



Adaptability and stability of novel eucalypt species and provenances across environments in Brazil at two assessment

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Abstract

The potential effects of climate change plus the expansion of eucalypt plantations to less favorable sites, beyond those where they are currently planted, requires exploring novel eucalypt germplasm to identify taxa less vulnerable to biotic and abiotic stress. To improve plant adaptation to new environments, the first step is breeding programs and/or forming base populations of new and different species. But, to achieve this, what species should be chosen from the almost 1000 existing eucalypt species? To tackle this question, this work evaluated various eucalypt species from different provenances at two assessment in five environments to verify (1) the need for environmental stratification; (2) the best species and provenances per environment, and (3) environmental stability, adaptability, and changes between assessment. The mortality and diameter at breast height of 27 eucalypt taxa originating from wild populations and seed orchards were evaluated. To evaluate the data, we took a factor analytic mixed modelling approach to define mega-environments (groups of similar sites) and characterize the interactions of these with the selected taxa. The analyses allowed both quantitative and graphical identification of optimal combinations of species and sites. Promising taxa identified include *Corymbia citriodora* subsp. *variegata*, *C. henryi*, *Eucalyptus longirostrata*, *E. major* and *E. urophylla*. We place the results of this process in the context of ongoing domestication and breeding of new taxa for challenging sites in Brazil.

Keywords Early selection · Factor analytic · Forest breeding · Forest improvement · Genotype × environment interaction (GEI)

Introduction

Most of the > 20 Mha of commercial eucalypt plantations are established using just nine relatively fast-growing species and their hybrids (Harwood 2011). Most of these plantations are established within a restricted range of environments between about 35° S to 35°

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N (Ferreira et al. 2019) where rainfall and other climatic conditions are favorable for maintaining relatively high growth rates. Most of Brazil's commercial eucalypt plantations lie in the most productive region between latitudes 15° S and 30° S (Ibá 2020). Conditions there are favorable for plantation growth, with infrequent water deficit, moderate temperatures and few major stressors (Elli et al. 2020). Eucalypt plantations in this zone are predominantly clonal, with most cultivars derived from *Eucalyptus urophylla* and *E. grandis* pure species and their hybrids. These species have the most advanced breeding programs in Brazil, comprising advanced generations of recurrent selection and controlled pollination orchards (Gonçalves et al. 2013; Assis et al. 2015; Silva et al. 2019a, b).

Published information on the detail of the breeding programs for these and other eucalypts that have been successfully introduced to Brazil, including the ancestral origins of families and provenances, is comparatively scarce. It is probable that many clonal selections (both pure species and spontaneous hybrids) have been made phenotypically from within the Brazilian eucalypt land race populations rather than as the result of systematic selection and breeding.

However, eucalypt plantations are now expanding to new regions with different, typically more-challenging, environmental conditions, thus, requiring species and provenances that are more resistant to biotic and abiotic stressors (Assis 2014). Besides the challenges of introducing eucalypts to new sites, climate change also influences and often increases pest and disease occurrence, as well as abiotic stresses in traditional eucalypt plantation regions (Silva et al. 2013). Selecting hardier species adapted to sites that are currently challenging may therefore also provide options for sites that will become less favorable in future due to climate change impacts (Bush et al. 2018). Domestication programs for alternative species that might be suited to more difficult sites in Brazil are currently in the early stages, with species and provenance screening being the focus.

These new challenges can be met by widening the available range of eucalypt genetic material currently planted and included in breeding programs. Existing breeds can be made more resilient and better adapted to stressful environments by screening novel provenances, and in some cases, by inter-specific hybridization (Lee et al. 2009). New plantations established in zones that have significantly less favorable climates and soils than traditional planting areas require screening of previously untested species, provenances, and taxa.

The first step to form base populations is to choose the species whose performance, traits and provenances are well known as well as their interaction with diverse environmental conditions (genotype \times environment interaction, GEI). The GEI can be used to define breeding zones by indicating the best species to grow at each site while allowing adaptation studies to the sites (Resende 2007; Malosetti et al. 2013; Araujo et al. 2019). Due to the choice of the adequate species and the provenance is fundamental for the success of eucalypts breeding programs (Eldridge et al. 1994). Moreover, it determines the most adaptable or the most stable genotypes among different environments (Malosetti et al. 2013; van Eeuwijk et al. 2016; Araujo et al. 2019) that can, therefore, be planted across various environments. To this end, Multi-Environmental Trials, based on a series of comparative trials (Smith et al. 2001), are used for identifying and exploring the mega-environments, a requirement for stratification purposes. GEI studies allow checking different genotype performances across sites while determining adaptability and stability over time (Araujo et al. 2019). Adaptability is related to the ability of a genotype to respond favorably to its environment, while stability is related to the predictability of its behavior (Finlay and Wilkinson 1963; Eberhart and Russell 1966). Adaptability and stability studies allow us to check how the effects of GEI act on the behavior of genotypes in the environments where they are tested, allowing the accuracy to make recommendations.

The objective of this work was to evaluate different eucalypt species and provenances at two assessment in five environments to determine (1) the need for environmental stratification; (2) the best species and provenances for a specific environment; and (3) the environmental stability and adaptability behavior over time.

Material and methods

This work builds on the early evaluations of *Corymbia* and *Eucalyptus* species undertaken by Silva et al. (2017). A total of 27 eucalypt taxa from wild populations and seed orchards were studied (Table 1).

The experimental plots had 7×7 plants per plot and area per plant ranging from 6 to 9.1 m², set up in five different environments/sites (Table 2; see also supplementary material FigS4). For each taxon, one plot per site was set up. Some taxa were missing at different sites: maj20967, lon20007, lon11156, lon20786, ccc11246 were missing at Aw-Bor; amp15281 missing at Cwa-Par; uroAV0022N01, maj20967, maj20009, maj15603 and ccv4q were missing at Aw-TM. The mortality, tree height, and diameter at breast height variables were evaluated at two assessment. The evaluated assessment ranged from 1.3 (Aw-TM site) to 2.6 (Am-Mac site) at the assessment 1 and from 3.3 (Cwa-Itam site) to 4.8 (Am-Mac site) years old at the assessment 2 (Table 2). The individual tree volume was calculated at each assessment considering the form factor of 0.5 for all taxa.

The taxa and sites were submitted to a traditional joint analysis using a mixed model and REML/BLUP procedure for DBH at each assessment, as follows:

$$y = X\tau + Z_g u_g + Z_{ge} u_{ge} + e$$

where y is the vector of observations; τ is the vector of fixed effects of sites (replications) and overall mean with associated design matrix X ; u_g is the vector of random genotypic effects of species and provenances within species with the associated design matrix Z_g ; u_{ge} is the random effects of species plot (analogous species x site interaction) and provenance within species plot (analogous provenance within species x site interaction) with the associated design matrix Z_{ge} ; e is the vector of residual effects. The Likelihood Ratio Test (LRT) was used to determine the significance of random effects.

A second approach consisted of applying a series of extended factor analytical (XFAk) models (Thompson et al. 2003; Meyer 2009) to $Z_{ge} u_{ge}$ effects, so that the genotypic covariance matrix of species and provenances within species in the environment could be written as: $(\Lambda\Lambda' + \Psi) \otimes I_g$, in that Λ is the matrix of environment loadings (with dimension number of sites (s) x quantity of retained factors (k)); Ψ is the within-site variance that is not accounted for by the factor loadings, also designed as specific variance; I_g is the identity matrix of species dimension (when adjusted species x site interaction) and provenance within species dimension (when adjusted provenances within species x site interaction). Models with up to $k=5$ (fa1 to fa5) and unstructured model (UN) were fitted and compared based on the Akaike's criterion (AIC).

The survival analysis was performed graphically for each assessment at the species and provenances levels. Besides, the graphical representation of site factor loadings as vector plots for the fa2 models was carried out so that the cosine of the angle between vectors is an estimate of the type-B correlation due to the first two factors while the vector length corresponds to the genetic variance (a similar approach was performed by Bush et al. 2015). The estimates and predictions of the environment loadings and genotypes' factorial scores

Table 1 Summary of *Eucalyptus* and *Corymbia* species and provenance data

Species (code)	Subgenus-section	Taxa code	Seedlot*	Provenance or origin	Latitude	Longitude
<i>Corymbia citriodora</i> subsp. <i>citriodora</i> (ccc)	<i>Blakella</i> <i>Maculatae</i>	ccc11246	DAF 11,246	Yeppoon	23° 07' S	150° 44' E
		ccc5298	DAF 5298	Kirrima	20° 3' S	146° 15' E
<i>C. citriodora</i> subsp. <i>variegata</i> (ccv)	<i>Blakella</i> <i>Maculatae</i>	ccv19664	ATSC 19,664	Barakula SF	26° 10' S	150° 20' E
		ccv19665	ATSC 19,665	Saddler Springs	25° 04' S	148° 02' E
		ccv20582	ATSC 20,582	Richmond Range	28° 33' S	152° 27' E
		ccv20787	ATSC 20,787	SSO Barclays Demiliquin	35° 01' S	145° 13' E
		ccv10220	DAF 10,220	Wolvi	26° 13' S	152° 49' E
		ccv10248	DAF 10,248	Brooyar	26° 45' S	151° 36' E
		ccv11185	DAF 11,185	Woondum	26° 15' S	152° 45' E
		ccv4q	DAF 4q	Cherry Tree	25° 13' S	149° 15' E
<i>C. henryi</i> (ch)	<i>Blakella</i> <i>Maculatae</i>	ccv1122	DSS1122	Woondum	26° 15' S	152° 45' E
		ccvA14C117	IPEF- A14C117	SSO Anhembi (CSIRO 14,426 e 14,434 Woondum and Wondai)	22° 40' S	48° 10' W
		ch20786	ATSC 20,786	SSO Barclays D	35° 29' S	145° 14' E
		ch5554	DAF 5554	Myrtle Creek	20° 23' S	148° 36' E
		ctAN0255N01	IPEF-AN0255N01	SSO Anhembi/SP (Kuranda)	22° 40' S	48° 10' W
		amp 15281	ATSC 15,281	Nerong S.F	35° 32' S	152° 10' E
		amp 18731	ATSC 18,731	Clouds CK SF & TSR	30° 00' S	152° 38' E
		braUS0003N01	IPEF-US0003N01	SSO Urbano Santos/MA	3° 12' S	43° 24' W
		camSE0006N01	IPEF- SE0006N01	SSO Selviria/MS (Notts Crossing and Katherine River)	20° 22' S	51° 25' W
		<i>E. longirostrata</i> (lon)	<i>Symphomyomyrtus</i> <i>Pumilio</i>	lon20007	ATSC 20,007	Starkvale Creek
lon20464	ATSC 20,464			Coominglah	24° 47' S	150° 55' E
lon11156	ATSC 11,156			Diamondy	26° 37' S	151° 17' E

Table 1 (continued)

Species (code)	Subgenus-section	Taxa code	Seedlot*	Provenance or origin	Latitude	Longitude
<i>E. major</i> (maj)	<i>Symphomyrtus Exsertaria</i>	maj15603	ATSC 15,603	27 K SE Gympie	23° 45' S	149° 04' E
		maj20009	ATSC 20,009	Blackdown Tableland	25° 38' S	152° 12' E
		maj20967	ATSC 20,967	Brooweena	23° 49' S	149° 04' E
<i>E. urophylla</i> (uro)	<i>Symphomyrtus Transversaria</i>	maj20491	ATSC 20,491	Blackdown	23° 49' S	149° 04' E
		uroAV0022N01	IPEF-AV0022N01	SSO Avaré/SP (Flores)	23° 6' S	48° 56' W

*Seedlot is the identification of the seeds collected from the species' origin sites, where it is possible to retrieve information about the material

Table 2 Technical data regarding the company, site climate, and geographical coordinates, planting date, and evaluated assessment

Site code	Am-Mac	Aw-TM	Aw-Bor	Cwa-Itam	Cwa-Par
City	Macapá, AP	Três Marias, MG	Borebi, SP	Itamarandiba, MG	Paraopeba, MG
Company	Amcel	Gerdau	Bracell	Aperam	Vallourec
Planting date	Jul/13	Dec/13	Jan/14	Jun/14	Feb/15
Assessment (years)	1 2.6 2 4.8	1.3 4.0	2.4 4.4	1.5 3.3	2.0 3.7
Spacing (m × m)	3.2 × 1.9	3.5 × 2.6	3.0 × 2.6	3.0 × 3.0	3.0 × 2.0
Latitude	00° 37' S	18° 12' S	22° 48' S	17° 54' S	19° 18' S
Longitude	51° 17' W	45° 14' W	48° 54' W	42° 52' W	44° 30' W
Altitude (m; sea level)	115	569	711	1003	750
Koppen Climate	Am	Aw	Aw	Cwa	Cwa
AAT (°C)	27.0	22.5	21.0	21.4	20.4
AAP (mm)	2400	1442	1350	1167	1300

were used to build the GGE biplot (Yan et al. 2000) and obtaining the detailed study of the GEI, as Nuvunga et al. (2015), Peixoto et al. (2016) and Araujo et al. (2019) to verify the stability and adaptability of the genotypes across the environmental gradients, thus identifying the mega-environments.

All analyses were carried out using ASReml 3.0 (Gilmour et al. 2015) and R (R Core Team 2019) software.

Results

In general, the fa2 model has a good fit for the variance structure for the Genotype × Environment Interaction (GEI) effects in the analysis (Table 3). In the Aw-TM and Am-Mac sites, mortality rates ranged from 2 to 60% and from 4 to 80% for assessments 1 and 2, respectively (Table 4). Overall, the highest mortality rate was recorded in the Am-Mac site where *E. longirostrata* (lon) survival rate was the lowest, 1% and 0% for assessments 1 and 2, respectively (Fig. 1a, b). In this site, at assessment 2, except for *C. torelliana* (ct), *E. brassiana* (bra), and *E. camaldulensis* (cam) species (87%, 70%, and 60% survival, respectively), the survival rates of all other studied species were very low (e.g., 4% for *E. amplifolia*). The ct species exhibited the highest survival rate in the Am-Mac site at both assessments (assessment 1–96%; assessment 2–87%) and, consequently, the highest Mean Annual Increment (MAI) in this environment (Fig. 1a, b). Furthermore, in the Aw-TM site, survival rates of cam, ct, and ccc were 100% whereas ch survival was the lowest at both assessments (92% and 86% for assessments 1 and 2, respectively).

For assessment 1, productivity ranged from 7.05 to 30.65 m³ ha⁻¹ year⁻¹ in the Am-Mac and Cwa-Par sites, respectively. For 2, it ranged from 4.98 to 35.74 m³ ha⁻¹ year⁻¹ in the Am-Mac and Aw-Bor sites, respectively (Table 4). At assessment 1, only the site × species interaction variance ($\hat{\sigma}_{\text{site} \times S}^2$) was significant (Table 4) while, at assessment 2, a significant effect was observed on the variance between species ($\hat{\sigma}_S^2$), site-species interaction variance ($\hat{\sigma}_{\text{site} \times S}^2$), and site × provenance interaction within species ($\hat{\sigma}_{\text{site} \times S(p)}^2$). From one assessment to another, the coefficients of determination increased for the species effect (\hat{S}^2)

Table 3 Summary of the number of variance parameters of genotype × environment interaction (GEI) matrix and Akaike's Information Criterion (AIC) for unstructured (us) and factor analytic (fa) variance models fitted to the eucalypt taxa MET dataset at evaluation assessments 1 and 2

	Model	Number of Parameters		AIC	
		Assessment 1	Assessment 2	Assessment 1	Assessment 2
Species level	us	21	21	10,727.86	12,333.33
	fa1	16	16	10,728.44	12,353.32
	fa2	20	20	10,726.53	12,333.59
	fa3	23	23	10,732.05	12,337.3
	fa4	25	25	10,735.78	12,439.99
	fa5	NC	NC	NC	NC
Provenance within species level	us	21	21	10,756.04	12,354.79
	fa1	16	16	10,760.09	12,365.01
	fa2	20	20	10,755.39	12,352.93
	fa3	23	23	10,759.92	12,358.6
	fa4	25	25	10,763.92	12,434.16
	fa5	26	26	11,671.49	13,339.4

NC Not converged

and site × provenance interaction within species ($\hat{C}_{site \times S(p)}^2$) while decreasing for species plot (analogous species × site interaction).

Separating the sites per sector indicated a complex GEI. If the taxa were in the same sector of the polygon it would indicate simple interaction; according to the GGE biplot theory (Yan et al. 2000), with a similar pattern for species (Fig. 2) and provenance within species (Supplementary material—Fig.S2.a and Fig.S2.b) at both assessments. The sites clustered into three mega-environments (1—Am-Mac; 2—Aw-Bor + Cwa-Par; 3—Aw-TM + Cwa-ITAM), the polygon vertices indicate the best performing species in each mega-environment (Fig. 2a, b). The aforementioned three mega-environments are supported by the type-B correlation (Fig. 3). The Aw-TM and Cwa-Itam, Aw-Bor and Cwa-Par sites have the highest genotypic correlations between pairs of environments. The genotypic correlation between the Am-Mac and Aw-Bor + Cwa-Par mega-environments is low (lower correlation with Aw-Bor—angle near 90 degrees at the assessment 1 and near 60 degrees at the assessment 2; approximately zero correlation with Cwa-Par site—angle close to 90 degrees in both assessments; Fig. 3) and negative genotypic correlation with Aw-TM and Cwa-Itam mega-environments (angle larger than 90 degrees in both assessments).

The best performances were observed for *Corymbia torelliana* in the Am-Mac mega-environment; *E. urophylla* in the Aw-Bor + Cwa-Par mega-environment; and *E. longirostrata* in the Aw-TM + Cwa-Itam mega-environment, all being the vertex genotypes in the polygon (Fig. 2a, b). The species of secondary importance are also identified, i.e., those that exhibited good performance in each of these mega-environments. Thus, good performances were observed for *C. citriodora* subsp. *variegata* and *C. citriodora* in the Mac mega-environment and for *C. henryi* in Aw-TM + Cwa-Itam (Fig. 2b).

A provenance effect was observed for *C. citriodora* subsp. *variegata*. The provenance effects change the species general performance at the species level analysis (Fig. 2) since different environment adaptations are observed between provenances. For example, the

Table 4 Estimates of variance components, genetic and non-genetic parameters, site phenotypic averages and standard errors (SE) of Diameter Breast Height (DBH) in different eucalypt species and provenances at two assessment intervals (Assessment 1: from 1.3 to 2.6 years after planting; Assessment 2: from 3.3 to 4.8 years after planting)

Genetic parameter	Assessment 1	Assessment 2
$\hat{\sigma}_S^2$ (species)	16.15 (16.82) ^{ns}	51.36 (29.86) ^{***}
$\hat{\sigma}_{S(p)}^2$ (provenance)	4.94 (2.66) ^{ns}	3.79 (2.58) ^{ns}
$\hat{\sigma}_{sitexS}^2$ (site × species)	63.38 (17.36) ^{***}	29.94 (10.05) ^{***}
$\hat{\sigma}_{sitexS(p)}^2$ (site × provenance)	1.63 (1.87) ^{ns}	6.00 (2.75) ^{**}
$\hat{\sigma}_e^2$ (residual)	283.34 (6.18)	243.19 (5.41)
\hat{S}^2	0.04	0.15
$\hat{S}_{(P)}^2$	0.01	0.01
\hat{C}_{sitexS}^2	0.17	0.08
$\hat{C}_{sitexS(p)}^2$	0.00	0.09
Mortality rate		
Aw-Bor	5%	5%
Cwa-Itam	5%	6%
Am-Mac	60%	80%
Cwa-Par	5%	6%
Aw-TM	2%	4%
Sites MAI averages (m ³ ha ⁻¹ year ⁻¹)		
Aw-Bor	26.28	35.74
Cwa-Itam	11.56	12.04
Am-Mac	7.37	4.98
Cwa-Par	30.65	26.97
Aw-TM	7.05	14.74

^{ns} = Non-significant for Likelihood Ratio Test (LRT)

^{**} and ^{***} = Significant for Likelihood Ratio Test (LRT) at 0.01 and <0.001 p-value levels, respectively; $\hat{\sigma}_S^2$; $\hat{\sigma}_{S(p)}^2$; $\hat{\sigma}_{sitexS}^2$; $\hat{\sigma}_{sitexS(p)}^2$ and $\hat{\sigma}_e^2$ are the estimated variances for species, provenance within species, site-species interaction, site-provenance within species interaction and residual respectively; \hat{S}^2 , $\hat{S}_{(P)}^2$, \hat{C}_{sitexS}^2 and $\hat{C}_{sitexS(p)}^2$ are the coefficients of determination of species, provenance within species, species plot (analogous species × site interaction), provenance within species plot (analogous provenance within species × site interaction)

Richmond Range (ccv20582), Wolvi (ccv10220), SSO Barclays Deniliquin (ccv20787) and Cherry Tree (ccv4q) provenances are adapted to Aw-Bor + Cwa-Par mega-environment whereas SSO Anhembi (ccvA14C117) and Woondum (ccv1122) provenances are adapted to the Aw-TM + Cwa-Itam and Am-Mac mega-environments, respectively (Fig. 4).

The average performance was similar over time (Fig. 5). The main changes were observed in the ranking of *E. longirostrata*, *E. amplifolia* (Fig. 5), assessment interaction between the performances of *E. urophylla* (uroAV0022N01) and Richmond Range (ccv20582) (provenance of *C. citriodora* subsp. *variegata*), better performance of both maj20491 (*E. major*) in assessment 2 and SSO Barclays D. (ch20786) provenance of *C. henryi* over time (Supplementary material—Fig.S3.a and Fig.S3.b). Additionally, few

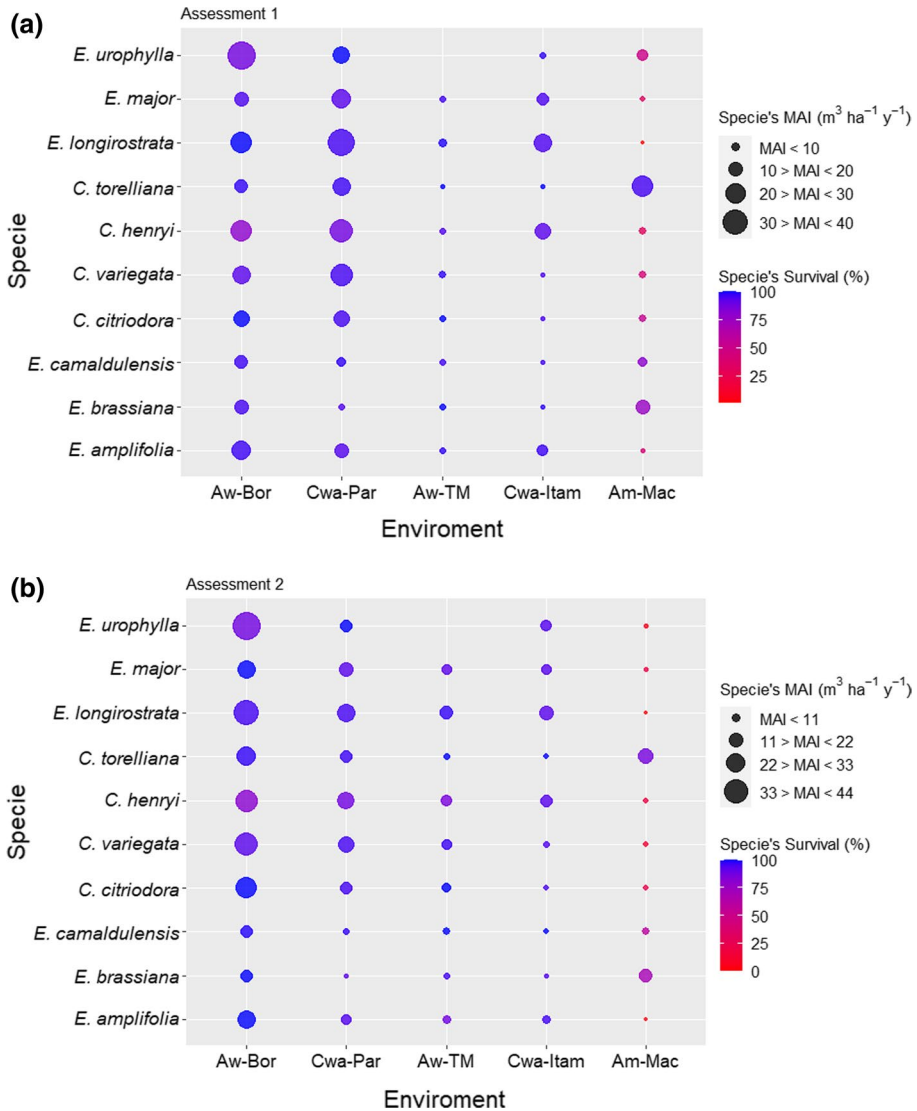


Fig. 1 Survival and Mean Annual Increment (MAI, $m^3 ha^{-1} y^{-1}$) of eucalypt species in five environments and two assessment ranges (Assessment 1, a: range from 1.3 to 2.6 years; Assessment 2, b: range from 3.3 to 4.8 years)

changes were observed in stability between the two studied assessments (indicated by the length of the dashed line perpendicular to the red arrow axis).

Eucalyptus urophylla exhibited the best mean performance and stability in both assessments (Fig. 5). Many *C. citriodora* subsp. *variegata* provenances had good mean performance and low stability in both assessments, however, the Saddler Springs

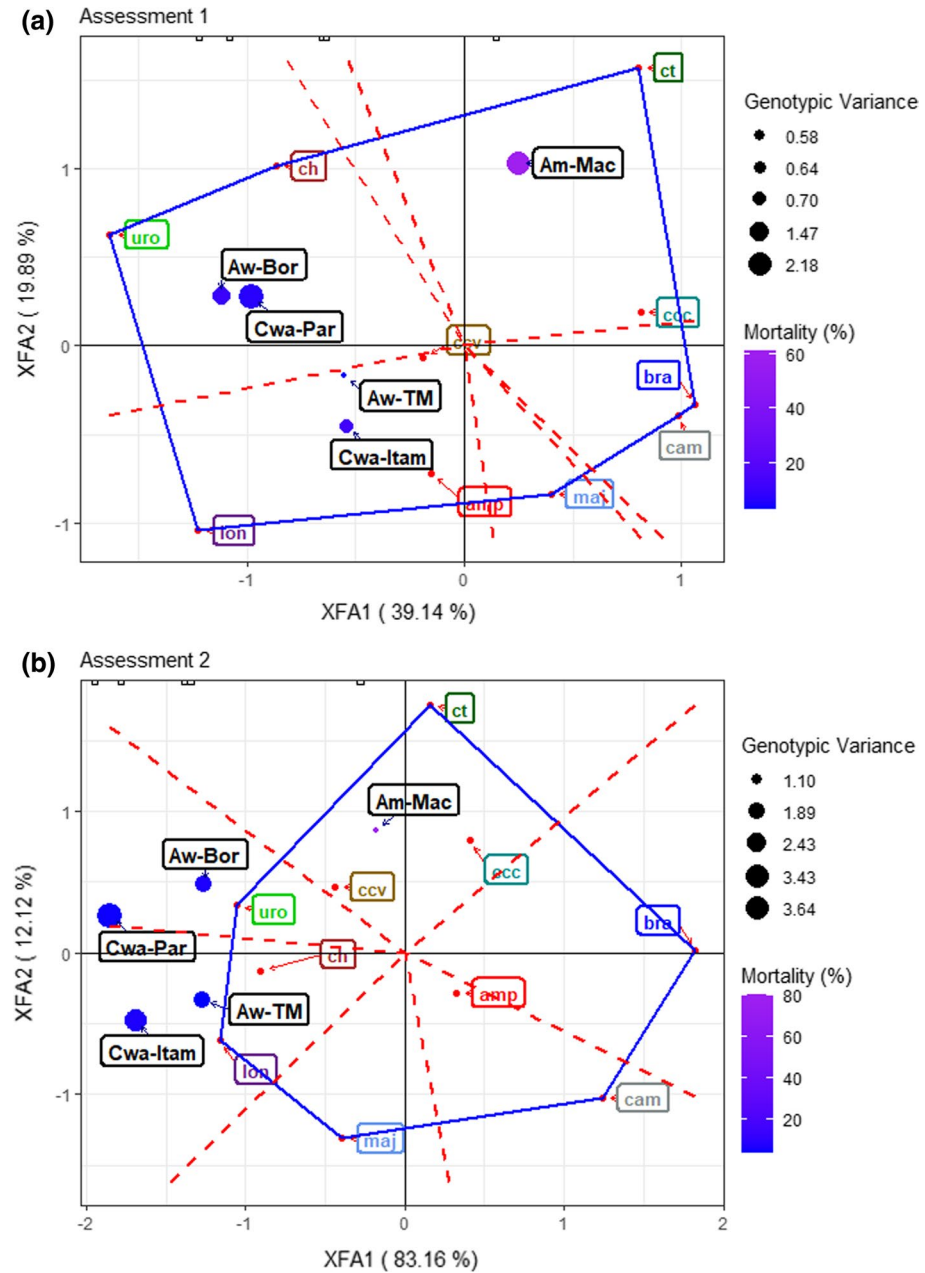


Fig. 2 Polygons of the Genotype-by-Environment interaction (GGE) biplots. Note—Sites: Borebi (Aw-Bor); Itamarandiba (Cwa-Itam); Macapá (Am-Mac); Paraopeba (Cwa-Par); Três Marias (Aw-TM). Assessment 1, a: range from 1.3 to 2.6 years; Assessment 2, b: range from 3.3 to 4.8 years for Diameter Breast Height (DBH)

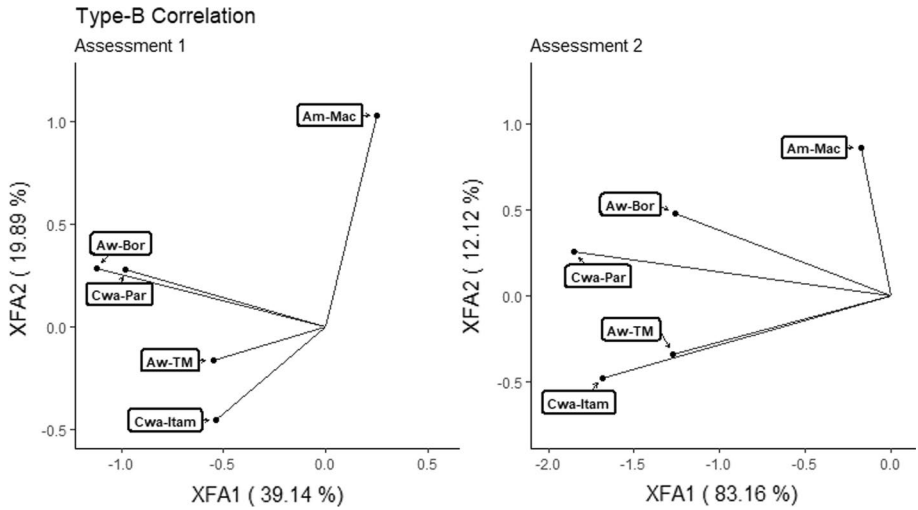


Fig. 3 Vector plot of the two factors from fa2 models showing the type-B correlation between pair of sites in Multi-Environment Trial with eucalypt taxa in two evaluated assessments

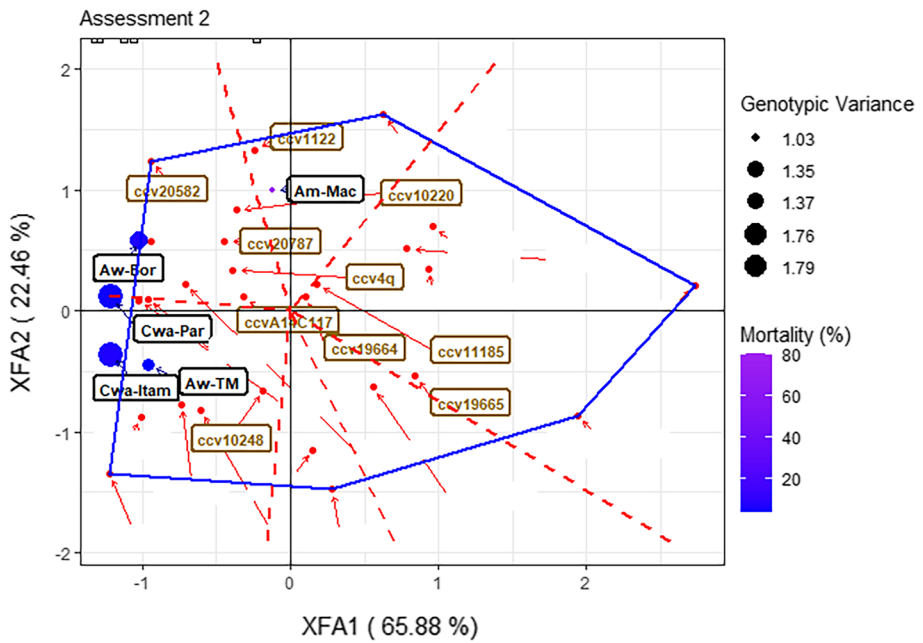


Fig. 4 Polygons of the Genotype-by-Environment interaction (GGE) biplots for provenances of the *Corymbia citriodora* subsp. *variegata*

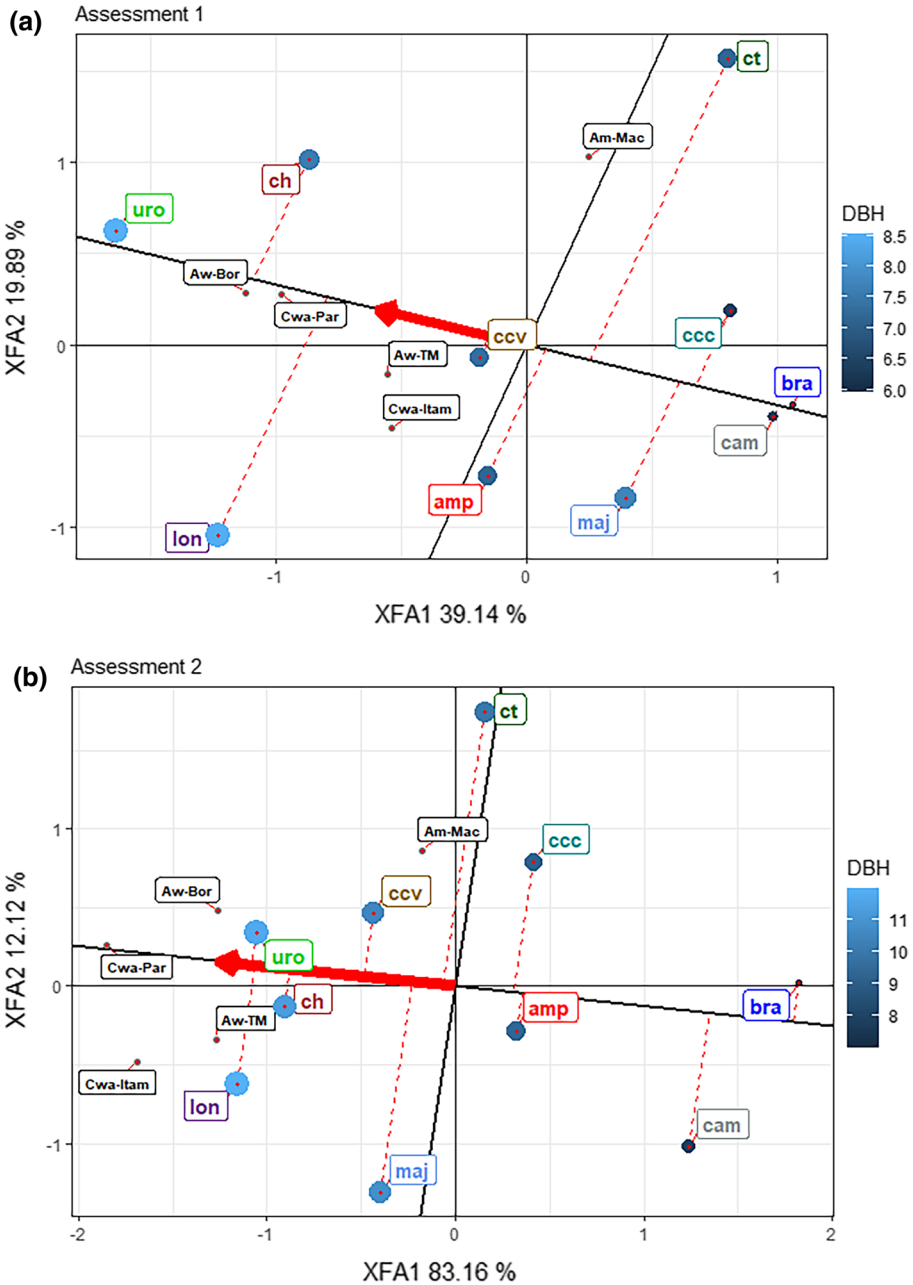


Fig. 5 Mean performance (BLUPs; in the direction of the red arrow) and stability (length of the dashed line perpendicular to the red arrow axis) for the Diameter of Breast Height (DBH) of several eucalypt species in two evaluated assessments. **Note:** Assessment 1, a: range from 1.3 to 2.6 years; Assessment 2, b: range from 3.3 to 4.8 years. Sites: Macapá (Am-Mac), Itamarandiba (Cwa-Itam), Três Marias (Aw-TM), Paraopeba (Cwa-Par) and Borebi (Aw-Bor). “Average-Environment Axis”: (AEC) line that passes through the average environment (red arrow) and the biplot origin

(ccv19665) provenance had a poor mean performance combined with high stability in both assessments (Fig.S3.a and Fig.S3.b).

Discussion

The survival rate generally decreased over time due to the increasing tree vulnerability to mortality in the forests (Allen et al. 2015) probably resulting from intensified competition between trees for site resources. However, the mortality between the first and second evaluations was comparatively higher in the Am-Mac site, emphasizing the difference between this site and all others. In fact, the Am-Mac site forms an independent mega-environment with the most contrasting and limiting conditions, exhibiting high mortality over time. Furthermore, the lower to negative genotypic correlation between Am-Mac and the other mega-environments is because the taxon more adapted to it (*C. torelliana*) different to the species identified for the sites. The stressor factor in this site is the occurrence of *Cylindrocladium* leaf spot (Silva et al. 2017, 2019b), a common disease in tropical regions (Rodas et al. 2005). Therefore, the Am-Mac site can be used to identify genotypes with tolerance to leaf spot disease and to allocate genotypes on sites/environment facing such stress.

Corymbia torelliana exhibited the lowest mortality in the most restrictive mega-environment, the Am-Mac site, highlighting the species high resistance to fungal diseases in Australia (Lee et al. 2005) and the potential for hybridization with members of the spotted gum complex (Genus *Corymbia* Section *Politaria*) for use in this region's breeding programs. Forestry breeding programs in Australia (Lee et al. 2005; Lee 2007; Dickinson et al. 2013) have already applied this strategy and reported that *C. torelliana* x *Corymbia* spp. hybrids improve rooting rate in stem cutting (Shepherd et al. 2008), resistance to biotic and abiotic factors (Lee et al. 2005; Aparecida et al. 2014) and, consequently, productivity (Lee et al. 2009). Additionally, *Eucalyptus brassiana* and *E. camaldulensis* had survival above 50% in the Am-Mac mega-environment and would be suitable for inclusion in a base population in a forestry breeding strategy in this region. This probably relates to the species natural distribution ranging from warm and sub-humid to warm and humid (Eldridge et al. 1994; Fonseca et al. 2010), similar conditions of the Am-Mac mega-environment.

A key strategy of breeding programs is to identify mega-environments to allocate superior genotypes in the target regions (Yan et al. 2000). In this study, three mega-environments were identified at the evaluated assessments. One question however remains, why is it possible to form two environments that clustered together Aw and Cwa? One explanation may be that the Koppen classification is based on average historical data, taking into account seasonality, as well as annual and monthly temperature and precipitation data, but climatic environmental variations between the years can influence it as well.

To this end, the environmental stratification method is suggested for improving breeding strategy and selecting superior material since it allows setting up orchards or seed production areas for the best-adapted germplasm species and provenances to identify and select the most stable and productive materials for each mega-environment. This is the core of some eucalypts species breeding programs in Brazil (Assis 2014; Castro et al. 2018; Silva et al. 2019a, b).

Eucalyptus longirostrata species was the best adapted to the Cwa-Itam + Aw-TM mega-environment (Diamondy and Starkvale Creek provenances) with satisfactory performance in the Aw-Bor + Cwa-Par mega-environment (Coominglah provenance). This result was similar to the *E. longirostrata* provenances in three Australian sites where differences

between provenances were observed in one of the sites (Henson and Smith 2007). Also, *E. longirostrata* was promising in subtropical regions in Australia and South Africa (Gardner et al. 2007; Lee et al. 2010).

Eucalyptus urophylla was expected to have the highest productivity across the trials since it is the main species planted in Brazil (Silva et al. 2019a) often in hybrid combination with other species. It is known to be particularly productive in the Brazilian subtropical regions (Gonçalves et al. 2013). However, this species' productivity was not the highest in all trials, for example it was neither the best adapted to the Am-Mac nor the Aw-TM+Cwa-Itam mega-environments. However, *E. urophylla* from a single seedlot (uroAV0022N01) was best suited to the higher-productivity mega-environment (Aw-Bor+Cwa-Par). Though this seedlot has not been selected for commercial deployment, it already shows some level of improvement in Brazil, and also exhibited high mean performance and stability at assessment 2. This seedlot comes from a seed orchard in Avaré (São Paulo state, Brazil), whose origin is Flores and Timor in Indonesia. As mentioned, *E. urophylla* has been worked by breeding programs in Brazil, with several productive clones being obtained, a work that has not yet been carried out for the other species that showed good performance in this study.

Corymbia citriodora subsp. *variegata* and *E. longirostrata* performance/productivity changed in response to environmental gradients (Brawner et al. 2013). These authors clustered these species according to moisture related (e.g. rainfall, wetness index), soil and temperature-related variables (e.g. minimum and average hottest temperature), unlike the present study. However, the study by Brawner et al. (2013) did not report on the *Cylindrocladium* leaf spot incidence, which may be the determining factor for the different results reported here. Our study indicates that *C. citriodora* subsp. *variegata*, mainly Woondum (ccv1122) provenance had trees with some level of tolerance to leaf spot disease. Saddler Springs, the most inland and driest provenance (ccv19665) of the *C. citriodora* subsp. *variegata* had the poorest mean performance. Conversely, the Richmond Range (ccv20582) provenance showed good potential and could form the basis of a breeding population. Genetic improvement of both *C. torelliana* and *C. citriodora* subsp. *variegata* would be beneficial. *Corymbia torelliana* was the only species with high tolerance to the *Cylindrocladium* leaf spot in our study, and significantly improves vegetative propagation success (Lee 2007). Growth of CCV provenances including Wolvi (ccv10220) and Woondum (ccv1122) was superior, and these would be suitable for inclusion in base populations that could be used to select material both for pure species deployment and hybridization with *C. torelliana*.

The *C. citriodora* subsp. *variegata* adaptability (Fig. 2), as well as the mean performance and stability of *E. longirostrata*, *C. henryi* and *E. urophylla* (Fig. 4), changed between the two studied assessments. This result indicates that these species' stability and adaptability may change over time and these changes must be considered in future tests. These changes may compromise the early selection of trees. Eucalypts are prone to these changes with studies showing that a genetic correlation between 2 and 5 years decreased from 0.83 to 0.73 (Moraes et al. 2014a, b). Thus, there is always some percentage, maybe even higher than 20% of non-genetic factor that should be considered as a risk of loss of superior material in an early selection that expresses its high performance only at a later assessment.

It is important to point out that some taxa were missing in some environments, which means that taxon-environment interactions can only be inferred for some combinations of species and site. However, the data still allow us to make some inferences on species performance, define mega-environments and the interaction between these. The lack of

within-site design did not allow the estimation of some parameters such as heritability for each site. In addition, it reduces experimental precision since only a single residual is allowed for all sites. However, by using a multivariate model, the environmental heterogeneity is captured, which softens the problems arising from the lack of design.

We suggest that as performance rankings were generally quite stable between assessments for the *E. longirostrata* provenances tested, there should be few concerns with changing adaptability between early and late assessments. However, the stability of Coomnglah (lon20464) provenance did change over time (Supplementary material – Fig.S3.a and Fig.S3.b). Only this provenance was tested in the Aw-Bor site, exhibiting good survival and better adaptation to the Cwa-Par and Cwa-Itam sites (Supplementary material – Fig.S1.a and Fig.S1.b). However, it is noteworthy that the *E. longirostrata* is not well adapted to hot and humid regions, with the occurrence of *Cylindrocladium* leaf spot in Brazil (Silva et al. 2017). Similarly, disease susceptibility led to research and development on this species being abandoned in Queensland (Pers. comm., D. Lee 2021). There is evidence in Brazil that the species is site-sensitive, requiring good edaphic conditions for acceptable growth (Silva et al. 2018). Early selection for disease resistance coupled with improved definition of acceptable sites will be required for future development of an improved breed of *E. longirostrata* in Brazil.

The temporal stability of *C. citriodora* subsp. *variegata*, *C. henryi* and *E. major* was low relative to *E. longirostrata*, with significant rank changes between assessments 1 and 2. Temporal effects on provenance ranking should be considered carefully when making early selections, especially in species that might be grown for longer rotation lengths (> 12 years) associated with timber production. However, temporal effects should not be of lesser concern for early selection of *E. longirostrata*. It is important to acknowledge that, in this study, there are variations in the site evaluation assessments, which will have affected the stability analyses. As a follow-on from this preliminary trial series, it will be important to progress to trials containing a wider range of genetic entries on sites within the mega-environments delineated as suitable here. These trials will allow more-accurate determination of genetic parameters and assessment-assessment correlations (i.e. temporal stability) for growth, disease and other key commercial traits.

The genotypic variance ranged from low to high in the Am-Mac environment from one assessment to another. This is closely related to survival rate, despite the high mortality at the earliest assessment, some trees were able to survive. Likewise, similar mortality rate results were found for eucalypt clones in the same region (Araujo et al. 2019). This study highlights the high expression of the genotypic value for productivity in the early stages in Am climate; however, at a later assessment, the survival and genotypic variance decreased. This result indicates that, in this environment, the first step towards population improvement is tolerance (survival) and, at a later stage, productivity should be targeted. In fact, if disease susceptibility of genotypes with higher growth potential has a detrimental effect on overall plantation productivity, then a balance must be achieved between two desirable but partly incompatible opposing goals (Brown and Rant 2013), i.e. selection for disease resistance and growth traits. A strategy of step-wise improvement can be adopted, starting with the best-adapted species for a particular mega-environment. Furthermore, early selection can be adopted based on genotypic value since the genotypic value is that of the candidate itself, i.e., species or provenance itself, rather than its progenies (Bernardo 2020). In the later stages, individual trees with high genotypic values can be selected in the breeding program.

Conclusions

1. The complex taxa and environment interaction observed allowed the identification of the best *Eucalyptus* and *Corymbia* species for each mega-environment. The environmental stratification identified three mega-environments to do this;
2. Significant changes in environmental stability and adaptability are observed between assessments 1 and 2 for some taxa including *Corymbia citriodora* subsp. *variegata*, *C. henryi* and *E. major*;
3. When more than one provenance was tested, a temporal effect of provenance was evident for *C. citriodora* subsp. *variegata*, *C. henryi* and *E. major* and should be considered in an early selection. However, the temporal effect of provenance is not a concern for *E. longirostrata* in a possible early selection.
4. The Am-Mac is the most suitable environment for early selection, due to the high disease stress in the first years after planting.

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