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Multivariate relationships in strawberry cultivated with native communities of arbuscular mycorrhizal fungi

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ABSTRACT. The mechanisms underlying the interactions between native mycorrhizal fungal communities and strawberry plants remain unclear. However, the identification of specific associations among variables and their influence on the total experimental variability when using inoculants based on arbuscular mycorrhizal fungi should enable the identification of the most relevant ones. Herein, our objective was to identify and characterize variables related to each other and to the total experimental variability among strawberry plants inoculated with native mycorrhizal communities. Experimental treatments included an uninoculated control and eight multi-specific inoculants from cultivated soils and native forests from reference strawberry-cultivation sites (Bom Princípio, Flores da Cunha, Ipê, and São José of Hortêncio) in Rio Grande do Sul State, Brazil. Morphological, productivity, and quality traits were evaluated. Inoculants obtained from agricultural ecosystems of Bom Princípio and Ipê did not influence the horticultural performance of strawberries, while those from Flores da Cunha largely explained total experimental variability, and therefore, should be considered when selecting the location to obtain inoculants for use on strawberry plants. Number of fruits, fruit flavor, chlorophyll a, and total chlorophyll contents, and, most importantly, root variables, should be included for experimental analysis of 'Albion' strawberry responses to multi-specific mycorrhizal inoculants from different locations.

Keywords: *Fragaria* X *ananassa* Duch.; mycorrhizal biotechnology; principal component analysis; Pearson correlation; canonical correlation.

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Introduction

Planning and establishing sustainable agri-food systems are two of the greatest challenges currently faced by horticultural production, which traditionally requires an excess of potentially contaminating chemical inputs (fertilizers and biocides), thus posing a threat to agroecosystems and the environment at large. As this scenario is the opposite of sustainable development goals envisaged on a global scale, there is an urgent need to promote agroecology as a science and driver of environmentally friendly crop management practices. Among the bio-tools that can contribute to enhancing sustainability in horticulture are arbuscular mycorrhizal fungi (AMF), which are naturally present in the soil and establish mutualistic associations with the roots of more than 80% of terrestrial flora, thereby improving the acquisition of water and nutrients by the plant host.

A case in point, strawberry (*Fragaria* X *ananassa* Duch.) is an AMF-responsive horticultural crop (Chiomento et al., 2019a). Whereas hydroponic cultivation of strawberries involves large-scale use of fertilizers that contribute to environmental contamination hazards in open drainage systems, mycorrhizal biotechnology can help minimize these inconveniences (Chiomento et al., 2021a). Therefore, researchers have focused on understanding how these microorganisms benefit strawberry plants. The evidence indicates that AMF improve the development of the strawberry root system (Chiomento et al., 2021a) and activate plant defense metabolism, such that berries actually acquire higher levels of phytochemicals (Chiomento et al., 2019a).

Overall, AMF do not show strict host specificity, indicating that plant root systems are often co-colonized by multiple fungal species (Öpik et al., 2009). Therefore, the use of mycorrhizal communities appears to be a promising strategy towards more sustainable horticultural models. Furthermore, plant development is

enhanced by indigenous or native AMF (Oliveira et al., 2017) because these microorganisms are physiologically and genetically better adapted to the edaphoclimatic and biogeographical conditions of the local agroecosystem than exotic AMF (Faye et al., 2013).

Indeed, the use of native AMF reportedly improves the adaptation of native hosts to nursery and field conditions (Maltz & Treseder, 2015). However, how mycorrhizal communities interact with strawberry plants in relation to their horticultural potential remains unclear. Principal component analysis (PCA) is a convenient way to determine the influence of the relationships among all the variables studied. This multivariate-covariance structure modeling technique aims to identify latent variables that represent linear combinations of a group of related variables.

The identification of specifically strong associations between variables and their influence on total experimental variability makes it possible to highlight those associations that are most relevance in each case. Thus, for example, while studying strawberry plants, Chiomento et al. (2021b) and Chiomento et al. (2023) adopted statistical analysis techniques that enabled them to describe the relationships among variables and generate other important information to guide reliable practical recommendations. However, information regarding the use of multivariate techniques to understand the effects of native AMF communities on strawberry horticultural potential is scarce at best. Thus, here, we aimed to identify and characterize variables closely related to each other and to the total variability in an experiment in which the strawberry, cultivar 'Albion', was grown together with native AMF communities.

Material and methods

Plant material

The study was conducted under hydroponic cultivation in a greenhouse in the municipality of Passo Fundo (28°15'46" S; 52°24'24" W), Rio Grande do Sul State, Brazil.

The day-neutral strawberry cultivar 'Albion' was used. The strawberry plants used in the experiment were produced by mother plants obtained from the nursery Llahuén/Chilean Patagonia (33°50'15.41" S; 70°40'03.06" W). In June 2016, the mother plants were transplanted into containers (5 L) filled with the commercial substrate Horta 2® and kept on 1.20 m high benches. In September 2016, the ends of the runners produced were removed from the matrices and transferred to a 72-cell tray (50 cm^3 per cell) filled with sterilized sand (120°C) for 20 min.

Experimental design

The experiment was laid in a completely randomized design with three replicates of a single plant per treatment. Treatments included eight multi-specific mycorrhizal inoculants (AMF communities) (Table 1) collected from soils at reference sites for strawberry cultivation in Rio Grande do Sul State, Brazil (Chiomento et al., 2019b), and a control (uninoculated) treatment. At each reference site, soils were collected from strawberry cultivation sites (SC) and native forest soils (NF). The collected inoculants were identified based on spore morphology and ontogeny.

Table 1. Description of AMF communities identified in soils of reference sites for strawberry cultivation in Rio Grande do Sul State, Brazil.

Sites	Ecosystem	Initials	Mycorrhizal community[1]
Bom Princípio	Agricultural	BP SC	*Acaulospora koskei*, *A. rehmii*, *Claroideoglomus* aff. *luteum*, *C. claroideum*, *C. etunicatum*, *Funneliformis* aff. *mosseae*, *Glomus* aff. *versiforme*, and *Glomus* sp. (*caesaris* like)
Bom Princípio	Natural	BP NF	*Acaulospora* aff. *scrobiculata*, *A. colossica*, *A. scrobiculata*, *Acaulospora* sp., *Acaulospora* sp1 (*E. infrequens* like), *Acaulospora* sp2 (*excavata* like), *Ambispora leptoticha*, *Claroideoglomus* aff. *luteum*, *C. claroideum*, *C. etunicatum*, *F. mosseae*, *G. microaggregatum*, *Glomus* sp1, and *Glomus* sp2
Flores da Cunha	Agricultural	FC SC	*C. claroideum*, *C. etunicatum*, *Funneliformis* aff. *geosporum*, *Glomus* aff. *versiforme*, *Glomus* sp. (*caesaris* like), and *Glomus* sp2
Flores da Cunha	Natural	FC NF	*A. colossica*, *A. koskei*, *A. lacunosa*, *A. mellea*, *A. tuberculata*, *C. claroideum*, *Dentiscutata savannicola*, *F. mosseae*, *Glomus* aff. *manihotis*, *Racocetra* sp., and *R. verrucosa*
Ipê	Agricultural	IP SC	*A. colossica*, *Acaulospora* sp., *Cetraspora pellucida*, *C. etunicatum*, *D. erythropa*, *D. heterogama*, *D. rubra*, *Funneliformis* aff. *geosporum*, *F. mosseae*, *Gigaspora* sp., *Glomus* aff. *caledonium*, *Glomus* aff. *manihotis*, *Glomus* sp. (*caesaris* like), and *Glomus* sp1
Ipê	Natural	IP NF	*Acaulospora* aff. *lacunosa*, *Acaulospora* aff. *scrobiculata*, *A. colossica*, *A. koskei*, *A. lacunosa*, *Acaulospora* sp. (*colossica* like M+), *A. spinosa*, *Claroideoglomus* aff. *luteum*, *C. etunicatum*, *D. biornata*, *F. geosporum*, *F. mosseae*, *Glomus* sp1, *Glomus* sp2, and *Scutellospora calospora*
São José do	Agricultural	SH SC	*A. foveata*, *Claroideoglomus* aff. *luteum*, *C. claroideum*, *C. etunicatum*, *Funneliformis* aff.

Hortêncio			*geosporum*, *Funneliformis* aff. *mosseae*, *F. mosseae*, *Glomus* aff. *versiforme*, *Glomus* sp. (*caesaris* like), and *Glomus* sp2
São José do Hortêncio	Natural	SH NF	*A. mellea*, *Acaulospora* sp2 (*excavata* like), *Claroideoglomus* aff. *luteum*, *C. claroideum*, *C. etunicatum*, *F. geosporum*, *F. mosseae*, *Gigaspora* sp., *Glomus* aff. *heterosporum*, *Glomus* sp1, *Glomus* sp2, and *Scutellospora* sp1

[1]Classification of Glomeromycota by Redecker et al. (2013).

Procedures

In October 2016, strawberry daughter plants were transplanted into 9 L polyethylene pots filled with sterilized sand. For the treatments inoculated with AMF, 10 g of inoculant soil collected at the reference sites for strawberry cultivation was added to the planting hole of daughter plants at the time of transplanting. A localized irrigation system was used to water the plants individually via dripper rods (2.4 L h^{-1} per emitter). Irrigation was applied four times a day (total wetting for 10 min.). Additionally, fert-irrigation was performed weekly (Furlani & Fernandes Júnior, 2004).

Measurements

The evaluated attributes included, 1) morphology, 2) productivity, and 3) quality characteristics.

The morphological traits were:

a) Crown diameter (CD, cm): measured with a digital caliper;

b) Height of the aerial plant body (HAP, cm) was measured using a ruler;

c) Crown number (CN);

d) Fresh mass of the aerial plant body (FMAP, g) and fresh mass of the root system (FMRS, g) were measured on an electronic analytical scale;

e) Dry mass of the aerial plant body (DMAP, g) and dry mass of the root system (DMRS, g). Tissues were oven-dried at 65ºC for 48h until constant mass and weighed on an electronic analytical scale;

f) Total root length (TRL, cm), root surface area (RSA, cm^2), and root volume (RV, cm^3) were analyzed through images using the WinRHIZO® software;

g) For measurement of TRL, roots were subdivided into the following diameter classes: very fine roots (VFR, Ø < 0.5 mm), fine roots (FR, Ø from 0.5 to 2 mm), and coarse roots (CR, Ø > 2 mm). TRL was determined according to the methodology of Böhm (1979);

h) Accumulation of dry mass in the aerial plant body (ADMAP, %) was determined according to Atif et al. (2016) using the following equation: $ADMAP=\left(\frac{DMAP}{FMAP}\right)\times 100$ (1), where DMAP and FMAP are the dry and fresh masses of the aerial plant body, respectively;

i) Accumulation of dry mass of the root system (ADMRS, %) was determined according to Atif et al. (2016), using the following equation: $ADMRS=\left(\frac{DMRS}{FMRS}\right)\times 100$ (2), where DMRS is the dry mass of the root system and FMRS is the fresh mass of the root system.

Productivity attributes were measured and calculated using the means of all harvests. The fruits were harvested when they were 85% red. The measured traits were:

a) Number of fruits (NF);

b) Fruit weight (FW, g): fruits were weighed on an electronic analytical scale.

As for quality attributes, these included total soluble solids content (SSC), total titratable acidity (TTA), and total anthocyanin content (TAC). One-hundred-gram fruits samples were used. The quality characteristics were determined as follows:

a) The Dickson quality index (DQI) was determined according to Dickson et al. (1960) using the equation $DQI=\frac{TDM}{\left(\frac{HAP}{CD}+\frac{DMAP}{DMRS}\right)}$ (3), where TDM = total dry mass, HAP = height of the aerial plant body, CD = crown diameter, DMAP = dry mass of the aerial plant body, and DMRS = dry mass of the root system;

b) Mycorrhizal colonization (MC, %) was determined using the following equation: $MC=\frac{TNFMR}{TNF}\times 100$ (4), following the methodologies of Phillips and Hayman (1970), and Trouvelot et al. (1986), where TNFMR is the total number of fragments with mycorrhizal roots, and TNF is the total number of fragments;

c) Chlorophyll a (CLA), b (CLB), and total (CLT) chlorophyll were measured with an electronic ClorofiLOG 1030 (Falker, Garches, France) chlorophyll-o-meter; 15 measurements were made in the central third of the leaf blade on each sampled plant;

d) Total soluble solids content (SSC, %) were determined with an analog refractometer;

e) Total titratable acidity (TTA, % citric acid): determined according to Zenebon et al. (2008);

f) Fruit flavor (FF): $FF=\frac{SSC}{TTA}$ (5), where SSC is the total soluble solids and TTA is the total titratable acidity.

g) Total anthocyanin content (TAC, mg of pelargonidin-3-*O*-glycoside equivalent per 100 g of fresh fruit [mg PE 100 g^{-1} FF]) was determined using the differential pH method (Lee et al., 2005).

Statistical analysis

Statistical analysis began with the estimation of the means and standard deviations for each variable in each treatment for descriptive characterization of the observations. Subsequently, PCA was applied to identify the variables most related to the treatments, in addition to identifying those that accounted the most for the experimental variability.

After applying PCA, Pearson's correlation analysis was performed, generating a matrix of correlation coefficients among the treatments and PCA dimensions, and among the measured variables and PCA dimensions. Subsequently, the number of conditions was obtained by the ratio between the highest and lowest eigenvalues of the X'X correlation matrix. A number of conditions ⩽100, indicated weak multicollinearity occurrence; a number of conditions between 100 and 1,000 indicated moderate to severe multicollinearity; and a number of conditions ⩾1,000, indicated severe multicollinearity (Montgomery et al., 2012). The variance inflation factor was obtained for each variable on the inverse diagonal of the correlation matrix X'X. Severe multicollinearity resulted when the variance inflation-factor value was >10 (Hair et al., 2009). The occurrence of multicollinearity among the explanatory variables was defined by obtaining values for the number of conditions ⩾1,000 and variance inflation-factor values >10. When moderate, strong, or high multicollinearity was detected, the variables that caused these results were removed from the dataset and a subsequent diagnosis was made to prove the effectiveness of removing variables from the dataset submitted to statistical analysis.

Finally, a canonical correlation analysis was performed to identify the existence of significant associations among the three groups of variables after identifying those with the lowest contributions to the main components, namely: 1) morphological variables (CN, FMAP, DMAP, FMRS, DMRS, ADMRS, TRL, RSA, VFR, FR, and CR); 2) productive variables (NF and FW); and 3) quality variables (SSC, TTA, FF, TAC, DQI, CLA, CLB, and CLT).

All statistical analyzes were performed in the R software (R Core Team, 2022) with a 5% error probability.

Results

The greatest variability, characterized by the highest standard deviations, occurred for FMRS, DMRS, VFR, FR, FW, TRL, RSA, and RV (Table 2). These results were expected because the evaluations of root systems typically show inherent high variability owing to the proper preparation of the roots for further evaluation. When checking variable means, considering the two mycorrhizal community ecosystems of origin i.e., cropping and forestland, the means of inoculants from agricultural ecosystems (SC) tended towards lower means than those from natural ecosystems (NF) for morphological variables and quality. The opposite was observed for production variables and those of the root system (Table 2).

Considering all the variables measured in our experiment, the results of PCA indicated that the first two components accounted for 41.30% of the total variability observed (Figure 1A), with FMRS, FF, ADMRS, NF, and DMRS accounting for the greater positive contributions, and VFR, FR, TRL, CLA, and CLT accounting for the greater negative contributions in the first two dimensions (Table 3, Figure 2A and B). These findings indicate that these variables were the most relevant in the analysis.

Table 2. Mean and standard deviation of morphological, productive, and quality variables of strawberry cultivar 'Albion', inoculated with mycorrhizal communities.

Trat[1]	CN[2]	CD	HAP	FMA	DA	FMR	DMR	ADA	ADR	VFR	FR	CR	NF	FW	SSC	TT	FF	TAC	TRL	RSA	RV	MC	DQI	CLA	CLB	CLT
	Mean																									
BP SC	7.0	6.3	27.1	167.8	39.4	162.7	57.7	23.4	35.1	791	184.7	13.0	86.3	1022	9.1	0.6	14.8	9.9	990	894	64.7	63.3	20.3	40.7	13.6	54.3
FC SC	6.0	6.9	27.1	200.2	46.3	251.9	97.5	23.1	35.6	686	131.5	0.9	90.6	1003	9.4	0.6	15.0	12.5	820	1026	125.4	93.3	31.2	40.7	15.0	55.8
IP	8.6	6.4	27.0	145.3	31.0	178.5	104.3	21.3	78.0	1608	338.4	25.6	89.3	1019	8.7	0.7	11.2	11.3	1973	983	44.7	53.3	29.8	39.0	14.4	53.5

SC																								
SH SC	9.3	7.5	25.7	172.0	40.2	188.6	79.4	23.4	37.8	1658	358.0	37.2	82.6	818	8.4	0.6	12.5	13.3	2055	1131	49.6	60.0	28.6	38.4	13.9	52.3
BP NF	7.6	6.7	27.0	171.3	35.9	231.7	105.6	21.0	42.5	512	144.1	18.1	82.0	990	8.1	0.6	13.6	10.5	698	843	97.7	60.0	33.9	40.0	14.1	54.2
FC NF	7.6	6.7	26.8	172.3	37.5	313.9	142.0	21.5	41.1	240	26.9	0.0	79.6	945	8.8	0.7	13.7	12.0	267	919	817.1	33.3	44.9	40.0	14.1	54.2
IP NF	9.3	6.7	25.6	189.3	41.6	292.7	205.4	21.8	128.4	283	62.8	7.9	98.0	1175	9.9	0.6	15.2	9.6	355	849	233.7	60.0	60.1	36.8	14.3	51.1
SH NF	8.0	6.4	25.0	167.0	45.1	240.5	112.7	26.9	59.4	390	81.5	0.0	87.3	1037	9.0	0.6	14.3	10.7	472	798	167.3	53.3	36.1	40.8	15.4	56.2
TES	9.3	6.8	26.0	180.2	40.8	298.9	116.0	22.7	36.5	161	60.8	22.2	83.6	920	9.0	0.5	15.8	4.3	244	637	175.7	0.0	36.7	40.6	16.4	57.1
Standard deviation																										
BP SC	1.7	1.0	3.6	9.5	3.6	26.3	14.0	1.0	3.0	51	41.2	16.7	10.2	108	0.2	0.0	0.8	1.9	37	87	13.7	11.5	7.5	0.7	0.8	1.4
FC SC	1.7	0.9	2.0	47.0	11.2	114.9	73.9	0.9	10.6	408	76.3	1.0	6.3	113	0.5	0.2	5.5	3.9	483	36	60.4	11.5	14.9	0.6	0.0	0.7
IP SC	1.5	0.3	0.5	5.1	1.3	143.3	65.7	0.2	70.4	439	157.1	22.3	3.2	102	1.5	0.1	2.4	2.5	608	366	35.3	15.2	16.5	2.3	0.8	2.2
SH SC	0.5	0.3	2.2	3.4	1.9	83.0	57.2	1.5	15.1	168	131.0	37.2	20.5	268	1.1	0.0	1.8	2.9	337	150	5.0	10.0	14.9	2.7	1.1	3.6
BP NF	0.5	0.5	3.0	20.1	2.4	84.0	61.1	1.1	12.7	211	130.7	31.3	12.4	126	0.7	0.2	5.3	1.4	367	46	49.6	17.3	20.8	1.5	0.9	2.4
FC NF	1.5	1.5	1.5	35.7	10.4	166.2	107.9	2.0	12.5	296	45.5	0.0	21.3	214	2.7	0.1	8.6	0.3	342	149	781.8	15.2	32.7	1.4	1.5	3.0
IP NF	1.1	1.2	1.5	42.2	12.5	253.9	162.9	1.8	117.6	268	24.1	13.7	13.4	107	1.0	0.0	2.5	0.6	279	122	174.5	10.0	43.0	0.4	0.4	0.8
SH NF	1.0	0.9	1.3	19.4	8.8	94.7	69.6	3.6	58.4	55	8.5	0.0	14.5	188	1.0	0.0	1.8	2.6	47	104	93.6	20.8	16.8	1.4	1.5	2.8
TES	1.1	0.6	2.0	16.6	1.7	187.6	82.1	1.3	12.3	90	24.1	20.3	15.3	109	1.0	0.0	1.6	1.6	105	186	141.2	0.0	21.2	1.7	0.0	1.7

[1]BP SC: Bom Princípio in agricultural ecosystem; BP NF: Bom Princípio in natural ecosystem; FC SC: Flores da Cunha in agricultural ecosystem; FC NF: Flores da Cunha in natural ecosystem; IP SC: Ipê in agricultural ecosystem; IP NF: Ipê in natural ecosystem; SH SC: São José do Hortêncio in agricultural ecosystem; SH NF: São José do Hortêncio in natural ecosystem; TES: control treatment (no application). [2]CN: crown number; CD: crown diameter (cm); HAP: height of the aerial part (cm); FMA: fresh mass of the aerial part (g); DA: dry mass of the aerial part (g); FMR: fresh mass of the root system (g); DMR: dry mass of the root system (g); ADA: accumulation of dry mass of the aerial part (%); ADR: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TT: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); RV: root volume (cm^3); MC: mycorrhizal colonization (%); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

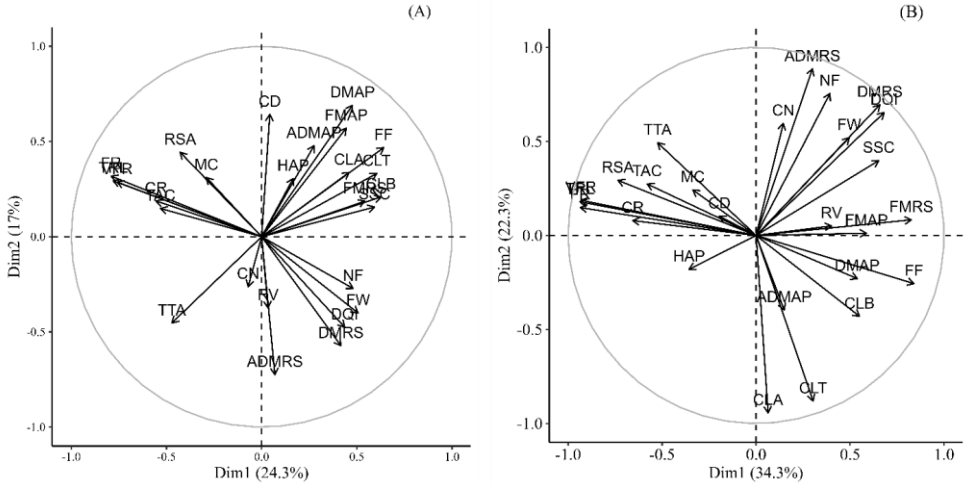

Figure 1. Biplot of principal component analysis with all variables (A) and with the removal of variables ADMAP, MC, RV, HAP, CD (B), considering the first two principal components. CN: crown number; CD: crown diameter (cm); HAP: shoot height (cm); FMAP: shoot fresh mass (g); DMAP: shoot dry mass (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMAP: accumulation of shoot dry mass (%); ADMRS: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); RV: root volume (cm^3); MC: mycorrhizal colonization (%); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

With this first PCA, we identified that ADMAP, MC, RV, HAP, and CD had greater contributions (positive or negative) to the last three components (Table 3 and Figure 2A). Thus, these five variables were removed from the database and PCA was repeated in their absence (Table 4), which increased the contribution of the first two components to 55.10% (Figure 1B). This finding further supported the contribution of the variables to the first two components (Table 4 and Figure 2B). This approach underlines to importance of highlighting and interpreting FMRS, FF, ADMRS, NF, DMRS, VFR, FR, TRL, CLA, and CLT to further explain the responses of strawberry cultivar 'Albion' to multispecific mycorrhizal inoculants from different locations and ecosystems.

By correlating the nine treatments with the PCA dimensions, the multispecific inoculants from Flores da Cunha in an agricultural ecosystem, Flores da Cunha in a natural forest ecosystem, and São José do Hortêncio in an agricultural ecosystem were most related to the first two dimensions, explaining 80.70% of the total variability (Figure 2C). Inoculants from Bom Princípio and Ipê in natural forest ecosystems were the most related to the third and fourth PCA dimensions, which explained a small proportion (6.20%) of the total variability. Similarly, neither Bom Princípio or Ipê inoculants in agricultural ecosystems, São José do Hortêncio in a natural forest ecosystem, or the AMF-uninoculated control exhibited relevant relationships with any PCA dimensions (Figure 2C). These results indicate that the AMF communities from Flores da Cunha stood out as the greatest explanation for the total experimental variability and should therefore be considered relevant for selecting the place of origin of those communities, regardless of the ecosystem.

Table 3. Contribution of all analyzed variables in the experiment in each dimension of the principal components.

Variable[1]	Dimension 1	Dimension 2	Dimension 3	Dimension 4	Dimension 5
CN	0.14473878	0.59600171	-0.735207058	0.27091429	0.003288286
CD	-0.19525433	0.10235777	-0.211385498	0.45872211	0.815462363
HAP	-0.35672799	-0.18006925	0.362391714	-0.60116650	-0.067033341
FMAP	0.58695841	0.01176892	0.392520174	0.33544070	0.466773610
DMAP	0.53816546	-0.22970054	0.440739494	0.62158187	0.249865382
FMRS	0.82560186	0.08312669	-0.160967264	-0.24669725	0.434385958
DMRS	0.65846002	0.69502536	-0.129912117	-0.16462613	0.118359059
ADMAP	0.14930128	-0.39674182	0.199318247	0.59308733	-0.160647408
ADMRS	0.29950918	0.88613040	-0.050720955	0.06177951	-0.319372646
VFR	-0.93226673	0.18730429	-0.029677664	0.22191746	-0.044955392
FR	-0.93533308	0.14848342	-0.103387251	0.25704469	-0.097802081
CR	-0.65594052	0.07910610	-0.627083326	0.29367994	0.029081701
NF	0.39295081	0.75518820	0.231780634	0.30639256	-0.303925220
FW	0.49520689	0.52011658	0.366527924	-0.09498770	-0.575959972
SSC	0.65271774	0.39857780	0.377779120	0.24363982	-0.161217514
TTA	-0.52403488	0.49349243	0.180688836	-0.51665766	0.069734914
FF	0.83993192	-0.25613601	0.162972651	0.25365365	0.018529328
TAC	-0.57921101	0.27365822	0.588309305	-0.06902752	0.352876143
TRL	-0.93663017	0.17900446	-0.054593808	0.22794770	-0.053067941
RSA	-0.73491768	0.29305739	0.437292247	0.10451164	0.384154170
RV	0.40112935	0.05070205	0.007400097	-0.64767507	0.501910213
MC	-0.33670240	0.24238002	0.852843184	0.21502303	-0.019733854
DQI	0.68116479	0.65403467	-0.134845392	-0.13347513	0.222878363
CLA	0.06392764	-0.94401016	0.210867816	-0.17895079	-0.126172067
CLB	0.55010856	-0.43014511	-0.345134215	0.22721200	-0.088348440
CLT	0.30346880	-0.88086268	-0.009726807	-0.02248478	-0.132173188

[1]CN: crown number; CD: crown diameter (cm); HAP: height of the aerial part (cm); FMAP: fresh mass of the aerial part (g); DMAP: dry mass of the aerial part (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMAP: accumulation of dry mass of the aerial part (%); ADMRS: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); RV: root volume (cm^3); MC: mycorrhizal colonization (%); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

Further, the biplot analysis showed that the AMF communities from Flores da Cunha were directly related to a greater extent to TRL, VFR, and FR, and to a lesser extent to RSA, CR, TTA, and TAC (Figure 3). The AMF community from São José do Hortêncio in an agricultural ecosystem, which correlated with the second dimension of the PCA (Figure 2C), was directly related to a larger extent to SSC, DQI, and DMRS and, to a lesser extent, to ADMRS, NF, FW, and CN.

The inoculants formed by the mycorrhizal communities of Bom Princípio in a natural forest ecosystem, Ipê in a natural ecosystem, São José do Hortêncio in a natural ecosystem, and the uninoculated control showed close associations with FF, FMAP, DMAP, CLA, CLB, and CLT (Figure 3). Consistently, mycorrhizal inoculants

obtained from the agricultural ecosystems of Bom Princípio and Ipê, which did not show significant relationships with any PCA dimensions (Figure 2C) did not show a close relationship with any measured variable either (Figure 3), indicating that neither inoculant influenced the horticultural performance of strawberries.

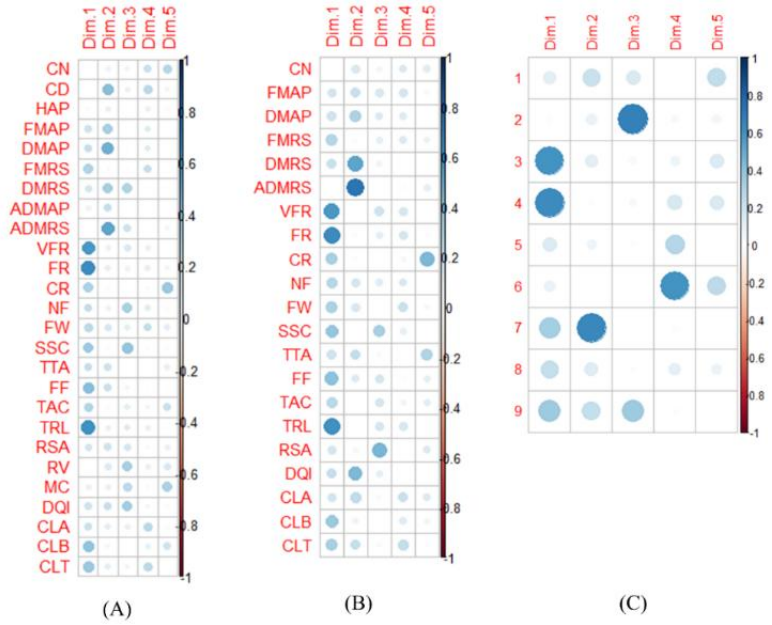

Figure 2. Pearson's linear correlation between the variables and dimensions of the PCA with all variables (A), with the removal of variables ADMAP, MC, RV, HAP, CD (B) and between the nine treatments (1: Bom Princípio in agricultural ecosystem; 2: Bom Princípio in a natural ecosystem; 3: Flores da Cunha in an agricultural ecosystem; 4: Flores da Cunha in a natural ecosystem; 5: Ipê in an agricultural ecosystem; 6: Ipê in a natural ecosystem; 7: São José do Hortêncio in an agricultural ecosystem 8: São José do Hortêncio in a natural ecosystem; 9: control without AMF inoculation) and the PCA dimensions (C). CN: crown number; CD: crown diameter (cm); HAP: shoot height (cm); FMAP: shoot fresh mass (g); DMAP: shoot dry mass (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMAP: accumulation of shoot dry mass (%); ADMRS: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); RV: root volume (cm^3); MC: mycorrhizal colonization (%); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

Table 4. Contribution of selected variables in each principal component dimension.

Variable[1]	Dimension 1	Dimension 2	Dimension 3	Dimension 4	Dimension 5
CN	0.11727387	0.61061542	-0.70067079	0.212097587	0.195906227
FMAP	0.63589565	-0.03698635	0.42166803	0.407698861	0.400833032
DMAP	0.55933712	-0.24652316	0.45886261	0.511804593	0.179169228
FMRS	0.80925726	0.04725673	-0.10110410	-0.295700911	0.459094067
DMRS	0.65770361	0.67691858	-0.11546590	-0.234981365	0.176373210
ADMRS	0.31349355	0.89664392	-0.10812597	0.004029388	-0.254588726
VFR	-0.92332096	0.21195671	0.01579715	0.243726543	-0.041367517
FR	-0.92530048	0.17396255	-0.07618078	0.291002128	-0.071291482
CR	-0.66322480	0.09470932	-0.59180470	0.375897581	0.172134992
NF	0.43705466	0.75506775	0.14873382	0.331459827	-0.296765250
FW	0.52813985	0.52587502	0.21517308	-0.093735233	-0.607737468
SSC	0.68732086	0.39071011	0.31892619	0.323724048	-0.227703337
TTA	-0.51955163	0.49475796	0.23758922	-0.543764830	0.013332758
FF	0.85967459	-0.27992181	0.10062019	0.343110707	-0.007341896
TAC	-0.55998885	0.26689216	0.69941290	-0.172345615	0.224425355
TRL	-0.92752986	0.20358729	-0.01269718	0.252858506	-0.042230927
RSA	-0.70608285	0.28656339	0.55708917	0.122136782	0.278680744
DQI	0.67729159	0.63226704	-0.09825831	-0.218120188	0.280662555
CLA	0.04867948	-0.94158828	0.15832103	-0.185189374	-0.213648585
CLB	0.52951370	-0.42891833	-0.39347854	0.134712593	-0.012516655
CLT	0.28285390	-0.87854513	-0.07017821	-0.070265244	-0.159654929

[1]CN: crown number; FMAP: fresh mass of the aerial part (g); DMAP: dry mass of the aerial part (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMRS: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

The number of conditions was classified as severe multicollinearity, with values of $1.5e^{17}$ and $3.6e^{17}$ for the groups of morphological and quality variables, respectively, and a variance inflation factor greater than 30 for the same groups. Based on this result, we removed VFR, FR, CR, FF, TTA, RSA, and CLT from the database, in addition to those already indicated by PCA (ADMAP, MC, RV, HAP, and CD). Thus, the number of conditions ranged from 9.72 to 40.81 (weak multicollinearity) and the variance inflation factor from 1.70 to 7.90, within the maximum limit of 10.00.

After the creation of the three groups, a new Pearson correlation analysis was conducted among the variables of each group (Figure 4). Thus, only trivial relationships were significant for morphological variables such as shoot dry mass and shoot fresh mass (Figure 4A). This result was also obtained by correlating the number and weight of fruits in the productive variable group (Figure 4B). No significant correlations were observed in the group of quality traits (Figure 4C).

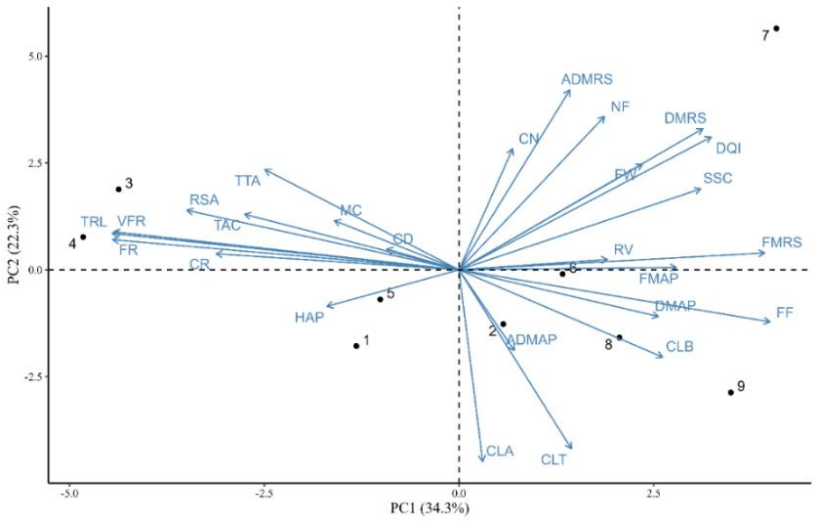

Figure 3. Principal component analysis for the variables and their association with the nine treatments studied (1: Bom Princípio in an agricultural ecosystem; 2: Bom Princípio in a natural ecosystem; 3: Flores da Cunha in an agricultural ecosystem; 4: Flores da Cunha in a natural ecosystem; 5: Ipê in an agricultural ecosystem; 6: Ipê in a natural ecosystem; 7: São José do Hortêncio in an agricultural ecosystem; 8: São José do Hortêncio in a natural ecosystem; 9: control without AMF inoculation). CN: crown number; CD: crown diameter (cm); HAP: shoot height (cm); FMAP: shoot fresh mass (g); DMAP: shoot dry mass (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMAP: accumulation of shoot dry mass (%); ADMRS: accumulation of dry mass of the root system (%); VFR: very fine roots (cm); FR: fine roots (cm); CR: coarse roots (cm), NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); FF: fruit flavor; TAC: total anthocyanin content (mg PE 100 g^{-1} FF); TRL: total root length (cm); RSA: root surface area (cm^2); RV: root volume (cm^3); MC: mycorrhizal colonization (%); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B; CLT: total chlorophyll content.

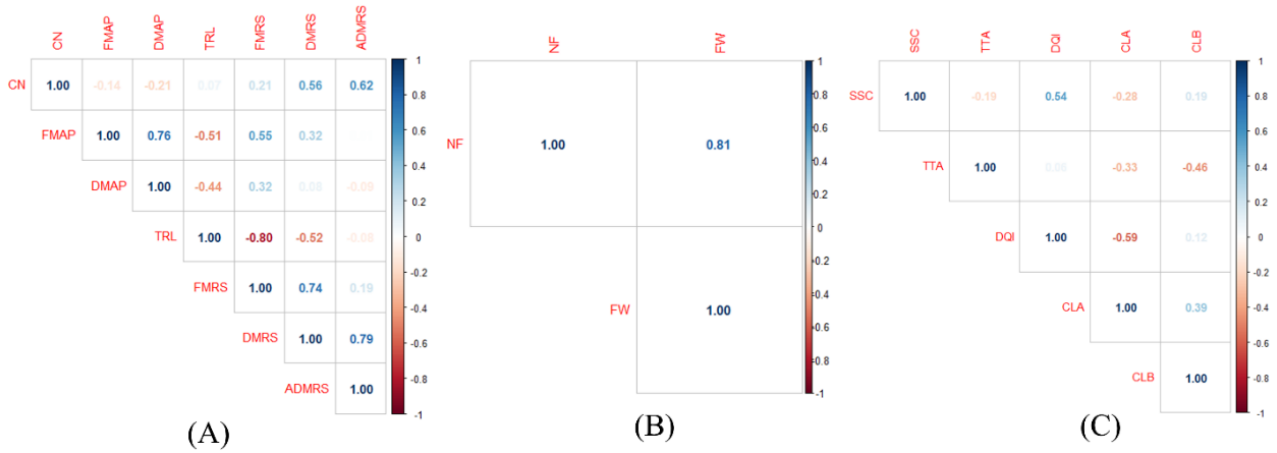

Figure 4. Pearson's linear correlation within groups of morphological (CN, FMAP, DMAP, FMRS, DMRS, ADMRS, and TRL), productive (NF and FW), and quality (SSC, TTA, DQI, CLA, and CLB) variables. CN: crown number; FMAP: shoot fresh mass (g); DMAP: shoot dry mass (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMRS: root system dry mass accumulation (%); NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); TRL: total root length (cm); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B.

To confirm the possible relationships of the variables among the three groups, canonical correlation analysis was performed, which showed no significant effects when relating the groups of morphological variables with those of the productivity variables (Table 5) or the latter with those of the quality variables (Table 6).

Table 5. Crossed canonical loads between morphological and productive variables.

Variable[1]	1º PC	2º PC
Morphological Variable		
CN	-0.1335	-0.5790
FMAP	-0.1852	-0.3901
DMAP	-0.1263	-0.2639
TRL	0.3636	-0.3507
FMRS	-0.1687	-0.0243
DMRS	-0.6183	-0.2569
ADMRS	-0.8067	-0.3728
Productive Variable		
NF	-0.8633	-0.5047
FW	-0.9958	0.0915
r	0.9978	0.9922
R^2	0.9957	0.6962
p-valor	0.1974	0.5912
RI 1	0.3048	
RI 2	0.9979	

[1]CN: crown number; FMAP: fresh mass of the aerial part (g); DMAP: dry mass of the aerial part (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); TRL: total root length (cm); ADMRS: accumulation of dry mass of the root system (%); NF: number of fruits; FW: fruit weight (g). r: canonical correlation; R^2: coefficient of determination; RI 1: redundancy index between morphological and productive groups; RI 2: redundancy index between productive and morphological groups.

Table 6. Crossed canonical loads between productive and quality variables.

Variable[a]	1º PC	2º PC
Productive variable		
NF	-0.9172	0.3982
FW	-0.5147	0.8572
Quality variable		
SSC	-0.7464	0.5639
TTA	-0.0160	0.0982
DQI	-0.5485	0.4205
CLA	0.7836	0.1765
CLB	0.0157	-0.0831
r	0.9816	0.7859
R^2	0.9636	0.4525
p-valor	0.2136	0.6801
RI 1	0.7338	
RI 2	0.3321	

[a]NF: number of fruits; FW: fruit weight (g); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B. r: canonical correlation; R^2: coefficient of determination; RI 1: redundancy index between productive and quality groups; RI 2: redundancy index between quality and productive groups.

These results show that the number and weight of fruits were not correlated with the morphological and quality variables of strawberries. However, when correlating the groups of morphological variables with those of quality variables (Table 7), the results were significant (p-value < 0.05) for the first three canonical pairs. Therefore, we found that higher DMAP provided fruits with lower TTA (1st pair), while higher root fresh mass provided fruits with higher TTA and lower TRL (2nd pair), and higher root dry mass and root dry mass accumulation provided higher DQI and fruits with lower chlorophyll A content.

Additionally, we observed that a higher DMRS will provide a higher DQI (1st and 3rd pair), and when a reduction in DMRS occurs, there will be a reduction in DQI (2nd pair). Finally, the relationship between a decrease in CN and a lower DQI was verified in the second canonical pair (Table 7).

Table 7. Cross canonical loads between morphological and quality variables.

Variable[1]	1º PC	2º PC	3º PC	4º PC	5º PC
Morphological variable					
CN	0.6503	-0.7917	0.5810	0.1633	0.3636
FMAP	0.5391	-0.4395	0.5102	-0.1666	-0.3623

DMAP	0.4348	-0.2913	0.3433	-0.3206	-0.3292
TRL	-0.6026	0.3893	-0.6669	-0.0264	0.0369
FMRS	0.6644	-0.5477	0.8083	-0.0091	0.2764
DMRS	0.7499	-0.7765	0.9224	0.1034	-0.0447
ADMRS	0.5468	-0.6706	0.6516	-0.0101	-0.3144
Quality variable					
SSC	0.5944	-0.5492	0.6353	-0.4335	-0.6139
TTA	-0.5200	0.3504	-0.2517	0.0919	-0.0185
DQI	0.7829	-0.7977	0.9414	0.1721	-0.0201
CLA	-0.4529	0.6676	-0.4813	-0.2913	0.1732
CLB	0.3710	-0.2335	0.3362	-0.6609	0.5508
R	1.0000	1.0000	1.0000	1.0000	0.7906
R^2	1.0000	1.0000	1.0000	1.0000	0.6326
p-valor	0.0001	0.0023	0.0048	0.4053	0.8205
RI 1			1.2263		
RI 2			1.2107		

[1]CN: crown number; FMAP: fresh mass of the aerial part (g); DMAP: dry mass of the aerial part (g); FMRS: fresh mass of the root system (g); DMRS: dry mass of the root system (g); ADMRS: accumulation of dry mass of the root system (%); SSC: total soluble solids content (%); TTA: titratable total acidity (% of citric acid); DQI: Dickson quality index; CLA: chlorophyll A; CLB: chlorophyll B. r: canonical correlation; R^2: coefficient of determination; RI 1: redundancy index between morphological and quality groups; RI 2: redundancy index between quality and morphological groups.

Discussion

Before and after the selection of variables, the PCA approach underlined the need to analyze and interpret FMRS, DMRS, ADMRS, FF, NF, FR, VFR, TRL, CLA, and CLT to explain the responses of the strawberry cultivar 'Albion' to multi-specific mycorrhizal inoculants from different locations and ecosystems. Specifically, PCA makes it possible to simultaneously reduce the dimensionality of a dataset and preserve its variability (Jolliffe & Cadima, 2016) because it is statistically coherent, computationally fast, and scalable (Price et al., 2010). The positive effect of mycorrhizal inoculation on the root system of the plant host (Chiomento et al., 2019a; Chiomento et al., 2021a) is attributed to molecular signaling between symbionts through the release of lipo-chito-oligosaccharides by AMF, which stimulates root formation in the host plant (Oláh et al., 2005).

The correlations between experimental treatments and PCA dimensions allowed us to verify that the multi-specific inoculants from Flores da Cunha in NF and SC ecosystems were directly related to TRL, VFR, FR, RSA, CR, TTA, and TAC. In contrast, the inoculant from the SC in São José was directly related to SSC, DQI, DMRS, ADMRS, NF, FW, and CN. For these ecosystems, 80.70% of the total variability was explained by the first two components, which agreed well with the general rule that at least 70.00% of the total variance in the PCA must be explained by the first two PCs (Rencher, 2002).

By and large, the contribution of mycorrhizal communities from Flores da Cunha to accounting for the total experimental variability observed was the greatest, and should be considered relevant for the selection of the place to obtain the inoculant, especially in the case of agricultural ecosystems. Strawberry crops were established at this soil-inoculant collection site from 2009 to 2016, using cultivar 'Albion' (Chiomento et al., 2019b), the same cultivar used in our study. This indicated that the fungal species collected from the NF and SC communities (Table 1) had the highest affinity for 'Albion' Because AMF are associated with a wide range of plants, clear host specificity is uncommon, although preferences for plant symbionts arising from effector proteins secreted by AMF to manipulate host cells and facilitate successful infection have been reported (van der Heijden et al., 2015). This alters the structure of the host, suppresses innate immune responses, and alters plant metabolism (Zeng et al., 2018).

Mycorrhizal inoculants obtained from agricultural ecosystems in Bom Princípio and Ipê did not show close relationships with any measured variable. Therefore, they did not influence the horticultural performance of strawberries. As the agricultural ecosystems of Ipê and Bom Princípio were affected by anthropization four and six years ago, respectively, and FC SC and SH SC had been modified for a longer time (Chiomento et al., 2019b), we believe that the mycorrhizal communities BP SC and IP SC were less adapted to strawberry monoculture. Despite the lack of AMF-host specificity, a substantial functional diversity can modulate the benefits generated by microorganisms, which include the plant symbiont, fungal species, and their relationships with environmental conditions (Koch et al., 2017).

When we inoculated strawberry plants of cultivar 'Albion' with AMF communities from natural ecosystems (NF), we observed a better performance of this horticultural crop in relation to morphological variables and fruit quality. Thus, we suggest that *F. mosseae* improves plant growth and fruit quality, as it is a coincident

species in communities from NF. The best performance of AMF inoculants from SC was observed for root system and fruit production variables. In this case, *C. etunicatum* and *Glomus* sp. (*caesaris* like) seem to promote strawberry root development and productivity, because they were the two species with equal abundance in the communities of SC.

In Brazil, only one AMF-based commercial inoculant is available, consisting of a single species [*Rhizophagus intraradices* (formerly *Glomus intraradices*)]. Traditionally, commercial inoculants are composed of only one fungal species (monospecific) that may not adapt to the conditions of a given agroecosystem. As the use of mycorrhizal species compatible with the plant symbiont intensifies mutualism, we emphasize that the multi-specific inoculants used here originated from soil adapted to strawberry cultivation (Table 1) (Chiomento et al., 2019b). In grassland ecosystems, the mycorrhizal plant root system is colonized by a community of several fungal species (Maherali & Klironomos, 2012). Researchers and industry must focus on studying the potential of multispecific inoculants composed of native fungal species as bio-tools for the sustainable plant cropping.

The inoculation of plants with AMF native to soils under the cultivation of this plant species contributes to improving its performance and adaptation to nursery and field conditions (Maltz & Treseder, 2015), presumably because indigenous AMF are genetically and physiologically adapted to their native hosts (Oliveira et al., 2017). Thus, for example, the restoration of *Picconia azorica* (Tutin) knobl, native forests was facilitated by the use of AMF, which was more appropriate to the ecological conditions of the environment and the host (Melo et al., 2019). As for strawberries, the addition of native mycorrhizal communities associated with the use of biochar reportedly increases mycorrhizal colonization and improves the development of the root system (Chiomento et al., 2021a).

In the Brazilian subtropics, indigenous AMF communities native to soils at the reference sites for strawberry cultivation (Chiomento et al., 2019b) can be used as bioinput to improve the horticultural potential of this crop in the field as well as under greenhouse conditions. Our findings indicate that the selection of multi-specific mycorrhizal inoculants enhances their positive effects on plant hosts through the maximum benefit of the symbiotic association. Prior to developing commercial inoculants, mycorrhizal genera, species, and strains must be studied for their potential to improve host development. As we verified the dynamic behavior of inoculants depending on their origin, such as those from Flores da Cunha, we believe that careful pre-selection of this bio-tool is indispensable for high-yielding strawberry crop production.

Conclusion

Principal component analysis applied before and after selection of variables, revealed that the number of fruits, fruit flavor, chlorophyll a and total chlorophyll contents, and, mainly, the characteristics of the root system, must be included in the experimental analyzes for further explanation of the responses of the strawberry cultivar 'Albion'. Particularly, AMF communities obtained from Flores da Cunha, Rio Grande do Sul State, Brazil, explained the greater proportion of total experimental variability and, therefore, should be relevant for selecting the place of origin of the AMF inoculants for use in strawberry crops, as they contain the fungal species with greater affinity for cultivar 'Albion' In contrast, the mycorrhizal inoculants obtained from the agricultural ecosystems of Bom Princípio and Ipê, Rio Grande do Sul State, Brazil, did not influence the horticultural performance of strawberry plants, probably owing to the recent intensive anthropization of these agroecosystems.

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