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Genotype x Environment interaction, stability, and adaptability in progenies of *Eucalyptus urophylla* S.T. BLAKE using the AMMI model

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Abstract

One of the determinant factors in the success of breeding programs that aim to select genotypes for different geographical regions is understanding the interaction between genotypes and environments (GxE). The objectives of this study were to evaluate GxE interaction, stability, and adaptability, and determine the need for environmental stratification of open pollinated progenies of *Eucalyptus urophylla*. Five progeny tests were established in study areas with different environmental conditions in southeast and mid-west Brazil. We used a complete randomized block experimental design with 138 to 167 progenies, and variations in the numbers of replicates and plants per plot. The trait measured was diameter at breast height (DBH) at two years of age and the AMMI method was used to determine patterns of GxE interaction. Significant effects were detected for genotypes, environments, and for GxE interaction. The effect of environment was responsible for the greatest proportion of the phenotypic variation, followed by the effect of genotypes and GxE interaction. Some progenies with greater productivity and stability were identified, although stability is not associated with productivity. The stratification of the selection in three specific environments is necessary due to the occurrence of a complex GxE interaction.

Keywords: *: Biplot analysis, eucalypts, forest breeding, stability*

Introduction

Eucalyptus urophylla belongs to a group known as the "Big Nine", which are the nine most cultivated species of the genus in the world (Harwood, 2011). The species is recommended for tropical and subtropical climate regions, as either pure stands or as hybrid combinations (Hodge and Dvorak, 2015). The characteristics of the species include high productivity and wood quality, moderate resistance to water deficit, and tolerance to pests and disease (Assis et al., 2015). As such, it can be planted in areas that are unfavorable for other eucalypt species (Scanavaca Junior and Garcia, 2003).

The success of genetic improvement programs relies on the selection of productive genotypes. This selection requires an understanding of the interaction between genotypes and environments (GxE) in order to minimize or exploit their effects and increase efficiency in genotype selection. Selection is usually based on growth traits, which present a complex pattern of inheritance, making it difficult to predict the responses of genotypes to different environments (Namkoong et al., 1966). Information about the nature and magnitude of this interaction are fundamental, particularly for the selection of characteristics with low heritability (Yan and Kang, 2002).

Although the environmental effect represents 80 % or more of variation, the effects of genotypes and the interaction between the two are the most relevant for selection (Yan and Kang, 2002). The GxE interaction reduces the correlation between phenotype and genotype (Rao et al., 2011) and interferes in genetic gains, which can create difficulties in selection. GxE interaction is one of the major challenges in plant breeding,

especially since it occurs across a diversity of soil and climatic conditions (Vencovsky et al., 2012).

In order to study GxE interactions, it is necessary to establish multi-environment experimental networks (Mustapha et al., 2014). The assessment of interaction in multiple environments can result in the adoption of two different selection strategies: i) stratification of heterogeneous areas in smaller and homogeneous sub-regions for selection; or ii) selection of stable genotypes based on performance in a variety of environments (Adebola et al., 2013; Funga et al., 2017). In order to estimate the GxE interaction, several statistical techniques have been used, including univariate, multivariate, mixed and non-parametric methods (Akbarpour et al., 2014). The least effective method among them to capture the patterns of GxE interaction are those based on analysis of variance and linear regression (Correia et al., 2010). On the other hand, multivariate techniques can be effective tools to study interaction, such as those that include biplots: Additive Main effects and Multiplicative Interaction (AMMI) and Genotype main effects and GxE interaction effects (GGE) (Li et al., 2017).

Gauch (2006) suggests that only one of these methodologies should be used and emphasizes the superiority of AMMI analyses in terms of visualization. Using this method, we obtain two biplot graphs. AMMI1 demonstrates the additive effects on the X axis (genotype means and environments) and the first multiplicative interaction axis, the Interaction Principal Component Analysis (IPCA), on the Y axis. Genotypes with scores similar to zero are stable. Genotypes to the right have higher productivity than the general mean of the measured trait. Grouped genotypes show similar adaptation and groups located near to an environment are similarly influenced by that environment. The second graph, AMMI2, plots the IPCA1 and IPCA2. Genotypes and environments located away from the source contribute to interaction and those with IPCA1 and IPCA2 scores close to zero are stable. When the points occupy the same quadrant in the graph the genotype and environment interact positively and when they are located on opposite quadrants, they interact negatively. Specific adaptation can be identified when the genotype shows positive interaction and high productivity in one environment (Funga et al., 2017). The AMMI model has been widely used for crop species (Akter et al., 2014), although less so for forest species (Chambel et al., 2005; Li et al., 2017).

The objectives of this study were to evaluate GxE interaction, stability, and adaptability using AMMI analysis, and determine the need for environmental stratification of open pollinated progenies of *E. urophylla*.

Materials and Methods

This study included the evaluation of five trials of open pollinated progenies of *E. urophylla*. The germplasm belongs to the Cooperative Program for Forest Improvement (PCMF) of the Institute of Research and Forest Studies (IPEF) and it is representative of the genetic material widely used in Brazil. Progeny

tests were established from 2009 to 2010 in five experimental areas: Anhembi and Itatinga, São Paulo State, belonging to the Department of Forestry Sciences, ESALQ/USP; Selvíria, Mato Grosso do Sul State, belonging to the Teaching, Research, and Extension Farm, FEPE-FEIS/UNESP; and Itamarandiba and Uberaba, Minas Gerais State, at the Aperam and Duratex forestry companies affiliated with PCMF. At each site, we recorded experimental and soil-climatic characteristics pertinent to the environment (Table 1). Management (soil tillage, fertility, weed control, and control of leaf-cutting ants and termites) followed commercial recommendations for each region (Gonçalves et al., 2013). The exception was in Selvíria where mineral fertilization was not used.

Table 1
Characteristics of the sites in which the five progeny tests were established

	Anhembi, SP	Itatinga, SP	Itamarandiba, MG	Uberaba, MG	Selvíria, MS
Spacing (m)	3.0×2.0	3.0×2.0	3.0×2.0	3.0×2.0	3.0×2.5
Repetition	4	4	4	8	5
Trees/Plot	6	6	6	5	5
Latitude	22°28'	23°13'	17°45'	19°18'	20°21'
Longitude	48°07'	48°34'	42°46'	48°01'	51°24'
Altitude (m)	472	827	910	850	375
Soil	NQ	LVAd	LVA	LAc	LVd
Climate	Aw	Cwa	Cwa	Aw	Aw
A.A.T. (° C)	21.8	19.7	22.6	22.6	24.8
A.A.P. (mm)	1300	1372	1100	1474	1309

A.A.T.: average annual temperature; A.A.P.: average annual precipitation; NQ: Typic Quartzipisamment; LVAd: Dystrophic Red-Yellow Latosol; LVA: Red-Yellow Latosol; LAc: Typical Acrylic Yellow Latosol; LVd: Typical Dystrophic Red Latosol. Aw: tropical climate with dry winter; Cwa: humid temperate climate with dry winter and hot summer.

We used a randomized block statistical design for the progeny tests with varying numbers of progenies in each environment (138 to 167). To extract a subset and balance the experimental data for use in the AMMI method (Yan et al., 2011), we discarded about 25 % of all genotypes. A total of 126 progenies were measured for diameter at breast height (DBH, cm) at two years of age. The choice of DBH as the measured trait is due to its correlation with volume, one of the main quantitative traits used in breeding programs (Martinez et al., 2012), and the measurement of DBH is highly accurate and easily obtained during data collection.

For the joint analysis of progeny tests and GxE evaluation, we used the AMMI method, combining two statistical procedures: analysis of variance (ANOVA) and singular value decomposition (SVD). The first decomposes the additive effects of genotypes and environments and the second partitions the multiplicative effects of the interaction of the main components (IPCA). The AMMI uses a linear model and treats the main and interaction effects as fixed (Crossa et al., 2012). The statistical model used follows Gauch and Zobel (1997):

$$Y_{ij} = \mu + g_i + e_j + \sum_{k=1}^{n} \lambda_k \gamma_{ik} \alpha_{jk} + \rho_{ij} + \varepsilon_{ij};$$

where: Y_{ij} is the mean response of genotype i in environment j; μ is the overall mean: g_i is the fixed effect of genotype i; e_j is the fixed effect of environment j; λ_k is the square root of the k-th eigenvalues of the matrices, $(\tau\upsilon)$ $(\tau\upsilon)'$ or $(\tau\upsilon)'$ $(\tau\upsilon)$, of equal non-zero eigenvalues, where $(\tau\upsilon) = \left[\widehat{\tau\upsilon_{ij}} \right]$ is the interaction matrix obtained as the residual of the adjustment to the matrices main effects, by analysis of variance, applied to the matrix of means; γ_{ik} is the i-th element (related to the factor τ) of the k-th eigenvector of $(\tau\upsilon)$ $(\tau\upsilon)$; a_{jk} is the j-th element (related to the factor υ) of the k-th eigenvector of $(\tau\upsilon)$,$(\tau\upsilon)$; ρ_{ij} is the noise present in the data; ε_{ij} is the mean experimental error; i is the genotype variations, $i = (1, 2, ..., g)$; j is the variations of environments, $j = (1, 2, ..., e)$; and p is the non-zero root of the characteristic, $p = (1, 2, ..., \min (g-1, e-1))$. The analyses were carried out using the software R 3.2.0 (R Development Core Team, 2017) with the statistical packages „agricolae" (Mendiburu, 2013), „klaR" (Weihs et al., 2005), and „plotrix" (Lemon, 2006). Statistical significance of the main components (IPCA) was obtained using the *F*-test described by Gollob (1968).

Results

Significant effects (Pr < 0.001) were detected for genotypes, environments, and the GxE interaction (Table 2). The effect of environment was responsible for the greatest proportion of total mean square (96.1 %), followed by the effect of genotypes and GxE interaction. The sum of squares of the interaction (SSGxE) was partitioned into four main component axes (IPCA): the first two were significant based on Gollob's test and explained 65.9 % of GxE variation (Table 2).

Table 2
Analysis of variance and decomposition of the GxE interaction of the principal components (IPCA) for the DBH trait in the five progeny tests.

Source of variation	df	MS	Pr	Exp. (%)	Ac. (%)
Genotype	125	138.3	< 0.001	-	-
Environmental	4	13812.5	< 0.001	-	-
G×E	500	24.6	< 0.001	-	-
IPCA 1	128	33.9	< 0.001	37.8	37.8
IPCA 2	126	25.5	< 0.001	28.1	65.9
IPCA 3	124	17.8		19.3	85.2
IPCA 4	122	13.9		14.8	100.0
Block (A)	20	287.1	< 0.001	-	-
Error	16612	14.4	-	-	-

df is the degrees of freedom; MS is the mean square; Pr is the probability of the test; Exp. is the percentage of variance explanation; Ac. is the accumulated percentage.

Biplot AMMI1 captured 90.6 % of the Sum of Squares (SS), including main effects, GxE interaction, and the IPCA1. In general, the distribution of the progenies on the axis in the abscissa was sparse, while the distribution in the ordinate was more concentrated. These results indicate that the progenies present more variability in productivity than in stability (Figure 1).

Itamarandiba was the only stable environment and Selvíria was the least stable environment. Of the 126 *E. urophylla* progenies evaluated in the five environments, 53.2 % (67) were considered stable (IPCA1 near zero), suggesting that they did not contribute to the complex GxE interaction. The environments in Anhembi, Itatinga, and Uberaba showed positive interaction with 60 progenies, but less than 50 % of these sites presented productivity above the mean DBH (Figure 1).
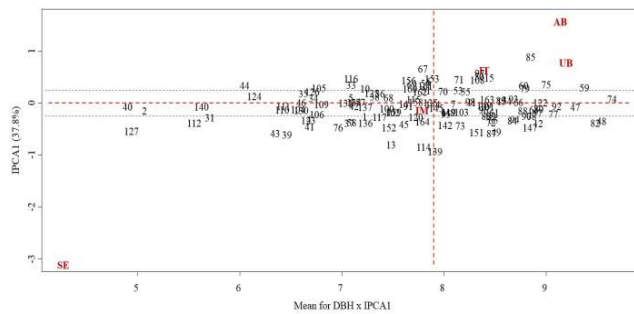
Figure 1
Biplot AMMI1 (Means for DBH×IPCA1) for 126 *Eucalyptus urophylla* progenies evaluated in five environments: Anhembi, SP (AB); Itamarandiba, MG (IM); Itatinga, SP (IT); Selvíria, MS (SE); and Uberaba, MG (UB).

Biplot AMMI2 shows the first two axes that concentrate the effects of the GxE interaction: IPCA1 and IPCA2. The environments in Itatinga and Itamarandiba had the least interactive effect on the progenies, as shown through the short length of the projections. Acute angles between projections means greater similarity in the response of the GxE interaction. As the angles between Uberaba and Itatinga and Uberaba and Itamarandiba were acute, the ranking of progenies do not vary widely among these environments. The lack of correlation was verified among the other pairs of sites with angles of approximately 90º (Figure 2).
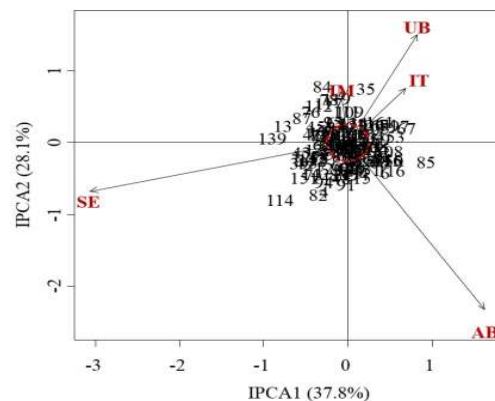
Figure 2
Biplot AMMI2 (IPCA1 × IPCA2) for productivity represented by DBH in 126 *Eucalyptus urophylla* progenies tested in five environments: Anhembi, SP (AB); Itatinga, SP (IT); Itamarandiba, MG (IM); Uberaba, MG (UB); and Selvíria, MS (SE).

Discussion

The effects due to environmental variation was lower than the 80 % reported by Yan and Kang (2002); however, the environment produced more pronounced effects than the other effects, as indicated by Gauch (2006). Thus, the effects of environment and its interaction with genotypes should not be neglected in breeding programs.

The results indicate divergence among the tested environments with a difference in growth of more than twice the DBH at two years after planting; the lowest level of growth was in Selvíria (mean DBH = 4.3 cm) and the highest in Uberaba (9.2 cm). This difference is largely due to the fact that mineral fertilization, which is fundamental for eucalypt growth in the first years after planting (Gonçalves et al., 2013; Silva et al., 2013; Melo et al., 2015), was not used in Selvíria.

The significant effects for genotype indicates genetic variation in relation to DBH, which can be further capitalized in breeding programs. The means among progenies ranged from 4.9 (40) to 9.7 cm (74), indicating a wide variability in performance. For almost 40 % of progenies, growth is within the range expected and similar to the results obtained by Pinto et al. (2014) and Nunes et al. (2016) for clones of *E. urophylla* and *Eucalyptus* sp., respectively, at three years of age.

The detected significant effects for the GxE interaction indicate that progeny responses vary in different environments (complex interaction), thus underscoring the need to analyze stability and adaptability to distinguish groups of genotypes adapted to several specific conditions and/or environments. Pupin et al. (2015) found significant GxE interaction for DBH at two years of age for the same set of *E. urophylla* progenies in these same five environments. In this previous study, the mean obtained was different and the Anhembi environment showed better performance in relation to the other study sites (10.5 cm). It is possible that the genotypes that contributed to a greater mean may have been excluded from the AMMI analysis in order to balance the data.

In the analysis of variance, the main additive effects (environments and genotypes) and the multiplicative effect of the interaction were decomposed and the first two axes were significant, indicating that the GxE interaction was concentrated in IPCA1 and IPCA2. The first two IPCA axes explain most of the variation of GxE (Table 2), although less than the 70 % discussed by Crossa et al. (1991). However, the AMMI method does not seek to recover 100 % of the SS_{GxE}, but rather the proportion most influenced by the effects of genotypes and environments, thus discarding the so-called noise (Duarte and Vencovsky, 1999). This was observed herein as the sum of squares of the IPCAs do not equal the total, leaving a small proportion of noise (6.8 %) consisting of unpredictable and uninterpretable responses (Verrissimo et al., 2012). Similar results were obtained by Mitrovic et al. (2012) and Akter et al. (2014) for annual crops. In these cases, the main feature of AMMI is the ability to capture the majority of the patterns in the first IPCA axes (Crossa et al., 1991).

In proportional terms, the first two IPCAs represent the largest portion of the SS_{GxE} (61.4 %), with 50.8 % of degrees of freedom. In yield trials of soybeans, Zobel et al. (1988) captured 71.0 % of SS_{GxE} with only 19 % of degrees of freedom, indicating that the AMMI model summarized the dataset much more effectively than in the current study.

Biplot AMMI1 indicates that many progenies are stable (Figure 1) although not necessarily productive; that is, stability is not related to productivity. The only stable environment identified in the present study was Itamarandiba. The mean DBH was slightly below the general average (7.78 cm < 7.90 cm), indicating that this environment is suitable for the expression of the genetic potential of the progenies. In progeny trials of *Pinus radiata*, for DBH at 6 to 10 years, Ivković et al. (2015) observed a correlation of the GxE interaction with climatic variables, mainly temperature and precipitation. In our case, levels of rainfall lower than the annual average during the study years may have caused the stability in Itamarandiba (2010 = 965 mm; 2011 = 915 mm; annual historic average of 1100 mm) (Inmet, 2017). Similarly, *E. grandis* families in Itamarandiba, under moderate and prolonged water stress, showed lower productivity levels of the stand and reduced environmental effects on the variation of the phenotype (Silva et al., 2018). Genotype management in a stable environment is more reliable since the genotype ranking will be determined primarily by genotypic effects (Duarte and Vencovsky, 1999). The least stable environment was Selvíria and the mean DBH was well below the other studied environments (4.3 cm). In Selvíria, the rate of survival was also low (54 %) and this was likely the result of limited silvicultural management. That is, the absence of adequate management contributed to an increase in unpredictable and uncontrolled conditions that augment the effects of the GxE interaction (Vencovsky and Barriga, 1992).

Although more than half of *E. urophylla* progenies presented predicable behavior, for selection and recommendation of genotypes, stability should be associated with productivity (Figure 1). Therefore, 32 progenies (25.4 %) can be considered stable and productive, presenting favorable traits for selection and recommendation due to the simple GxE interaction for these progenies. These results are similar to those observed for *E. grandis* progenies in five experiments established between latitudes 08o 89′ to 32°10′ in Brazil and Uruguay (Silva et al., 2018).

Anhembi, Itatinga, and Uberaba showed positive GxE interaction, with 24 genotypes identified as the most productive and stable, which could form a select set of genotypes adapted to these environments (Figure 1). Six of the ten best progenies in terms of both stability and productivity were identical to those obtained by Pupin et al. (2015), who used the Harmonic Mean of Relative Performance of Genetic Values (HMRPGV; Resende, 2007) for all *E. urophylla* progenies. Only one of the high ranking progeny identified by the HMRPGV was not included in the AMMI analysis conducted herein. If we compare the results of AMMI and HMRPGV methodologies, although they agree in terms of productivity, some progenies were less stable in the AMMI analysis. Because the HMRPGV method considers genotypic and non-phenotypic stability, it explores the data in different ways. Despite the differences observed, the use of varying methodologies can be

complementary, offering robust results for the recommendation of genotypes, such as the group of progenies identified in both studies.

Biplot AMMI2 shows the first two axes in which the effects of the GxE interaction are concentrated. Itatinga and Itamarandiba exerted the least interactive effect on the progenies, since they presented shorter projections than the other experimental areas (Figure 2). The angle between the projections determines the phenotypic correlation between environments (Mohammadi and Amri, 2011). Thus, the results suggest that the environments can be divided into three specific groups: i) Uberaba, Itatinga, and Itamarandiba; ii) Anhembi; and iii) Selvíria (Figure 2). The need environmental stratification was also constated in *Eucalyptus saligna* in Brazil (Oliveira et al., 2018), in *Pinus radiata* in Australia (Ivković et al., 2015) and in *Salix* spp in USA and Canada, which used AMMI analysis (Fabio et al., 2017).

Genotypes with scores similar to zero and concentrated around the origin for the two IPCA axes are less sensitive to GxE interaction (Figure 2). Progenies plotted further away from the origin are more responsive and strongly influenced by the GxE interaction, which enables the identification of specific adaptations. Stability is indicative of the progenies respective adaptive amplitudes, that is, stable genotypes tend to be broadly adapted to environments (Duarte and Vencovsky, 1999). Thus, 40 progenies (31.7 %) were considered to be widely adapted and could be recommended for all five environments. Among them, we identified a group of 20 progenies (15.9 %) as having greater productivity, stability, and adaptability. In comparison with Pupin et al. (2015), only six progenies were consistent across both studies for these three characteristics. We detected a few cases of progenies with adaptation specific to an environment, including: four progenies in Itamarandiba; and one progeny each in Uberaba and Anhembi. Two progenies can be considered adapted to the environment in Selvíria, as their performance was superior to the others, although not in terms of productivity.

Conclusion

The effects of the environment and GxE interaction are more pronounced than genotype effects and should not be neglected in the process of selection. There are progenies with greater productivity and stability, although stability is not associated with productivity. The stratification of the selection in three specific environments is necessary due to the occurrence of a complex GxE interaction.

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