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Climate and water availability impacts on early growth and growth efficiency of Eucalyptus genotypes: The importance of GxE interactions

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ABSTRACT

Predicting Eucalyptus plantation productivity in the face of climate change is a key challenge for intensively managed forest plantations around the world. Forest industry tree improvement and advanced silvicultural programs are charged with maximizing forest production but face challenging selection choices where Eucalyptus genotypes may be sensitive to genetic × environment interactions (GxE). Our study investigated the importance of GXE interactions by measuring the early (establishment to 2.6 years old) cumulative growth response of 30 selected genotypes of *Eucalyptus globulus*, *E. nitens*, *E. badjensis*, *E. smithii, E. nitens* × *globulus* and *E. camaldulensis* × *globulus* hybrid seedlings established across contrasting water availability conditions (High vs Low Irrigation). We compared the same genotypes at a low vapor pressure deficit (VPD) and clayey soil (North site) and a high VPD sandy soil (South site) in order to evaluate the stability of these genotypes across environmental gradients and thus evaluate the importance of genetic versus environmental impacts on growth. Stand growth was evaluated at 2.6 years when leaf area index (LAI) reached canopy closure in order to estimate a growth efficiency relationship (GE) with current annual increment (CAI). As expected, irrigation increased cumulative growth and LAI for all taxas, except for *E. smithii* at the North site. Genotypes showed large significant differences of performance within and across sites under each irrigation treatment. However, a strong relationship between North and South cumulative volume at age 2.6 years was observed for irrigated genotypes but not for non-irrigated genotypes. This suggests that a large GxE interaction may be expected under low water resource availability conditions associated with strong effects in ranking change of evaluated taxas and genotypes. Comparing taxas with at least two genotypes or more in our experiment, GE increased under High Irrigation for all taxas across sites. However, *E. nitens* × *globulus* hybrids showed small differences between High vs Low Irrigation treatments GE relationships compared to *E. nitens* and *E. globulus* genotypes. Our results suggest the need for strategic allocation of genotypes to contrasting drought risk environments and the need to assess our understanding of how particular genotypes interact with water stress conditions.

1. Introduction

Eucalyptus plantations occupy more than 20 million hectares globally (Ribeiro et al. 2015) and Eucalyptus is one of the most intensively managed commercial forest species in the world leading to a doubling of growth rates in many areas (Binkley et al. 2017). Increased productivity has been achieved through a combination of silvicultural improvements (site & soil preparation, weed control, fertilization) and selection of the appropriate genotypes (Stape et al. 2004, Du Toit and Dovey 2005). In fact, studies show that genetic gains can only be achieved under the best silvicultural treatments that effectively ameliorate site limiting factors and maximize site-specific resource availability (Dye 2000, Ryan et al. 2008, Stape et al. 2010, Dutkowski and Potts 2012). However, large uncertainties exist regarding how genetic × site resource availability interactions may impact genetic improvements (Harper et al. 2009, Baesso et al. 2010, Medlyn et al. 2011) and the future selection of Eucalyptus genotypes (White et al. 2009b, Bleby et al. 2012). Resolving this uncertainty may be particularly

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critical for Mediterranean Eucalyptus species because of declining water availability under certain climate change scenarios that may impact the direction of current genetic tree improvement programs and plantation productivity estimates across the landscape (Fearnside 1999, Whitehead and Beadle 2004, White et al. 2009a, Austin and Van Niel 2011, Ling et al. 2012, Rody et al. 2012, Dye 2013, Fensham et al. 2014, Correia et al. 2014). In fact, clonal deployments of Eucalyptus plantations by the forest industry have not always achieved expected results, especially where large environmental gradients exist on a given landscape (Huth et al. 2008, Crous et al. 2013). Consequently, clonal forestry practices are shifting toward specifically matching clonal material to a site rather than selection of a group of clonal materials for broader site conditions. However, despite the use of regional genetic trials for testing genotypes, we lack information on the performance of highly selected genotypes over large environmental gradients (Johansson and Tuomela 1996, Pita et al. 2003, Costa E Silva et al. 2004, Dos Reis et al. 2006, Silva et al. 2006). Therefore, studies that examine the magnitude and stability of growth response for genotypes under manipulated resource availability or environmental gradients may provide insights on the importance of GxE interactions under climate change scenarios (Watson et al. 1999, Mummery and Battaglia 2002, Whitehead and Beadle 2004, White et al. 2009b).

Our study investigated the genetic × environment growth response of 30 selected contrasting Eucalyptus genotypes established under two water availability conditions (summer irrigated vs control) at two sites with different atmospheric demand and soil conditions. Our main objective was to evaluate the stability of volume growth for contrasting genotypes under divergent water and environmental limitations. Specifically, we evaluated two key questions 1) how stable is volume growth for different genotypes under contrasting water availability and 2) are genetics or resource availability more important as drivers of volume growth, leaf area and growth efficiency across sites with contrasting atmospheric demand and soil types?

2. Materials and methods

2.1. Site description

Our study was conducted at two sites with contrasting water availability conditions in south central Chile (Fig. 1).

The North site was located in Constitución city, Maule region of Chile (35° 18′ 49.14″ S, 72° 23′ 23.66″ O). Land use history was a forest nursery area that had Eucalyptus sp. seedling production and cuttings orchards. The site is located 3 km from the coast and approximately 20 m.a.s.l. Soils are derived from granitic sediments, classify as a Huelon soil series (CIREN, 1999), fine loam, mixed, thermic Aquic Xerochrepts with a clayloam surface and clay texture at depth. They are moderately well drained along the profile, and present < 5% slope (Table 1). Mean annual temperature during the last three years at the site was 12.6 °C with a minimum temperature of 9.1 °C in July and a maximum of 16.1 °C in January. Total precipitation during our experiment was 829 mm year^{-1} in 2014 (first growing season) and 967 mm year^{-1} in 2015 (second growing season). The South site is located 9.6 Km south of Yumbel, Bio-Bio region, central south Chile (37° 8′0.01″S, 72°27′34.70″W) (Fig. 1). Previous land use at the site was a *Pinus radiata* D. Don hedge field that was harvested, stumps were removed mechanically, and remaining residues were crushed and incorporated by harrowing. Soils are an Arenales soil series (CIREN, 1999), a mixed, thermic Dystric Xeropsamments corresponding to young, deep and coarse volcanic black sands of andesitic and basaltic volcanic origin deposited by rivers in flat areas with < 3% slope. Soils are very rapidly drained, have a low soil water holding capacity, and soil texture is sandy loam in the first 20 cm; deeper soil horizons have a sandy texture with increasing content of coarseness and gravel with depth. The water table may fluctuate in these soils between 70 cm (winter) to 120 cm (summer) in many areas (CIREN, 1999; Rubilar et al. 2013), and local assessments in winter showed a water table depth of 150 to 300 cm in winter. Soil texture was determined by Boyoucos, bulk density using 100 cm^3 diameter core cilinders and weighing oven dried soil at 105 °C of each core. Soil water holding capacity was estimated as the difference between permanent wilting point (PWP) and field capacity (FC) points determined using a pressure plate apparatus (Soil Moisture Inc., USA). Organic matter, total N and C were determined using a CHN Infrared mass spectroradiometer (SERCON Scientific Inc.) and mean values of each soil property every 20 cm depth increments were obtained from soil samples excavated on each block at each site (Table 1). Mean annual temperature during the last three years at the site was 13.8 °C with mean monthly records of 7.6 °C in July (minimum) and 20.5 °C in January (maximum) temperatures. Rainfall was 1252 mm year^{-1} in 2014 (first growing season) and 1102 mm year^{-1} in 2015 (second growing season) (Fig. 2). Monthly rainfall and maximum daily VPD information from each site obtained from 15-minute data records from nearby (< 1km) weather stations is presented in Fig. 2.

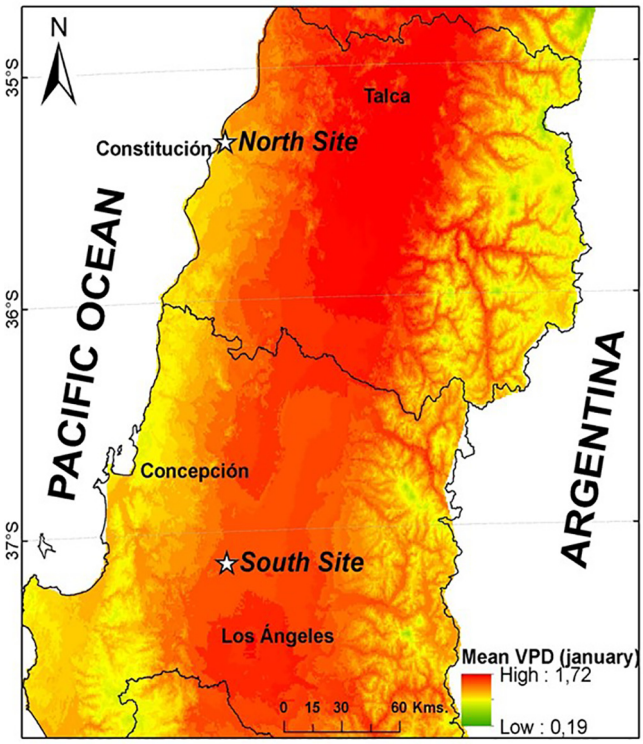

Fig. 1. Location of study plots in a north coastal, low atmospheric demand and clay soil site (North site), and a central valley, high atmospheric demand and sandy soil site (South site) in central Chile.

2.2. Genotypes and experimental design

At both sites, soil preparation lines were 3 m wide and, subsoiled to 80 cm depth. A Savanah D8 plow subsoiler was used to create 15–30 cm mounds to facilitate seedling establishment. Between July and August 2013 at both sites, 30 Eucalyptus genotypes, evaluated as top-ranking selections by the tree improvement programs of CMPC and ARAUCO forest companies, were planted in a randomized complete factorial block design with 3 replicates for each of two irrigation treatments (Low and High). Plant genetic material consisted of 17 cuttings and 2 seedlings of *Eucalyptus globulus* (EG), 6 cuttings of *E. nitens* × *globulus* hybrids (ENG or *E.gloni*), 2 seedlings of *E. nitens* (EN), and single cuttings of *E. camaldulensis* × *globulus* (ECG or E.camglo), *E. badjensis* (EB) and *E. smithii* (ES). Plants were established at a 3 × 2 m spacing (1666 trees ha^{-1}), and experimental plots consisted of 5 × 5 trees with 3 × 3

Table 1
Mean soil physical properties values at the North and South sites evaluated from soil pits excavated to 1 m depth for each block at each site. Standard error of each soil property is indicated in parenthesis.

Site	Depth (cm)	B.d. (grcm^{-3})	SWHC	O.M.	clay	silt	sand	N Total	C Total
			%						
North									
	0–20	1,25 (na)	8,50 (1,82)	1,57 (0,29)	48,1 (2,93)	32,6 (2,42)	19,1 (5,22)	0,12 (0,02)	1,43 (0,32)
	20–40	1,32 (na)	5,29 (1,99)	1,40 (0,35)	41,4 (2,83)	35,8 (3,59)	22,7 (3,10)	0,10 (0,01)	1,17 (0,22)
	40–60	1,42 (na)	4,67 (1,71)	1,71 (0,27)	32,3 (10,6)	40,0 (6,03)	27,5 (5,46)	0,09 (0,01)	1,07 (0,20)
	60–80	1,42 (na)	4,70 (1,65)	1,76 (0,36)	37,5 (18,0)	36,8 (13,6)	25,5 (5,58)	0,07 (0,02)	0,94 (0,26)
	80–100	1,42 (na)	4,56 (1,37)	1,55 (0,32)	33,2 (19,9)	39,8 (11,6)	26,8 (9,56)	0,06 (0,02)	0,81 (0,31)
South									
	0–20	1,50 (na)	4,46 (1,25)	1,28 (0,68)	0,99 (1,27)	12,3 (2,36)	86,6 (2,49)	0,13 (0,09)	1,54 (1,02)
	20–40	1,45 (na)	4,79 (0,98)	0,44 (0,12)	1,50 (1,16)	5,16 (4,35)	93,3 (4,02)	0,03 (0,01)	0,36 (0,14)
	40–60	1,43 (na)	5,07 (0,90)	0,30 (0,05)	2,06 (0,92)	3,53 (4,34)	94,3 (3,71)	0,01 (0,00)	0,21 (0,08)
	60–80	1,43 (na)	4,88 (0,83)	0,27 (0,10)	2,06 (1,01)	4,31 (3,49)	93,6 (2,75)	0,01 (0,00)	0,13 (0,05)
	80–100	1,43 (na)	5,15 (0,98)	0,22 (0,06)	0,90 (1,27)	6,80 (2,97)	92,2 (3,19)	0,01 (0,00)	0,10 (0,01)

B.d. = Soil Bulk density, SWHC = Soil water holding capacity, O.M. = Organic matter, N Total = Total Nitrogen, C Total = Total Carbon, na = not available.

trees internal measurement plots.

Our analyses included a) all individual genotypes and b) higher level taxa (species or hybrid) that had at least two tested materials. The latter was used to minimize the effect of a single taxon that are not currently deployed extensively for commercial plantings but are included in operational tree improvement programs. For example, *E. globulus* and *E. nitens* have been extensively planted in Chile since the 80́s, but during the last 5 years an increasing area has been planted with *E. gloni*, a high value hybrid combining desirable fiber and pulp yield gains, high resistance to drought and cold temperatures, and low susceptibility to forest pests.

From October 2013 to January 2014 a sprinkler system irrigated the

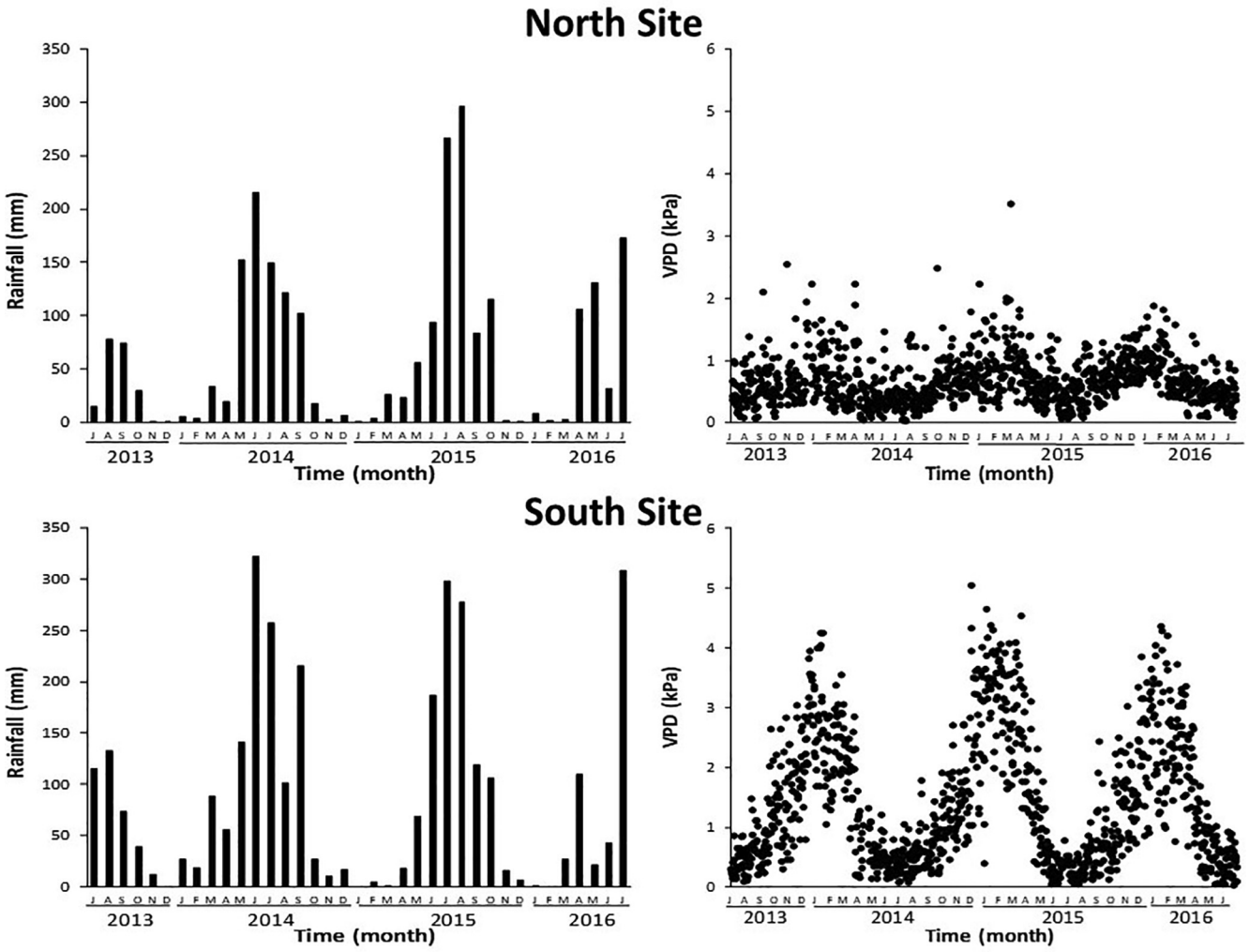

Fig. 2. Seasonal variation in rainfall (mm month^{-1}) and maximum daily vapor pressure deficit (kPa) at the low atmospheric demand and clay soil site (North site), and the central valley high atmospheric demand and sandy soil site (South site) from July 2013 to July 2016.

experimental areas at both sites to ensure early survival during summer months for both treatments. In January (South site) and February (North site) 2014, a drip irrigation system was installed to provide a controlled delivery of water supply on the experiment. Irrigation was applied until April 2014 during the first year, from October to June (unusual extended dry season) in 2015, and from November to April in 2016. The irrigation treatment (defined as "High Irrigation") supplied water daily in order to maintain soil water availability above mid-range between permanent wilting point (PWP) and field capacity (FC) of the soil during all the years of evaluation. The "water-stress" treatment (defined as "Low Irrigation") received no additional water, except during the first 6 months after planting where irrigation was applied to provide a maximum of 25% of the range between PWP and FC to ensure early establishment of all planted trees. The High Irrigation treatment at the North site added 1268 mm ha^{-1} of water in 2014–2015 (November to June) and 726 mm ha^{-1} of water in 2015–2016 (December to March), and for the Low Irrigation treatment 12 mm ha^{1} of water were applied in 2014–2015 and no irrigation was supplied in 2015–2016. At the South site, the High Irrigation treatment added 393 mm ha^{-1} of water in 2014–2015 (December to April), and 178 mm ha^{-1} of water in 2015–2016 (November to April). The Low Irrigation treatment added 89 mm ha^{-1} of water in 2014–2015 (January to February) and 40 mm ha^{-1} of water during 2015–2016 (November to March). A summary of annual irrigation inputs for each study site is presented in Table 2. Nutrient additions were applied to eliminate any potential nutritional deficits. During spring (September-November) of each growing season (2014 and 2015), individual trees at both sites were fertilized with a commercial fertilizer at a rate of 64 g of N + 46 g of P + 9.2 g of K + 5.4 g of Mg + 11 g of S + 3 g of B. Fertilizer was applied by hand, broadcasting the fertilizer mix approximately within a 1 m band from the planting line. Pre-planting and post planting broadcast weed control was applied to the whole area (2.5–3.0 Kg ha-1 Glyphosate) during the first and second growing seasons in order to maintain weed free conditions in the experiments at both sites.

2.3. Measurements

We estimated stem volume using annual measurements of tree diameter and height. We measured ground line diameter (GLD) at 10 cm above ground level (± 0.1 cm) until 1 year of age and diameter at breast height (DBH, ± 0.1 cm) afterwards. Tree height was measured using a height pole. We estimated individual tree volume (VOLt) as: $Diameter^2$ (GLD or DBH) *HT*0.33; and volume per hectare estimates (VOLha) were obtained by summing individual tree volumes for each plot and scaled to the hectare level for each of treatments and sites (North site High Irrigation, VolN-high; North site Low Irrigation, VolN-low; South site High Irrigation, VolS-high; South site Low Irrigation, VolS-low).

Tree survival for each plot was evaluated annually and current annual increment (CAI) was estimated for the last growing season as the difference between 2015 and 2016 cumulative annual volume growth estimates.

Leaf area estimates for each plot at 1.8 years after planting (May 2015) were obtained from the midday (11:00 to 14:00) photosynthetically active radiation (PAR) interception, measuring PAR below the canopy (n = 12) and outside it (n = 3) using a ceptometer (Li-191R & Li-250, LICOR Scientific, Lincoln, Nebraska USA). Leaf area index was calculated using Beeŕs law with a light extinction coefficient of 0.5 and appropriate corrections for deviation of sun angle (Chen and Black 1991). Finally, growth efficiency (GE) was estimated as the ratio of CAI and leaf area index (LAI) estimates.

Table 2
Summary of annual water inputs at each site considering annual rainfall and Low and High Irrigation treatments. Annual inputs presented for 2016 only consider until March 2016.

Site	Year	Rainfall (mm $year^{-1}$)	Low Irrigation (mm $year^{-1}$)	High Irrigation (mm $year^{-1}$)
North	2014	829	0	68
	2015	967	12	1406
	2016	12	0	520
South	2014	1302	18	55
	2015	1102	83	384
	2016	2	28	132

2.4. Statistical and data analyses

We applied ANOVA to evaluate differences in growth, survival, leaf area index and growth efficiency among genotypes at each site for each irrigation treatment (site specific response to soil water resource availability). Graphical comparisons of the magnitude of ranking change and direction (increase or decrease in ranking) for each evaluated genotype were made by comparing cumulative volume growth at each site under both irrigation treatments, and also under each irrigation treatment between sites. We estimated the percent cumulative growth gains attributed to differences in resource availability or genotype differences across sites or within a single site considering all genotypes or within *E. globulus*, *E. nitens* and *E. nitens* × *globulus* hybrid taxa. For each irrigation treatment, we used regression analyses to assess differences in stand volume estimates accumulated after 31 months (2.6 years) at each site for all evaluated genotypes and taxa with more than a single genotype (*E. globulus, E. nitens* and *E. nitens* × *globulus* hybrids). Statistical analyses considered blocks and genotypes as random effects and irrigation treatments as fixed effects using SAS software version 9.4 and modules PROC REG and PROC MIXED and the Satterwhite degrees of freedom option (SAS Institute Inc., Cary, NC, 2004). Linear and nonlinear regression analyses were evaluated between leaf area index (LAI) and annual growth (CAI). Models were compared using the Akaike Information Criteria (AIC) and RMSE values using the Fit Curve procedure in JMP statistical software (JMP Pro 14, SAS Institute Inc.) and PROC REG and PROC NLIN procedures (SAS version 9.4 SAS Institute, Inc., Cary, NC, 2004.). Residual plots were also used to evaluate final models. Linear models R^2 was used to compare among linear models and pseudo R^2 values to compare nonlinear models; however, R^2 values were not used for comparison between linear and nonlinear models. Model comparisons used a full versus reduced model approach or dummy variables to test differences between sites and irrigation treatments.

3. Results

3.1. Site, Irrigation and genotype effects on growth

All growth parameters (GLD, DBH, HT, Volt, VOLha, CAI and LAI) showed large effects of irrigation and genotype but almost no genotype × irrigation interactions except for VOLt at the North site and Surv at the South site (Table 3, Fig. 3). Across all genotypes and sites, irrigation improved growth by an average of 23% for GLD, 27% for DBH, 25% for HT, 87% for VOLt, 87% for VOLha, 87% for CAI and 85% for LAI, and no effects were observed in survival and growth efficiency (Fig. 3, Table 4). For both sites, a larger influence of irrigation was observed on cumulative volume growth than on ???, but the South site showed a larger response compared to the North site (Table 4 and Figs. 2 & 3). In fact, the largest absolute response to irrigation was observed at the harsher southern site for *E. nitens* genotypes, which could be considered the less adapted species to this sandy soil dry environment. Under low irrigation, the lowest cumulative growth was observed at the South site for the *E.camglo* hybrid. For particular genotypes from all taxa and across sites, the smallest response in cumulative growth to irrigation was observed for *E. smithii* (5%) at the North

Table 3
Analyses of variance p-values testing irrigation, genotype and interaction effects evaluated at each site for root collar diameter (RCD), diameter at breast height (DBH), individual tree height (HT), individual tree volume (VOLt), stand volume (VOLha), survival (Surv), current annual increment (CAI) and leaf area index (LAI).

Site	Effect	RCD	DBH	HT	VOLt	VOLha	Surv	CAI	LAI
North Site	Irrigation	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	0.2839	< **0.001**	< **0.001**
	Genotype	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	0.4826	< **0.001**	< **0.001**
	Irrigation × Genotype	0.0778	0.1637	0.2822	**0.0418**	0.0519	0.6652	0.0680	0.1988
South Site	Irrigation	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	0.2826	< **0.001**	< **0.001**
	Genotype	< **0.001**	< **0.001**	< **0.001**	< **0.001**	< **0.001**	**0.0340**	< **0.001**	< **0.001**
	Irrigation × Genotype	0.9833	0.9844	0.7711	0.2767	0.2848	**0.0146**	0.3362	0.6787

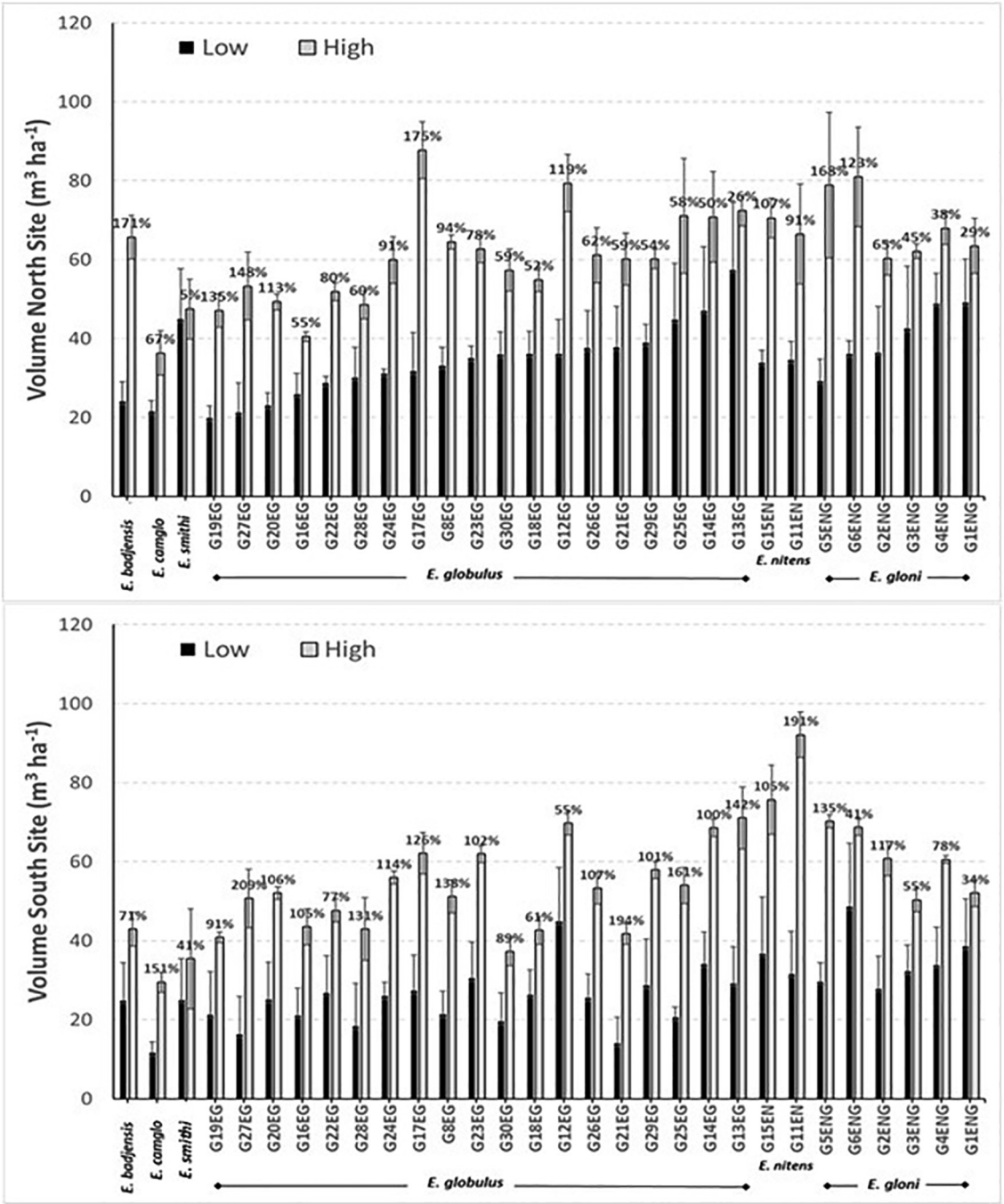

Fig. 3. Cumulative volume (m^3 ha^{-1}) after 31 months since planting (columns) and percent growth loss in the low irrigation treatment compared to the High Irrigation treatment (number above the columns) at each evaluated site for all considered taxa (EG, *Eucalyptus globulus*, EN, *Eucalyptus nitens*, ENG: *Eucalyptus nitens* × *globulus* (E.gloni), ECG: *E. camaldulensis* × *globulus* (*E.camglo*), ES: *E. smithii*, EB: *E. badjensis*). Vertical bars correspond to standard error of plot means (n = 3).

Table 4
- Comparison of estimated percentual cumulative gains between High vs Low Irrigation means or comparison of maximum and minimum values for each irrigation treatment. Differences were evaluated for all growth parameters after 31 months at each site for all genotypes, only *E. globulus*, only *E. nitens* and only *E. nitens* × *globulus* hybrids (*E. gloni*).

Site	Effect	GLD	DBH	HT	VOLt	VOLha	Surv	ICA	LAI
North Site	All Genotypes								
	Low vs High Irrigation (mean)	21%	21%	25%	76%	75%	1%	77%	64%
	Low Irrigation (max vs min)	42%	45%	44%	180%	187%	17%	171%	538%
	High Irrigation (max vs min)	27%	30%	36%	125%	142%	13%	140%	112%
	E. globulus								
	Low vs High Irrigation (mean)	23%	23%	25%	77%	76%	1%	79%	62%
	Low Irrigation (max vs min)	40%	45%	40%	180%	187%	13%	171%	538%
	High Irrigation (max vs min)	27%	30%	29%	117%	117%	13%	116%	112%
	E. nitens								
	Low vs High Irrigation (mean)	20%	21%	37%	103%	99%	2%	105%	41%
	Low Irrigation (max vs min)	6%	5%	6%	2%	2%	0%	9%	19%
	High Irrigation (max vs min)	12%	6%	2%	10%	6%	4%	17%	36%
	E. gloni								
	Low vs High Irrigation (mean)	18%	18%	26%	70%	70%	1%	68%	79%
	Low Irrigation (max vs min)	21%	23%	14%	68%	68%	8%	68%	202%
	High Irrigation (max vs min)	15%	9%	10%	30%	34%	8%	40%	53%
South Site	All Genotypes								
	Low vs High Irrigation (mean)	26%	33%	25%	97%	100%	1%	96%	106%
	Low Irrigation (max vs min)	80%	73%	42%	352%	315%	42%	280%	320%
	High Irrigation (max vs min)	39%	47%	54%	225%	212%	29%	199%	137%
	E. globulus								
	Low vs High Irrigation (mean)	29%	36%	27%	108%	109%	3%	105%	107%
	Low Irrigation (max vs min)	39%	51%	40%	164%	218%	29%	193%	264%
	High Irrigation (max vs min)	28%	28%	22%	88%	91%	17%	80%	137%
	E. nitens								
	Low vs High Irrigation (mean)	18%	32%	36%	104%	145%	16%	144%	79%
	Low Irrigation (max vs min)	25%	15%	2%	60%	16%	26%	23%	44%
	High Irrigation (max vs min)	2%	9%	14%	22%	22%	0%	15%	8%
	E. gloni								
	Low vs High Irrigation (mean)	18%	26%	20%	75%	71%	3%	67%	128%
	Low Irrigation (max vs min)	21%	23%	13%	84%	74%	8%	56%	232%
	High Irrigation (max vs min)	7%	11%	13%	30%	39%	23%	37%	79%

GLD: Ground line diameter, DBH: diameter at breast height, HT: total height, VOLt: Individual tree volume, VOLha: Stand volume, SURV: Survival, ICA: current annual increment, LAI: leaf area index

site, and the largest response to irrigation was observed for *E. globulus* (G27EG, 209%) at the South site.

The range of responses in cumulative (RCD, DBH, HT, Volt, Volha, Survival, LAI) and incremental growth (CAI) variables indicated large differences among genotypes at each site (Tables 3 and 4). Comparing the best and worst genotype, the largest differences were observed under Low Irrigation at the South site, except for LAI where maximum differences among genotypes were observed under Low Irrigation at the North site. Analysis of cumulative volume means of each taxon comparing High Irrigated vs Low Irrigated treatments showed similar percentual gains for the North and South sites (Table 4). Comparing the maximum and minimum cumulative growth values, small percentual gains differences were observed between *E. nitens* genotypes at the North site under Low Irrigation (< 10%) compared to the South site (Fig. 3, Table 4). However, All other taxa exhibited larger percentual gain differences in maximum and minimum values under Low Irrigation (Table 4). For *E. globulus* and *E. gloni* genotypes, the range in response for maximum and minimum values observed at the North and South sites was similar for each irrigation treatment. Interestingly, for *E. globulus* and *E. gloni*, the ranking of responses under Low Irrigation did not match the response under the High Irrigated treatment.

Contrary to cumulative and incremental growth variables, tree survival showed no effects of irrigation across genotypes at the North site, but an interaction was observed between genotype and irrigation treatment at the Southern site (Table 3).

Analysis at the taxa level showed that, on average, all taxa had more than 90% survival, except for a 79% survival observed for *E. nitens* under Low Irrigation and 77% survival for *E. smithii* under High Irrigation. For *E. globulus*, *E. nitens* and E. gloni, only one genotype showed < 90% survival under Low Irrigation at the North site (G20EG, 88%) but several genotypes exhibited lower survival under Low Irrigation at the South site (G11EN, 88%; G15EN, 70%; G16EG, 81%; G21EG, 77%; G22EG, 85%; G27EG, 85%). Interestingly, *E. gloni* showed the best taxa survival under Low Irrigation (greater than90%) with an average of 97% (Table 4).

3.2. Stability of genotypes and ranking change

Individual genotype cumulative volume responses to irrigation were not the same across sites. In fact, volume growth at the North site under High Irrigation (VolN-high) showed a good correlation (adj-R^2 = 0.51, $p < 0.001$) with volume growth under High Irrigation at the South site (VolS-high). However, a poor relationship (adj-R^2 = 0.14, p = 0.020) was observed for volume growth under low Irrigation at both the North (VolN-low) and the South site (VolS-low) (Fig. 4). The same relationships for both sites analyzed for *E. globulus* showed a significant strong linear relationship of volume growth with irrigation (VolS-high = 13.515 ns + 0.649**VolN-high, adj-R^2 = 0.52, $p < 0.001$) but no relationship with Low Irrigation (VolS-low = 16.205* + 0.262 ns*VolN-low, adj-R^2 = 0.06, p = 0.151). A similar response was also observed for E. *gloni*, for both irrigation (VolS-high = 6.854 ns + 0.777**VolN-high, adj-R^2 = 0.64, p = 0.034) and no irrigation (VolS-low = 29.549* + 0.142 ns*VolN-low, adj-R^2 = 0.02, p = 0.779) treatments.

Analysis of ranking change by comparing individual genotype change in stand cumulative volume indicated a large effect of site and irrigation treatments (Fig. 5). Larger ranking changes occurred at the North sites compared to the South site due to irrigation treatment (Fig. 5a and 5c). Also, larger ranking changes were observed under Low compared to High Irrigation conditions between sites (Fig. 5b and 5d).

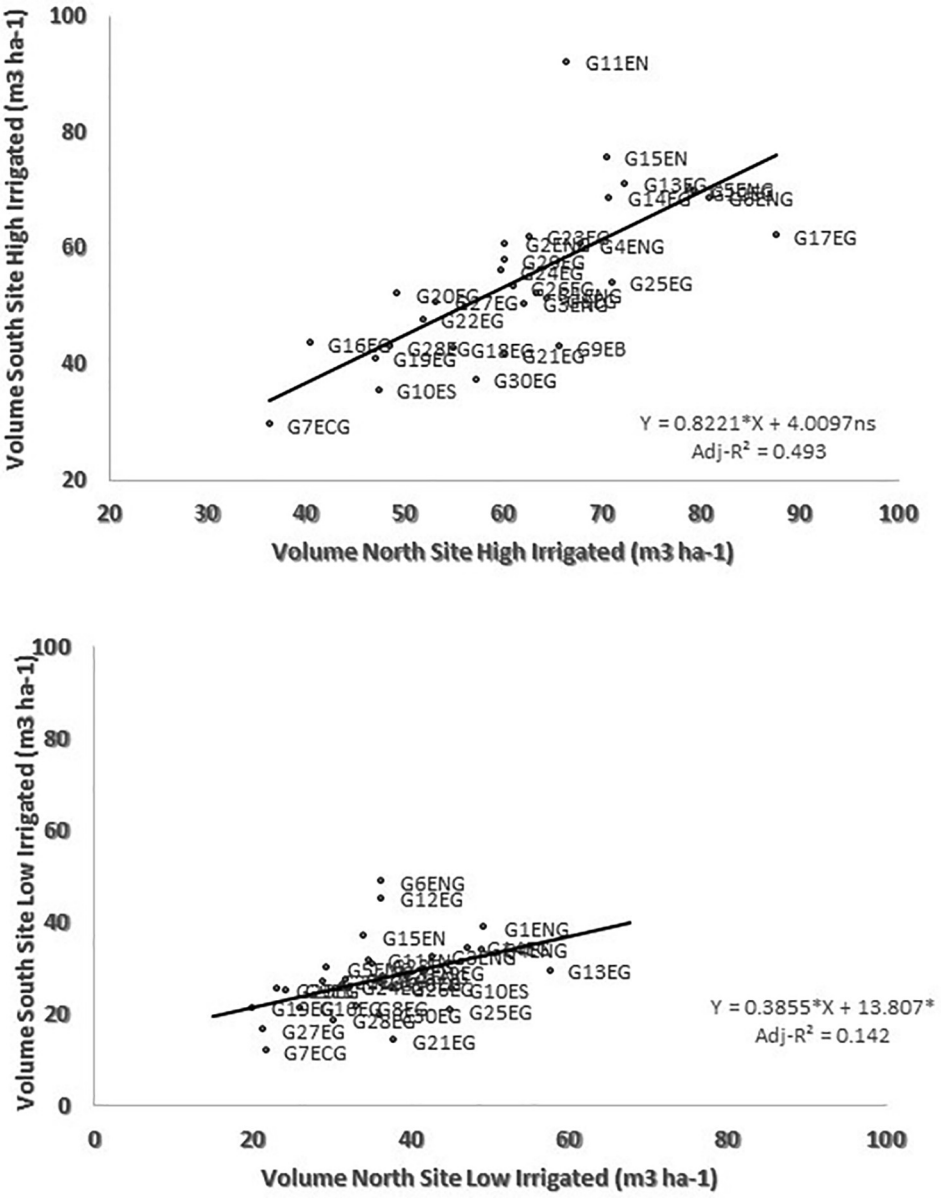

Fig. 4. Regression comparisons between cumulative volume (m^3 ha^{-1}) after 31 months since planting for all genotypes under a) High Irrigation (VolN-high versus VolS-high) and b) Low Irrigation (VolN-low versus VolS-low) conditions at each site. Letters after genotype number (G1 to G30) indicate taxa being compared for stability under High Irrigated vs. Low Irrigated treatments.

Only 3 genotypes under the High Irrigation treatment showed no change between sites (G14EG, G7ECG and G5ENG). Consistently, *E. nitens* showed a large positive ranking change under High Irrigation and the effect was more pronounced at the North site (Fig. 5a, 5b and 5d). Also *E. badjensis* showed a large positive ranking change under High Irrigation at the North site but this was not the case at the South site. In contrast, *E. smithii* showed a negative ranking change under High Irrigation at both sites. Among all taxa, E. *camglo* was the most consistent genotype, showing almost no rank change (< 3) under all evaluated conditions.

E. globulus taxa showed the widest range of site-specific responses being the most well represented taxa in our study. The effect of high irrigation on *E. globulus* showed a positive ranking change for 8 genotypes (< 50%) at the North site and 11 genotypes (58%) at the South site. A strong positive ranking change due to high irrigation was also observed at both sites for G8EG, G17EG, G27EG, and a moderate positive change for G20EG and G24EG. However, it was surprising that even though 6 (South site) and 9 (North site) genotypes showed negative change in ranking due to higher water availability, only two genotypes (G18EG and G30EG) were the same at both sites. Site comparisons showed that a large number of *E. globulus* genotypes were negatively affected by changing site from North to South under Low Irrigation (10 genotypes, 52%), which was a smaller number compared to High Irrigation treatment conditions (7 genotypes, 36%). Only genotypes G21EG, G25EG and G30EG showed a consistent negative direction of ranking change under High Irrigation and Low Irrigation conditions (Fig. 5b and 5d). This suggests a strong environmental effect on these genotypes with higher growth at the North site irrespective of the irrigation treatment. Conversely, only genotypes G20EG and G24EG showed a positive North vs South ranking direction regardless of irrigation treatment.

We observed a consistent positive ranking change under High Irrigation at both the North and South sites for all *E. nitens* genotypes (Fig. 5a and 5c). Also, *E. nitens* genotypes showed positive ranking change from the South to the North site, regardless of irrigation treatment (Fig. 5b and 5d). For E. *gloni*, the second most represented taxa

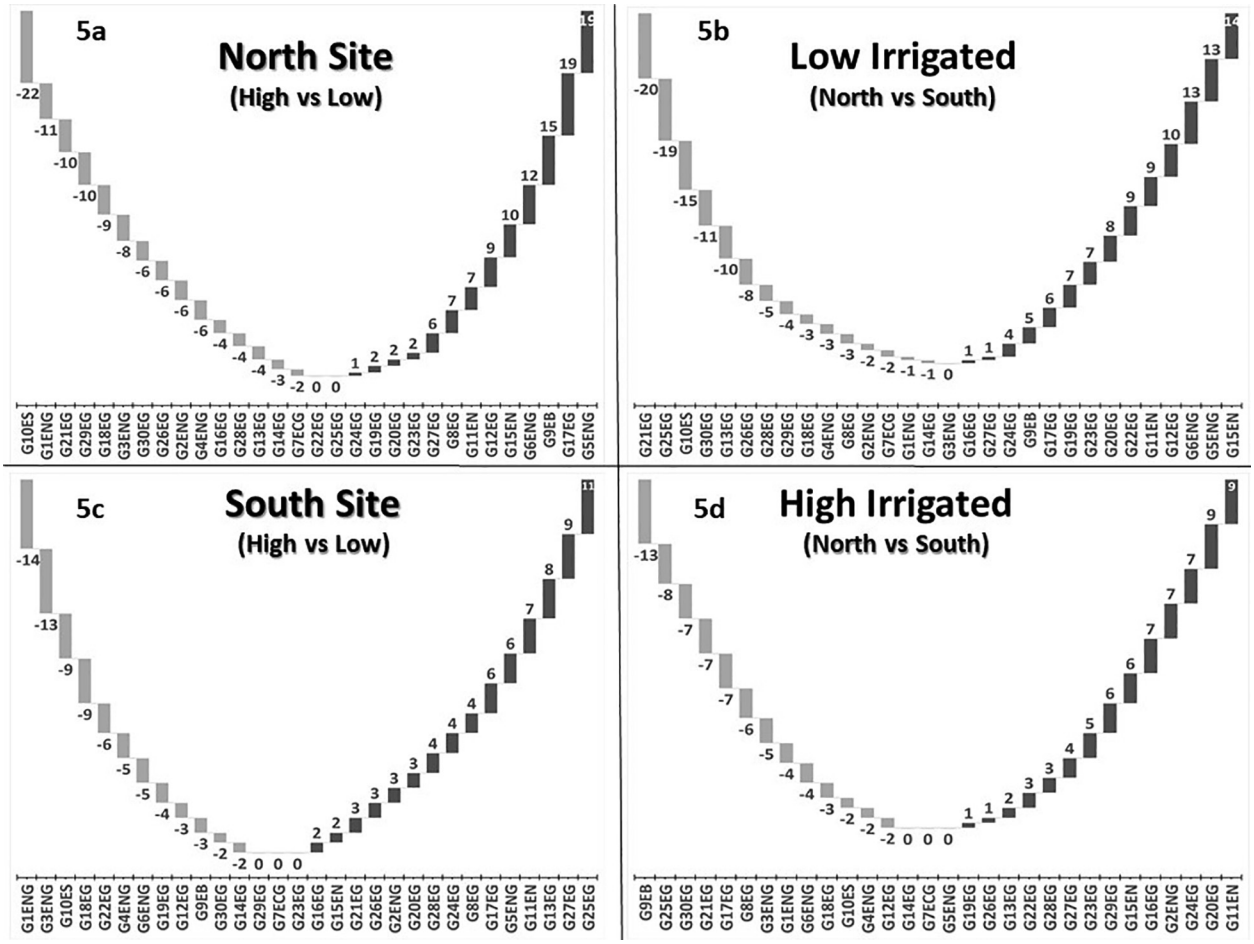

Fig. 5. Rank change in stand cumulative volume (VOLha) at 31 months since planting among genotypes (G1 to G30). The graphs on the left (5a and 5c) show the rank change for genotypes within a study site for High Irrigated vs. Low Irrigated treatment conditions while the graphs on the right side (5b and 5d) show rank changes for genotypes between sites for the same irrigation treatment . For all the figures, left light gray bars with negative values indicate genotypes with a decrease in ranking and right dark bars with positive values indicate genotypes with an increase in ranking. The size of each bar estimates the magnitude of rank change.

trees growing in the High Irrigation treatments showed a positive rank change for 2 genotypes and a negative rank change for 4 genotypes at the North and South site, but specific genotypes were not the same at both sites (Fig. 5a and 5c). We observed counterintuitive responses of some genotypes. For example, within High Irrigation treatments, G2ENG showed a negative ranking change at the North site but exhibited a positive ranking change at the South site. Conversely, G6ENG under High Irrigation showed a positive rank change at the North site but showed a negative ranking change at the South site.

3.3. Leaf area index & growth efficiency

Irrigation had a large impact on leaf area across genotypes and for individual taxa and in average this response was larger (106% vs 64%) at the South than at the North site (Table 4). Except for *E. nitens* genotypes at the North site, larger differences in LAI among genotypes within each taxon or within all genotypes were observed under Low Irrigation compared to High Irrigation treatments (Table 4). In the case of E. *nitens* at the North site, differences in LAI between genotypes under High Irrigation were larger than under Low Irrigation (36% vs 19%) (Table 4 and Fig. 6).

We observed a positive relationship between CAI and LAI suggesting that CAI variation could be predicted from LAI across sites and treatments (Fig. 6a). Several linear and nonlinear regression models were tested to evaluate the growth efficiency relationship (GE) between leaf area and current annual increment for all genotypes. Analysis including all genotypes for both sites and irrigation treatments suggested that a Michaelis Menten nonlinear model (MM) was the most common best fit to the data (Table 5, Fig. 6). Full versus reduced model comparisons of MM nonlinear models for site and irrigation effects showed that for all genotypes, site effect was not significant ($F = 1.420$, $p = 0.242$) but irrigation treatment models were different ($F = 31.645$, $p < 0.001$). Site comparisons for individual taxa, except for *E. nitens* ($F = 4.131$, $p = 0.031$), also showed no effects for *E.globulus* ($F = 0.183$, $p = 0.832$) and *E. gloni* ($F = 2.344$, $p = 0.103$). Analyses evaluating irrigation effects showed significant differences between High and Low Irrigation treatments for *E. globulus* ($F = 29.599$, $p < 0.001$) and *E.gloni* ($F = 5.021$, $p = 0.009$). In the case of *E.nitens*, independent site and irrigation treatment effects showed that a common model for the South Site Low & High Irrigation treatments together with the North Site High Irrigation was independent of a North Site Low Irrigation treatment model ($F = 13.825$, $p < 0.001$) (Table 5, Fig. 6).

The b parameter of our MM nonlinear models represents the mean LAI value at which a maximum CAI (asymptotic) value is attained (a parameter). In general, the nonlinear regression models for all genotypes showed better fits for Low irrigation than for High Irrigation conditions and, except for the *E. globulus* taxa, the b parameter of the MM model was not significant for *E. gloni* and *E. nitens* which suggested that a maximum mean value or MM asymptote (a parameter) was able to represent High irrigation conditions (Table 5, Fig. 6). Interestingly, LAI for High irrigation treatments started at values above 3 units (Fig. 6b and 6c), and small changes in CAI growth rates were observed

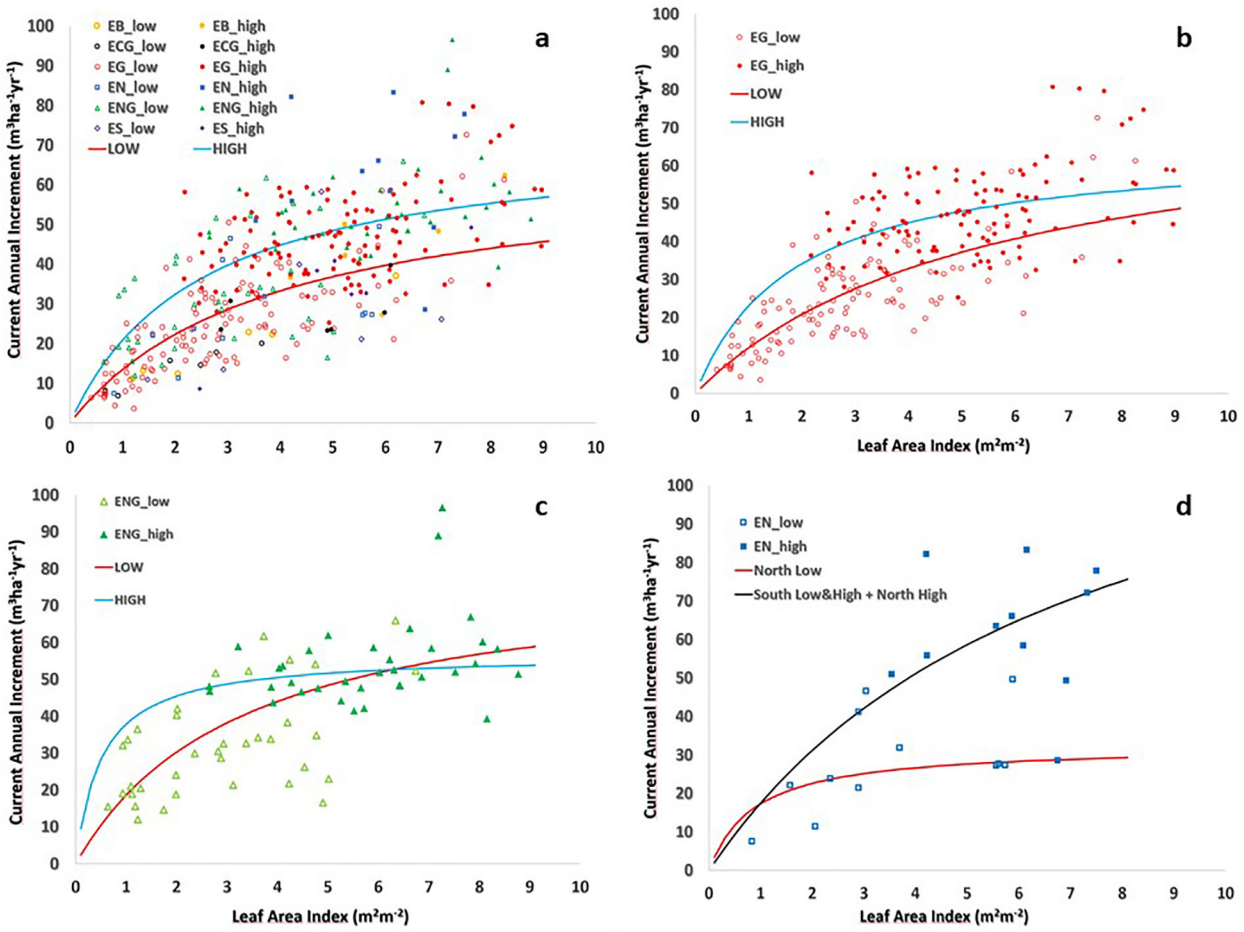

Fig. 6. Nonlinear models adjusted for the leaf area index (LAI) and the current stem volume annual increment (CAI) relationship for the High vs Low irrigation treatments for a) all evaluated genotypes, b) *E. globulus* taxa, and c) *E. gloni* taxa. The same relationship was adjusted for d) *E. nitens* taxa at the South site (both High & Low irrigation treatments) and the North High irrigation, which followed a common regression, and the North Low Irrigation treatment. Nonlinear Michaelis Menten models had the form CAI ($m^3ha^{-1}yr^{-1}$) = a*LAI/(b*LAI).

Table 5
Nonlinear Michaelis Menten models adjusted for the LAI and CAI (growth efficiency) relationship for all genotypes or specific *E. globulus*, *E. nitens* and *E. gloni* taxa that showed significant effects of irrigation treatments (High vs Low). Michaelis Menten models are represented by the expression CAI = a*LAI/(b*LAI) and goodness of fit of linear and nonlinear models was evaluated by Akaike information criteria (AIC), root mean square error (RMSE) and pseudo-R^2 values.

Model	Effects	Parameters		AIC	RMSE	pseudo-R^2
		a	b			
All Genotypes	Low & High	98.520**	6.113**	2788.35	11.94	0.52
	Low	64.972**	3.819**	1346.56	10.07	0.43
	High	72.311**	2.461**	1396.34	12.08	0.14
E. globulus	Low & High	99.270**	6.297**	1723.78	10.50	0.58
	Low	78.288**	5.527**	813.20	8.50	0.55
	High	65.673**	1.848*	857.19	10.19	0.14
E. gloni	Low & High	74.455**	2.578**	476.15	9.11	0.61
	Low	80.315**	3.310*	245.86	10.46	0.53
	High	56.766**	0.498 ns	223.01	6.60	0.05
E. nitens	Low & High	120.53 ns	7.246 ns	203.39	17.99	0.39
	North Site Low	32.429**	0.871 ns	47.18	3.37	0.29
	South Low&High + North High	142.22*	7.129 ns	133.74	13.16	0.69

ns = not significant, * $p < 0.05$, ** $p < 0.001$.

above this level, except for *E. nitens* South-Low&High + North-High models that showed an asymptotic behavior at higher LAI values (Fig. 6d). High irrigated treatments showed lower LAI values to attain their maximum CAI asymptotic behavior (Fig. 6b and 6c), except for *E. nitens* at the South Low&High + North High Irrigated plots (Fig. 6 d). Interestingly, under both irrigation treatments, and except for *E. nitens* North Low site, genotypes and treatments ranked *E. nitens* > *E.globulus* > *E.gloni* for the maximum observed LAI value at which the CAI asymptotic value was attained (Table 5 and Fig. 6b, 6c and 6 d). However, the ratio between a and b parameters, that is, the slope of the GE relationship, ranked *E.gloni* > *E. globulus* > *E. nitens* for Low Irrigation treatments and *E. nitens* > *E. gloni* > *E. globulus* for the High

Irrigation treatments.

4. Discussion

This study evaluated the stability of stem volume growth for contrasting *Eucalyptus* genotypes under divergent water and environmental limitations. A limited number of experiments have tested how species (or other taxon) perform in contrasting environments under controlled conditions. In our study, increased growth in the High Irrigation treatment was anticipated given the range of responses observed in comparative regional studies evaluating productivity-site water availability relationships under Mediterranean climates (Beadle and Turnbull 1992, Macfarlane et al. 2004). Similar responses have also been observed in sub-tropical environments (Ngugi et al. 2004, Stape et al. 2004). In addition, several (Beadle and Turnbull 1992)process based models have shown the major importance of site soil water availability and atmospheric demand affecting fast growing species productivity (Battaglia and Sands 1997, Hingston and Galbraith 1998, Battaglia et al. 1999, Sands and Landsberg 2002, Almeida et al. 2004, Battaglia et al. 2004). Growth increases were greater at the South site under High Irrigation compared to results observed at the North site, and may be attributed to the lower water holding capacity of this sandy soil and its higher atmospheric demand. The *E. nitens* taxa showed the highest growth rates under this limited water availability site and our results agree with Honeysett et al. (1992) who reported less sensitivity on aboveground volume of this species under water stress. In fact, compared to other taxa under the Low Irrigation treatment, *E. nitens* was one of the best performers at the South site. However, at the North site, the growth increase of *E. nitens* was in the range of the other taxa, possibly because of its higher leaf area and/or lack of this species ability to acclimate to warmer spring and summer temperatures, leading to a longer seasonal effect on productivity at the South site. (e.g. Battaglia et al. 1998, Rodriguez et al. 2009, Watt et al. 2014).

The “Low irrigation” treatment in the South site received some water additions in order to sustain trees close to permanent wilting point. For *E. badjensis* and the *E. camglo* hybrid the response to water additions were similar to previously reported responses (Lemcoff et al. 2002, Rad et al. 2011, Bi et al. 2014). However, the relatively high growth rates under Low Irrigation of *E. smithii* at the North and South sites were surprising and suggests a strong mechanism of drought tolerance compared to other tested taxa (Mitchell et al., 2013) and/or that lower hydraulic conductance under fine textured soils may trigger conservative mechanisms to reduce transpiration that may favor this species (Sperry et al. 1998, McDowell et al. 2008). Silva et al. (2017) showed large and rapid decline in predawn water potential of *E. smithii* under drought compared to other hybrids, suggesting reduced drought tolerance of this species that may be benefited at the lower VPD North site.

The broader range of responses observed for *E. globulus* and *E. gloni* hybrids at our experiment may be due to the larger number of tested genotypes for these taxa compared to others in our experiment. However, Dutkowski and Potts (2012) suggest that there is significant variation in drought susceptibility for *E. globulus* observed in the range of environments under natural selection of this taxa in Australia. But also, large differential responses among genotypes of *E. globulus* have been shown over water availability gradients in other studies (Costa E Silva et al. 2004, Silva et al. 2006).

Survival was lowest under Low Irrigation at the South site for *E. nitens* and *E. globulus*. Interestingly, most *E. globulus* genotypes that showed poor survival also showed low performance in individual tree cumulative growth, except for EG21. This response differed markedly from *E. nitens* which showed the highest growth rates of all evaluated genotypes under Low Irrigation which suggests strong water stress adaptation for growth but not for early survival (Meo 2010).

The largest differences in genotypes performance were observed comparing the Low Irrigation treatment of both sites when comparing all genotypes as a whole, but also within each taxon. In fact, a poor relationship was observed among genotypes' volume growth under Low Irrigation compared to High Irrigation (Fig. 4). These results suggest that selection of genotypes may be highly biased if water stress limitations are not considered within these Mediterranean environments and large GxE interactions may play a critical role for matching genotype to site. Contrasting effects of environment on genetic performance in growth variables at the family and clonal level have been reported for intensively managed conifers (McKeand et al. 2006, Baltunis and Brawner 2010, Raymond 2011) but large GxE interactions have been shown for Eucalyptus families and clones in Australia, despite some materials showed high stability across environments (Silva et al. 2006, de Oliveira et al. 2018, Pupin et al. 2018). Previous GxE studies have shown that the importance of abiotic factors clearly depends on the environmental extent and the range and type of limiting factors being considered (Li et al. 2017, Ukrainetz et al. 2018). Our results also showed larger rank changes when comparing genotypes under different irrigation treatments within a single site (same soil-climate conditions, Fig. 5a and c). The same was observed when sites were compared under Low Irrigation, accounting for the effect of soil and climate interacting under restricted soil water availability conditions (Fig. 5b and 5d). The effect of reduced environmental limitations showed smallest changes in rank among genotypes when sites were compared under High Irrigation and also when comparing better irrigated volume growth between sites for all or for specific taxa (Figs. 4 and 5).

Our results suggest that stability of *Eucalyptus* sp. genotype performance increases for sites under high resource availability and may be reduced under limited water resource availability within these Mediterranean environments. Stratification of selection of genotypes for specific environments have been proposed under these scenarios before (Li et al. 2017, Pupin et al. 2018). Unexpected negative ranking changes under better irrigation for specific *E. globulus*, *E. gloni,* and also the lack of response to irrigation for *E. smithii* suggest that complex interactions may be expected for hybrids of new species being considered for enriching genetic programs under complex climate change scenarios (Ngugi et al. 2004, Mokotedi 2010, Mitchell et al. 2013, Mitchell et al. 2016). In practical terms, comparing all of the genotype's response under each irrigation treatment (Table 4), suggests that genetic gains from matching the best genotype to sites are significantly larger for sites with reduced or limited water availability (Fig. 3). Nonetheless, our comparison of all evaluated taxa may have some limited interpretation given that we only tested a single genotype for E. *camglo*, *E. badjensis* and *E. smithii*. These lesser known commercially improved materials may represent potential interesting opportunities under climate change scenarios that may not only impact water resources but also biotic risks for intensively managed plantations (McDowell et al. 2008, Pinkard et al. 2014, Mitchell et al. 2016). In fact, more complex scenarios for biotic interactions may be expected given that environmental effects also affect performance of biotic agents (Pinkard et al. 2014, Mitchell et al. 2016).

4.1. Leaf area and growth efficiency

Similar to cumulative volume growth responses, the High Irrigation treatment increased CAI and LAI, similar to previous studies incorporating irrigation or analyzing water availability across regional gradients (Campoe et al. 2013, Albaugh et al. 2016, da Silva et al. 2016). In our study, at least at this stage of stand development, water availability but not site environmental effects (except for *E. nitens* taxa), changed the proportional relationship between annual growth rate and leaf area (i.e. growth efficiency) (Fig. 6a). In fact, leaf area was higher under irrigation treatments for all genotypes (Fig. 6b and 6c) and similar effects have been reported for *E. globulus* and *E. nitens* irrigated trees (White al. 2016).

Smethurst et al (2003) examined a similar gradient of LAI on *E. nitens* plantations from several fertilization experiments in Australia

and described a comparable nonlinear asymptotic GE relationship between LAI and stemwood biomass increment using a three parameter Michaelis Menten model. In contrast to our study, and maybe due to the small range in annual rainfall among their sites (850–1444 mm yr^{-1}), these authors found no site or treatment effects on their GE relationship explained by a single model across sites. Our independent GE models may be explained by the large water availability and site atmospheric demand differences imposed, as has been shown in previous studies (Stape et al. 2010, Fontes et al. 2006; Whitehead and Beadle, 2004). Also, leaf area production may have been enhanced in our study due to summer irrigation (Yu et al., 2019). Similar to our study, Smethurst et al (2003) showed that growth rates per unit LAI were higher at lower LAI and lower at high LAI levels. They also observed that for *E. nitens*, an asymptotic behavior in their GE relationship was reached around LAI values of 5 units. Interestingly, White et al. (2010) modelled optimum LAI as a function of annual water stress (e.g. ratio between annual evapotranspiration and potential evaporation) for *E. globulus* and *E. nitens* plantations and observed that LAI reached an asymptote at 5 units for sites under no water stress. Different from Smethurst et al (2003), our study showed that for the North Low irrigated site, *E. nitens*, *E. globulus* and *E. gloni* taxa, LAI reached an asymptote at 3 units of LAI. Similar results have been observed for tropical and subtropical *Eucalyptus* species (da Silva et al., 2016; Stape et al.,2004). However, the strong early asymptotic behavior and high LAI levels observed for both the *E. nitens* genotypes at the North site Low Irrigation treatment was unexpected.

Adjusted models for all genotypes showed higher GE relationships for High irrigated genotypes compared to Low Irrigated across sites at lower LAI levels but the inverse situation was observed at higher LAI values where High irrigated treatments reached an earlier asymptotic behavior (Fig. 6, Table 5). In fact, all genotypes in the High Irrigated treatments showed an earlier asymptotic behavior than under Low Irrigated treatments (except for *E. nitens* North Low Irrigation treatment, Fig. 6). GE models showed higher slopes for *E. nitens* compared to *E. globulus* and *E. gloni* suggesting a larger response in GE of *E. nitens* to irrigation. In fact, *E. nitens* irrigated trees showed the largest growth rates for the same range of LAI values compared to other taxa under irrigationFor the Low Irrigation treatments, the smaller maximum CAI were observed in *E. nitens* at the North site (North Low). In the case of *E. globulus* and *E. gloni*, similar maximum CAI were observed for both taxa; however, *E. gloni* showed a higher GE relationship compared to *E.globulus* (Fig. 6, Table 5). The smaller number of tested genotypes for *E. nitens* may limit the interpretation of our previous statement for this taxon. However, our results clearly suggest that *E. globulus* may be less sensitive to water deficit affecting aboveground productivity compared to *E. nitens*. These responses may also suggest a conservative response of *E. globulus* under water stress, a more sensitive response to water stress signals, as suggested by White et al. (1996) and Hodecker et al. (2018), or a response in its aboveground: belowground ratio (Fontes et al. 2006, Ryan et al. 2008, Stape et al. 2008, Drake et al. 2019). However, results from previous studies comparing *E. globulus* and *E. nitens* under irrigation versus non irrigated conditions suggest that drought can cause larger negative effects on *E. globulus* root biomass compared to *E. nitens* (Moroni et al., 2003). Interestingly, *E. gloni* showed similar response patterns to *E. globulus*, higher GE compared to *E. globulus*, and closer GE relationships between High and Low Irrigated treatments compared to the other taxa.

Our results suggest that volume growth and ranking of performance for selected genotypes may be stable for environmental gradients were water availability is not a major limitation. Furthermore, our results suggest that although resource availability plays a major role on driving volume growth and leaf area, genetics also interact, showing the importance of genotype selection in constrained environments. Interestingly, small effects of genetics were observed on growth efficiency across the water availability gradients in our study. Understanding genetic × water resource availability/demand environment interactions under manipulated studies will increase our understanding of the potential risks of traditional genetic selections under climate change scenarios and the effects on forest productivity. However, more detailed physiological comparisons are needed to provide a more in depth framework of a drought tolerant/more risky or drought avoidance/less risky strategy for these species or clonal differences at this level (White et al. 1996, Whitehead and Beadle 2004, Mokotedi 2010, Zeppel 2013).

5. Conclusions

Our goal in this study was to determine the stability of volume growth for different genotypes under contrasting water availability and to assess the importance of genetics versus resource availability as drivers of volume growth, leaf area and growth efficiency across sites with contrasting atmospheric demand and soil types. Increased survival, individual tree and stand growth and leaf area were observed across all genotypes and sites under improved water resource availability treatments at these Mediterranean sites. However, specific genotypes showed a higher stability with improved resource availability under soil-site conditions (lower VPD and clay soils) that reduced water stress. Interestingly, across sites, large effects of increased water availability on nonlinear growth efficiency relationships were observed for all genotypes and *E. globulus*, *E. nitens* and *E. gloni* taxa.

Genotypes may show large differences of volume growth performance within and between sites under improved or reduced water availability (irrigation treatments). However, low growth performance, stability and larger ranking changes may be observed when comparing sites with higher water stress suggesting a larger expression of GxE interactions within harsher environments. Differences in response to water resource limitations should be carefully taken into consideration for future genetic selection considering site specific expected risks of drought and climate change.

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