAL		-0.018	-0.068	-0.005	0.064	0.109	0.172	0.023	0.276

OIL - average orthotropic internode length. PIL - plagiotropic internode length. OBL - length of new orthotropic branches. PBL - average plagiotropic branch length .CBD - largest crown-base diameter. OBD - diameter of new orthotropic branches. FP/FR - number of flowers produced per rosette. FR/BR - number of remaining fruits per branch. RF/FR - number of remaining fruits per rosette. ODM - dry matter of eliminated orthotropic branches. NLP - number of leaves produced from plagiotropic branches.NON - number of orthotropic branch nodes .NPN - number of plagiotropic branch nodes .NOB - number of orthotropic branches. NPB - number of new plagiotropic branches produced. YLD - yield of processed grains. %FR - percentage of flowering rosettes on plagiotropic branches. %DEV – development.

When only the direct effects of the secondary traits on YLD were analyzed, OIL showed the highest correlation (–0.870), which is mainly because of the direct contribution from the primary trait NOB (–0.625). The negative sign indicates that genotypes with shorter orthotropic internodes would be more productive; however, when we add the indirect effects affecting the OIL variable, its relationship with YLD is practically nullified (–0.036). The relationships from NON (0.653) and PIL (0.551), both acting on the primary variable NOB, contributed to this nullification.

The second highest total direct relationship with YLD was found for the OBD trait, whose effect was 0.678. The positive sign indicates that genotypes with larger orthotropic branch diameters (OBD) are more productive. The greatest direct contributions to the establishment of this relationship (OBD with YLD) originate from the primary traits NOB (–0.310) and ODM (0.345), highlighting the balance between the two primary variables, which can be visualized by measuring OBD. When the indirect effects are considered, the relationship is reduced to 0.391 after receiving the opposite influence, mainly via OIL (–0.394) and CBD (–0.223), ultimately reducing the association between OBD and YLD to the moderate (but true) category.

These results place the OBD trait in a very prominent position in genotype selection. It is recommended that selection be performed with a view to increasing OBD, since besides the positive direct effect on grain yield, that trait contributes indirectly to reducing NOB and increasing ODM, which in turn have a greater direct effect on YLD than does OBD.

The secondary trait that also exerted a significant total direct effect on YLD was PIL (0.521); this relationship was markedly influenced by the primary trait NOB (0.758). However, when the indirect effects are considered, this relationship is drastically changed (0.275) due to the action of the secondary trait OIL (–0.632), which is mostly manifested upon the primary trait NOB (–0.455), and as previously mentioned NOB does not have a true association with YLD (–0.951).

Among the primary traits, NOB showed the highest negative correlation with YLD, whose total effect was –0.626, having a direct contribution from the secondary trait NON (–0.967) and an indirect mitigation effect from OIL (0.422). This fact allows for the definition of the existence of a moderate, yet true association between these traits. The ODM variable showed the highest positive association with YLD, whose total effect was 0.603, receiving a direct contribution from the secondary trait NON (0.577).

A comparison of the genotypic-correlation and path-coefficient estimates after the correlation was decomposed into direct and indirect effects revealed which variables have the most influence on the yield of the coffee crop, making it possible to focus on the variables that will provide greater gains with indirect selection. Indirect gains obtained via correlated responses for the variables selected here will be efficient and potentiated in Conilon coffee genotypes under the programed cycle pruning system.

CONCLUSIONS

Path analysis was efficient in identifying the traits that exerted the most influence on the yield of Conilon coffee after programed cycle pruning.

The primary traits that most influenced the yield of Conilon coffee after programed cycle pruning were *number of orthotropic branches* and *orthotropic branch dry matter*. The secondary traits that provided the greatest direct contribution were *orthotropic branch diameter* and *orthotropic and plagiotropic internode lengths*.

In the selection of Conilon coffee, producers should choose genotypes that, after programed cycle pruning, have vigorous orthotropic branches with a larger diameter and among them, those with the shortest orthotropic and plagiotropic internode lengths.

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