

The interactions of climate, spacing and genetics on clonal *Eucalyptus* plantations across Brazil and Uruguay



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A B S T R A C T

Intensively managed plantations account for 1.5% of the world's forests, but they meet one-third of the demand for wood products. *Eucalyptus* plantations are among the most productive, with rates of growth depending heavily on genetics, silviculture, and climate. The TECHS Project examines productivity at 36 locations across a 3500 km gradient from Brazil to Uruguay, testing the interacting influences of genetics, temperature and precipitation on stemwood production. Across all sites and genotypes, stemwood production in the middle of the 6-year rotation (the peak period of growth) averaged 22 Mg ha⁻¹ yr⁻¹. Production varied by fivefold across sites, and by about 2-fold among genotypes within each site. The best clones at each location grew 1.5–4 Mg ha⁻¹ yr⁻¹ more than the average for all clones, underscoring the importance of matching genotypes to local site conditions. Contrary to patterns for natural forests across geographic gradients, *Eucalyptus* production declined with increasing temperature, dropping by 2.5 Mg ha⁻¹ yr⁻¹ for a 1 °C temperature increase. The temperature effect was likely driven in part by the geographic covariance of temperature and rainfall, as rainfall tended to decline by 78 mm yr⁻¹ for each 1 °C increase in temperature. Stemwood production increased an average of 1.5 Mg ha⁻¹ yr⁻¹ for each 100 mm yr⁻¹ increase in precipitation, but when the covariation of temperature and precipitation were included the apparent influence of precipitation declined to 0.4 Mg ha⁻¹ yr⁻¹ for each 100 mm yr⁻¹ increase in precipitation. Future results will determine if within-site reductions in ambient rainfall have the same apparent influences as the rainfall pattern across the geographic gradient, as well as quantifying the importance of insects and pests in affecting growth. The supply of wood from intensively managed plantations will be strongly influenced by both temperature and precipitation at plantation locations, and with changing climates.

1. Introduction

Forests are a dominant vegetation type around most of the world, from frigid regions with very short growing seasons to the hottest tropical areas that have sufficient water supplies to support trees. We depend on forests for the production of fuel and wood products, and global consumption of wood products more than doubled from 1950 to 1990. Total global consumption of wood stabilized in about 1990 at a level of 3.5 billion m³ yr⁻¹, split about equally for fuel and for industrial products (Sutton, 2014). More than 80% of the world's wood supply was taken from natural forests in 1950, with planted forests

supplying less than 20% (Whiteman, 2014). The proportional contribution of wood supplied from natural forests has declined steadily to less than half the global demand in 2015, with actual harvest rates from natural forests declining since 1995. This shift to reliance on planted forests to supply the demands for wood products resulted from increasing area devoted to planted forests (rising by 50% from 1990 to 2015; Payn et al., 2015) combined with accelerating growth rates. Planted forests account for about 7% of all forests (Whiteman, 2014). The most intensively managed, fast-growing plantations account for only 1.5% (54 million ha) of the world's forests, but they supply one-third of the non-fuelwood supply (INDUFOR, 2012). The most

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commonly planted species are pines in temperate and subtropical areas (*Pinus*, 42% of planted areas) and eucalypts (*Eucalyptus* 26% of planted areas) in subtropical and tropical areas.

The growth of forests varies across climatic gradients and species (Lieth and Whittaker, 1975; Roy et al., 2001), and plantations of suitable *Eucalyptus* species in the Tropical and Subtropical regions of Brazil are among the most productive forests in the world (Stape et al., 2010; Flores et al., 2016). Intensive research and development into forest growth resulted in a 4-fold increase in wood productivity in Brazil from 1970 to 2015 (Fig. 1). High rates of growth depend on application of results from research programs in genetic improvement (Resende et al., 2012) and silvicultural practices including site preparation, fertilization, spacing and weed control (Gonçalves et al., 2013). Climate strongly influences the growth of planted forests of *Eucalyptus*; a doubling of precipitation from 800 mm yr⁻¹ to 1600 mm yr⁻¹ along a 100-km gradient in Bahia led to a 3-fold increase in wood growth (from 10 Mg ha⁻¹ yr⁻¹ to 30 Mg ha⁻¹ yr⁻¹; Stape et al., 2004). The addition of supplemental water within sites also increases *Eucalyptus* wood growth, by 20–80% (Stape et al., 2008; Ryan et al., 2010).

Sustaining or increasing the high rates of *Eucalyptus* growth will depend on a variety of changes in the future. Annual variations in precipitation can alter gross primary production and wood production by one-third to one-half (Stape et al., 2008), and any regional changes in climate would likely result in regional changes in production. Statistical and ecophysiological models that incorporate rainfall are commonly used to predict growth (Almeida et al., 2010; Scolforo et al., 2017). Short rotations (commonly about 6–8 years) allow land owners to change land use in responses to changing markets. Increases in the value of agricultural crops could lead to allocation of *Eucalyptus* forests to drier sites, which would require more specific genotypes and new management practices. Most intensively managed *Eucalyptus* plantations use genetically identical clonal trees within each stand to maximize uniformity and growth (Binkley et al., 2002; Stape et al., 2010), and genotypes differ substantially in rates of water use, the efficiency of wood production per unit of water transpired, and in responses to droughts (Hubbard et al., 2010; Blackman et al., 2017). Changes in silviculture could also be important, such as reducing the number of trees planted per hectare to reduce drought-related mortality (Hakamada et al., 2017). Besides these abiotic factors, exotic pests and diseases that harm *Eucalyptus* plantations have been increasingly reported in South America in the last decade with damages levels depending on genotypes and climate (Wingfield et al., 2013). Deployment

of *Eucalyptus* clones requires many years of silvicultural evaluation (Resende et al., 2012). A long-standing goal of tree breeders and ecophysiologicalists is understanding the survival and growth of a large and diverse group of clones (derived from hybrids of various species) across large areas, and how this knowledge can be used to develop manageable ideotypes for tactical and operational decisions (Marcatti et al., 2017; Scolforo et al., 2017).

These impending changes in factors that drive the biological productivity of planted *Eucalyptus* forests led to the creation of an experimental research platform to investigate the influence of climate (water and thermal stresses), spacing and genetics on survival and growth at the level of individual trees and stands. The TECHS Project (Tolerance of *Eucalyptus* Clones to Hydric, Thermal and Biotic Stresses, www.ipef.br/techs/en) was launched in 2011 as a collaboration among people from 26 forest companies, 9 universities, and research institutions from Brazil, Uruguay, and the United States. The TECHS Project comprises 36 experimental sites across a 3500-km gradient from the Amazon Region to Uruguay (Tables 1 and 2), examining:

1. How the growth of clonal *Eucalyptus* plantations relate to patterns in climate;
2. How production ecology factors (light and water use, efficiency of resource use, photosynthate allocation) account for the influence of climate;
3. The role of genotypes in determining growth responses to climate;
4. How spacing can mitigate drought effects, survival and growth at the scales of individual trees and plots of trees; and
5. How genotypes can be grouped into ideotypes regarding their ecophysiological responses to hydric and thermal stresses and susceptibility to pests and diseases for operational deployment.

This paper provides a description of the TECHS Project, and basic mid-rotation results for growth patterns and interactions between genetics and environmental conditions. A variety of detailed investigations will come from the Project in the next few years.

2. Experimental design, site descriptions, and core measurements

The core design for TECHS has 18 clones of *Eucalyptus* (Table 3), with 11 clones planted at each of 36 sites for a planned rotation length of 6 years (Figs. 2–4). Only 27 sites are included in this paper, as the others were planted later and had not reached the mid-rotation point

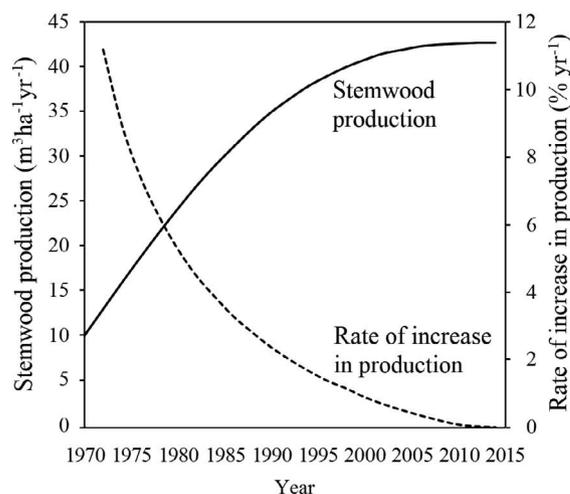


Fig. 1. The productivity per ha of *Eucalyptus* plantations across Brazil increased by 4-fold from 1970 to 2015, as a result of intensification of management and development of fast-growing genotypes. The rate of increase in productivity is currently near 0 (data from IBA, 2015). Image of a typical 7-year-old plantation being harvested with stemwood production across the rotation (mean annual increment) of 25 Mg ha⁻¹ yr⁻¹ (approximately 50 m³ ha⁻¹ yr⁻¹).

Table 1
Climate description for 27 of the TECHS sites (column descriptions at bottom of table), for the growth period (24–36 months) presented in this paper.

TECHS	Lat Degrees	Long	Alt m	Tavg °C	Tmx	Tmn	AGDD	T < 2 °C Number of days yr ⁻¹	T > 35 °C	RH %	RAD MJ m ⁻² d ⁻¹	VPDday kPa	VPDlight	P mm yr ⁻¹	PET	AET	DEF
1	-14.34	-48.73	545	25.5	31.4	19.6	7472	0	39	61	21.9	1.6	2.2	1321	1644	1091	552
2	-24.21	-49.97	770	19.0	23.2	14.7	5081	0	0	73	17.0	0.8	1.1	1495	1183	1137	46
3	-19.70	-45.41	727	22.8	28.7	16.9	6480	0	14	64	18.7	1.3	1.9	946	1298	939	359
4	-19.31	-42.42	243	23.6	28.5	18.7	6771	0	5	68	17.6	1.2	1.7	964	1215	957	258
5	-18.58	-42.93	873	21.8	27.4	16.1	6099	0	0	68	18.7	1.1	1.6	932	1307	915	392
6	-30.19	-51.62	150	21.6	26.2	16.9	6022	0	9	74	15.7	0.9	1.3	1805	988	976	13
7	-18.02	-50.90	681	24.0	30.2	17.8	6944	0	21	62	19.0	1.5	2.1	1628	1470	963	507
8	-11.86	-38.37	218	25.3	30.0	20.6	7405	0	3	70	17.5	1.3	1.8	896	1479	878	601
9	-18.73	-47.92	969	21.8	26.8	16.7	6110	0	1	66	18.8	1.1	1.6	1412	1319	1021	298
10	-23.03	-48.53	869	19.8	24.3	15.2	5382	0	0	74	17.9	0.8	1.2	1376	1162	1004	158
11	-18.71	-52.59	783	23.7	29.1	18.2	6805	0	9	66	19.0	1.3	1.8	1290	1273	862	411
12	-19.76	-40.13	36	25.2	29.8	20.6	7362	0	3	72	18.6	1.1	1.6	832	1520	832	688
13	-20.90	-51.90	361	26.5	32.7	20.3	7828	0	72	63	21.4	1.7	2.4	1155	1406	1133	274
14	-19.96	-51.59	480	24.6	30.8	18.3	7121	0	33	69	18.0	1.3	1.8	1392	1383	1093	291
15	-11.21	-48.64	255	27.0	33.3	20.6	8000	0	80	66	20.1	1.7	2.3	1204	1520	1012	507
17	-18.25	-45.10	806	22.9	28.7	17.0	6491	0	7	62	20.2	1.4	1.9	792	1610	746	864
20	-22.35	-46.97	633	23.1	29.7	16.4	6576	0	22	62	17.8	1.5	2.1	1224	1274	1022	252
22	-24.23	-50.53	888	19.8	23.9	15.6	5379	0	0	77	15.5	0.7	1.0	1554	1079	1050	29
23	-27.53	-50.10	870	17.4	22.7	12.0	4517	13	0	82	16.3	0.5	0.8	2055	950	949	1
24	-22.73	-49.00	656	21.4	28.4	14.4	5972	0	11	69	16.7	1.1	1.6	1701	1147	1018	129
26	-16.78	-44.31	926	23.3	29.4	17.2	6675	0	6	64	20.8	1.4	1.9	477	1457	477	980
27	-25.98	-50.11	916	19.0	24.8	13.1	5101	10	1	76	14.4	0.8	1.2	1487	819	817	1
28	-26.11	-50.21	812	18.5	23.6	13.3	4896	8	0	78	14.7	0.7	1.0	1487	935	933	2
29	-3.44	-43.07	81	28.0	32.7	23.2	8375	0	61	72	18.4	1.4	1.9	1560	1781	865	916
30	-17.32	-43.77	848	22.4	28.7	16.0	6336	0	5	62	20.6	1.4	2.0	507	1491	507	984
31	-16.34	-39.60	200	23.9	28.2	19.5	6880	0	0	76	18.3	0.9	1.3	982	1314	808	506
33	-23.85	-48.70	695	21.0	26.0	16.0	5822	0	4	72	16.9	0.9	1.4	1357	1185	1130	55

Tavg = mean annual air temperature; Tmx = average maximum air temperature; Tmn = average minimum air temperature; T < 2 °C = number of frost days; T > 35 °C = number of days with Tmx > 35 °C; AGDD = accumulated growing degree days considering based on temperatures between 5 and 35 °C; RH = average relative humidity; RAD = average global radiation; P = total precipitation; VPDday = average vapor pressure deficit for 24 h; VPDlight = average vapor pressure deficit of the photoperiod; PET = potential evapotranspiration by Penman–Monteith equation; AET = actual evapotranspiration by water balance of Thornthwaite-Mather and using a specific water holding capacity of the soils; DEF = water deficit by water balance of Thornthwaite-Mather and using a specific water holding capacity of the soils.

used in this evaluation. Each clone was planted in a single plot, with 8 lines × 30 trees (24 × 90 m plot), with trees at a spacing of 3 × 3 m (1111 trees ha⁻¹). One edge of each plot had 5 rows (each with 8 trees) available for destructive sampling throughout the duration of the Project. Each plot was split, with half receiving full ambient rainfall. Rain-removal troughs were installed in the other half-plot (about a year after planting) to remove about 33% of rainfall. The rain-removal treatments were applied shortly before the mid-rotation point, so no results are available to include in the current paper.

The plot-level design was complemented with an individual-tree design, with varying spacing per tree leading to a range of ambient water supply per tree. The single-tree experiment had one plot for each clone, with uniform spacing of 3-m within 7 columns, and variable spacing between 27 trees within rows (from 0.25 m to 7.15 m, or ~13,000 trees ha⁻¹ to ~450 trees ha⁻¹). All plots were fertilized intensively during the first year (70 kg N ha⁻¹, 45 kg P ha⁻¹, 85 kg K ha⁻¹, 500 kg Ca ha⁻¹, 90 kg Mg ha⁻¹, 40 kg S ha⁻¹, 3 kg B ha⁻¹, 1 kg Cu ha⁻¹, and 1 kg Zn ha⁻¹) to alleviate any nutrient limitation. The schedule of fertilizer application varied among site, with the total application divided among 2–4 applications from the preplanting through 12 months. Herbicides were used to keep the plots weed-free.

The large gradient in environmental conditions (Tables 1 and 2) led to a division of sites into warmer Tropical sites and cooler Subtropical sites. Following discussions among companies' breeders, 11 commercial Brazilian *Eucalyptus* clones were selected among thousands available. Four clones were chosen based on expected suitability for a wide range of environmental conditions (termed "plastic" clones, Table 3), and were planted across all TECHS sites. Seven clones were chosen for

suitability for warmer conditions, and were planted at all Tropical sites. Seven other clones were chosen for cooler conditions and were planted at all Subtropical sites. Each site therefore tested the four plastic clones and seven regional clones, along with a site-specific clone chosen at the discretion of the local landowner (not included in these mid-rotation results).

Genotype grouping was performed using multilocus genotypes for 20 microsatellites to estimate pairwise individual-level genetic distances among the 18 clones (pure species of *E. grandis*, *E. urophylla*, *E. saligna*, *E. dunnii*, *E. benthamii*, and hybrids) and 4 seedlots pure species (*E. grandis*, *E. saligna*, *E. urophylla* and *E. camaldulensis*) as references. The matrix of genetic distances was used to graphically represent distance relationships between the clones and pure species with an unweighted pair group method with arithmetic mean (UPGMA, Faria et al., 2011). The heterozygosity of the 18 clones was assessed using approximately 60,000 single-nucleotide polymorphisms (SNPs) following the methodology described in Silva-Junior et al. (2015). The results basically confirmed the breeders' expectations regarding two main genetic pools for clones in this study: (i) taxonomic section Maidenaria (clones F6, J1, I9, M4 and N5 of *E. dunnii* or *E. benthamii*); and (ii) Transversaria and Exsertaria sections (all the others; Fig. 5).

The sites showed a range of about 10 °C for both the maximum (23–33 °C) and minimum (12–23 °C) average annual temperatures (Table 1). During the 12 months of mid-rotation evaluation, the cooler sites experienced more than 8 frost days, while in the hottest sites the maximum daily temperature higher than 35 °C was observed in 40 or more days. Annual average precipitation ranged from about 400 mm to

Table 2

Locations for the 27 TECHS sites in this paper, and soil characteristics (0–40 cm depth, details for column heading are below table).

Site	Nearest city	Region	State	Soil order	Clay	Silt	Sand	Organic matter	pH	P	K	Ca	Mg	Cation exchange capacity	Water holding capacity
					%			g L ⁻¹		mg L ⁻¹ soil	mmolc L ⁻³				L m ⁻²
1	Niquelândia	T	GO	Oxisol	39	18	43	40.0	4.2	0.0	0.7	1.0	1.0	62.7	166
2	Arapoti	T	PR	Oxisol	71	22	7	34.3	4.1	0.0	0.6	1.0	1.0	91.4	240
3	Bom Despacho	T	MG	Oxisol	79	19	2	45.0	4.4	0.0	0.5	1.0	1.0	76.5	246
4	Belo Oriente	T	MG	Oxisol	59	10	31	31.3	4.0	1.5	1.2	4.8	1.3	71.7	179
5	Guanhães	T	MG	Oxisol	44	13	43	35.0	3.9	0.5	0.9	1.3	1.0	91.1	160
6	Eldorado do Sul	ST	RS	Ultisol	27	19	54	25.0	3.7	0.5	1.0	1.0	1.0	128.0	145
7	Rio Verde	T	GO	Entisol	6	5	89	19.0	4.5	2.5	0.3	9.5	1.0	35.8	59
8	Inhambupe	T	BA	Ultisol	18	7	75	18.0	4.1	4.5	0.8	1.0	1.0	37.3	89
9	Estrela do Sul	T	MG	Oxisol	80	9	11	43.0	3.9	1.0	0.8	2.0	1.0	88.8	215
10	Botucatu	ST	SP	Oxisol	20	9	71	30.0	4.3	3.5	2.2	4.0	1.0	66.7	100
11	Chapadão do Sul	T	MS	Oxisol	15	9	76	23.5	4.3	1.5	0.5	3.0	1.0	55.0	91
12	Aracruz	T	ES	Oxisol	30	12	58	18.0	4.0	1.5	0.7	2.5	1.0	40.7	130
13	Três Lagoas	T	MS	Oxisol	14	9	77	11.0	4.0	3.0	5.2	24.5	4.5	62.7	87
14	Inocência	T	MS	Entisol	10	8	82	10.5	4.1	1.0	6.8	28.5	5.0	64.8	79
15	Brejinho de Nazaré	T	TO	Entisol	10	8	82	7.5	4.2	0.0	4.1	35.5	5.0	64.6	77
17	Três Marias	T	MG	Oxisol	14	5	81	15.5	4.1	0.5	2.9	11.5	2.0	47.4	76
20	Mogi Guaçu	T	SP	Oxisol	41	16	42	34.0	4.1	4.5	1.2	8.0	1.5	97.2	165
22	Telemaco Borba	T	PR	Oxisol	56	23	21	52.0	4.0	3.5	3.8	37.5	11.0	183.8	214
23	Otaclício Costa	ST	SC	Inceptisol	43	28	29	44.5	3.9	0.5	7.5	67.0	10.5	338.0	205
24	Borebi	T	SP	Entisol	8	3	89	12.0	4.6	2.0	5.5	73.0	10.0	104.5	57
26	Coração de Jesus	T	MG	Oxisol	35	6	59	32.0	3.9	1.5	5.1	48.5	7.5	120.6	118
27	Antônio Olinto	ST	PR	Ultisol	14	5	81	25.5	3.9	3.5	4.5	31.5	6.0	141.5	76
28	Três Barras	ST	SC	Oxisol	60	24	16	51.0	3.8	1.5	1.6	30.5	5.5	291.1	225
29	Urbano Santos	T	MA	Entisol	9	5	87	16.0	4.1	0.0	1.4	36.5	15.5	91.4	64
30	Bocaitíva	T	MG	Oxisol	76	14	10	47.5	3.9	2.0	1.6	48.5	26.5	209.1	225
31	Eunápolis	T	BA	Ultisol	25	3	73	24.5	5.4	5.0	1.5	25.5	9.0	60.0	88
33	Buri	ST	SP	Oxisol	52	20	28	51.0	4.3	10.5	1.0	11.0	14.5	135.5	196

Region: Tropical (T), Subtropical (ST).

Soil order: by US taxonomy, [Soil Survey Staff \(1999\)](#).Clay and sand were quantified by densimeter method ([Embrapa, 1997](#)).Organic matter was determined by Walkley-Black method ([Embrapa, 1997](#)).Extractable P, K, Ca, e Mg were extracted by ion exchange resin ([van Raij et al., 2001](#)).

CEC (cationic exchange capacity).

WHC (water holding capacity, 0–2 m depth, [Stape et al., 2004](#)).**Table 3**The 18 TECHS genotypes of *Eucalyptus*, genetic heterozygosity, and the climate where each clone was developed for operational use.

Clone	Genotype	Clone type	Heterozygosity	Climate of the clone origin region ^a
A1	<i>E. urophylla</i>	Plastic	0.245	Cwa
B2	<i>E. urophylla</i> x <i>E. grandis</i>	Tropical	0.247	Aw
C3	<i>E. grandis</i> x <i>E. camaldulensis</i>	Plastic	0.294	As
D4	<i>E. grandis</i> x <i>E. urophylla</i>	Tropical	0.243	Aw
E5	<i>E. urophylla</i>	Tropical	0.243	Cwa
F6	<i>E. benthamii</i>	Subtropical	0.091	Cfb
G7	<i>E. urophylla</i>	Tropical	0.251	Cwa
H8	<i>E. grandis</i> x <i>E. urophylla</i>	Tropical	0.258	Am
I9	<i>E. dunnii</i>	Subtropical	0.105	Cfb
J1	<i>E. benthamii</i>	Subtropical	0.092	Cfb
K2	<i>E. saligna</i>	Plastic	0.211	Cfb
L3	<i>E. urophylla</i> x <i>E. globulus</i>	Subtropical	0.230	Cfb
M4	<i>E. dunnii</i>	Subtropical	0.102	Cfb
N5	<i>E. dunnii</i>	Subtropical	0.106	Cfb
O6	<i>E. grandis</i>	Subtropical	0.181	Cfb
P7	<i>E. urophylla</i> x <i>E. tereticornis</i>	Tropical	0.234	As
Q8	<i>E. grandis</i>	Plastic	0.240	Af
R9	<i>E. urophylla</i>	Tropical	0.251	Aw

^a Köppen climatic classification ([Alvares et al., 2013b](#)).

2000 mm ([Fig. 4](#)), and potential evapotranspiration ([Thornthwaite and Mather, 1957](#)) ranged from about 800 to 1800 mm yr⁻¹. Accounting for the water holding capacity of soil at each site, the annual water deficit (water balance of [Thornthwaite and Mather, 1957](#)) ranged from 0 for cooler and wetter sites to over 800 mm yr⁻¹ on the hotter, drier sites.

Soils varied substantially among the TECHS sites, including one site on a clayey Inceptisol, five sites on sandy Entisols, four sites on highly weathered, high-clay Ultisols, and seventeen on highly weathered Oxisols ([Table 2](#)). Soil water holding capacity (0–2 m depth) differed by up to fourfold across sites, increasing from about 75 mm m⁻¹ for soils with 10% clay to over 200 mm m⁻¹ for soils with 80% clay. All soils were very acidic, with low to moderate levels of extractable phosphorus, nutrient cations, and cation exchange capacity. Cation exchange capacity related more strongly to soil organic matter ($r^2 = 0.45$, $P < 0.001$) than to clay content ($r^2 = 0.2$, $P = 0.05$).

The diameter at breast height (DBH, 1.3 m above ground level), total height (H), and live crown depth of all trees and sites were measured every 6 months. Stemwood biomass was estimated by allometric equations developed from destructive sampling of 93 trees from the 18 clones (3–6 trees per clone) at site 33 (which uniquely was planted with all 18 genotypes). The sampled trees were selected to cover the range of DBH. After harvesting, DBH and total height (H) were measured. Stemwood was separated from the other components of the tree and weighed on site individually, and representative samples were collected and dried at 65 °C to constant weight for dry mass determination.

Dry mass (B, in kg tree⁻¹) of the stemwood compartment was calculated using the linearized model of [Schumacher and Hall \(1933\)](#),

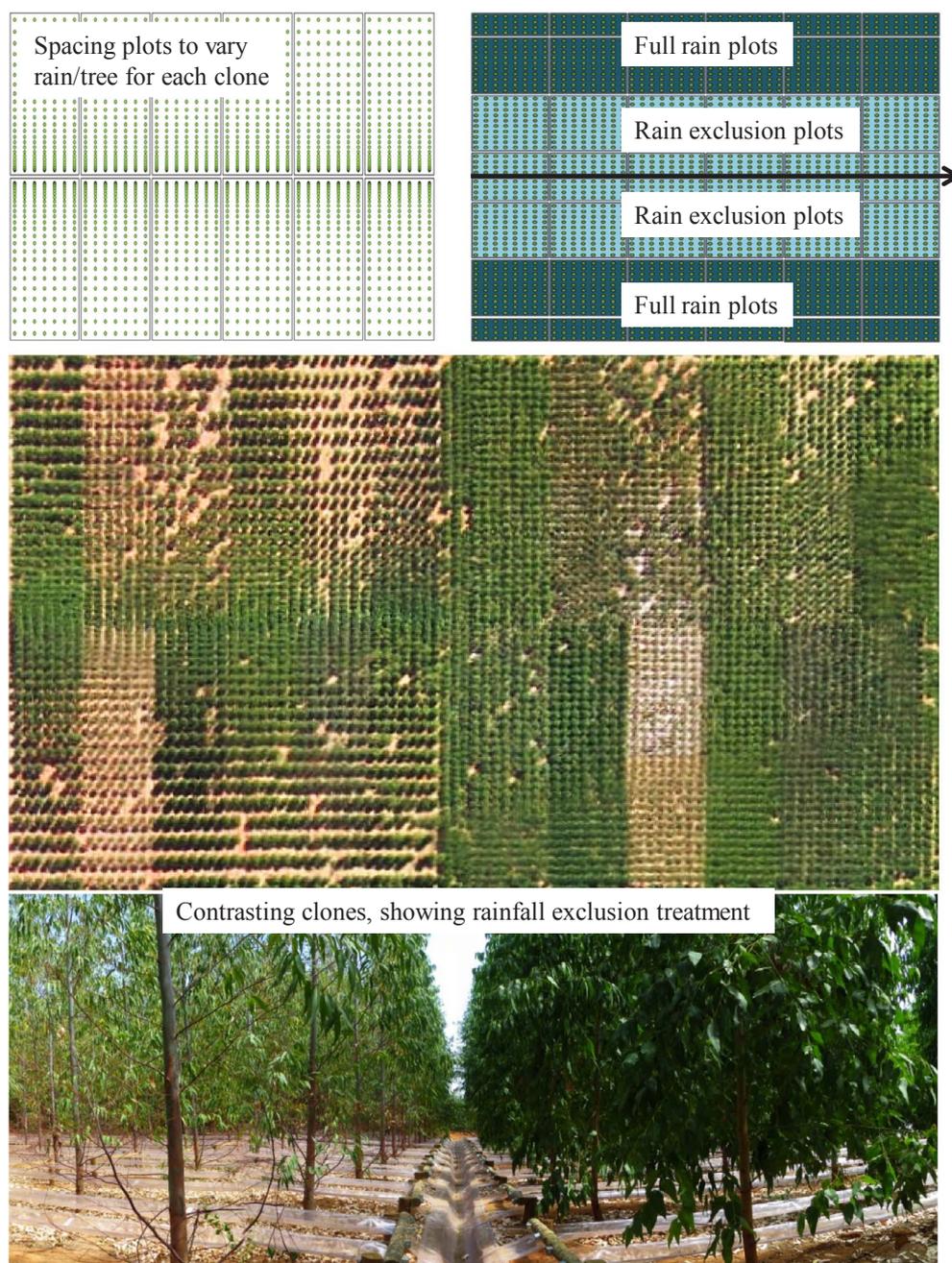


Fig. 2. Diagram (upper) and photograph (middle) of TECHS design. For the individual-tree experiment with spacing (left side of upper and middle images), each of the 12 clones used at each site was planted in 7 lines of trees (3 m spacing) and 27 variable spacing between trees within rows (ranging from 0.25 to 7.15 m apart), providing a range from 1.5 m² tree⁻¹ (~13,000 trees ha⁻¹) to 23 m² tree⁻¹ (~450 trees ha⁻¹). The rainfall removal experiment (right side of upper and middle figures) planted trees in single-clone plots (24 × 30 m, with trees at 3 × 3 m spacing), with additional rows of trees to allow for destructive sampling. The rainfall removal troughs are shown for 2 clones in the bottom image.

with specific intercept “a” for each clone j ($R_{adj}^2 = 0.98$, MAE = 0.04 kg tree⁻¹) (Mattos, 2015):

$$\ln B_j = a_j + 1,8534 \ln(DBH) + 1,1414 \ln(H)$$

The best allometric equation was selected by the graphical analysis of normality and distribution of the residuals, the range of prediction of mean absolute error (MAE, Willmott and Matsuura, 2005), and the adjusted determination coefficient. The coefficients were fitted using the ordinary least squares of the function *lm* in R (R Core Team, 2014). The “a” intercept varied from -4.4530 to -4.0682. Stemwood production between years 2 and 3 was estimated for each clone and site as the summation of the individual tree stem biomass increases (based on

clone-specific allometrics), dividing by the plot area and expanding to a hectare basis (Mg ha⁻¹ yr⁻¹).

Leaf area index (LAI) was estimated based on the theory of Norman and Jarvis (1975), using a ceptometer (AccuPAR LP-80, Decagon Devices Inc., 1999). The method accounts for sky conditions at the time of radiation measurement, effects of the canopy structure, and foliage optical properties, assuming random foliage orientation distribution radiation extinction coefficient of 0.5 (Campbell, 1986, Wang et al., 2007; see Mattos, 2015 for more details).

The patterns of stemwood production across gradients in precipitation and temperature were evaluated with CurveExpert version 2.4 (<http://www.curveexpert.net/>). The best-fit equation was chosen

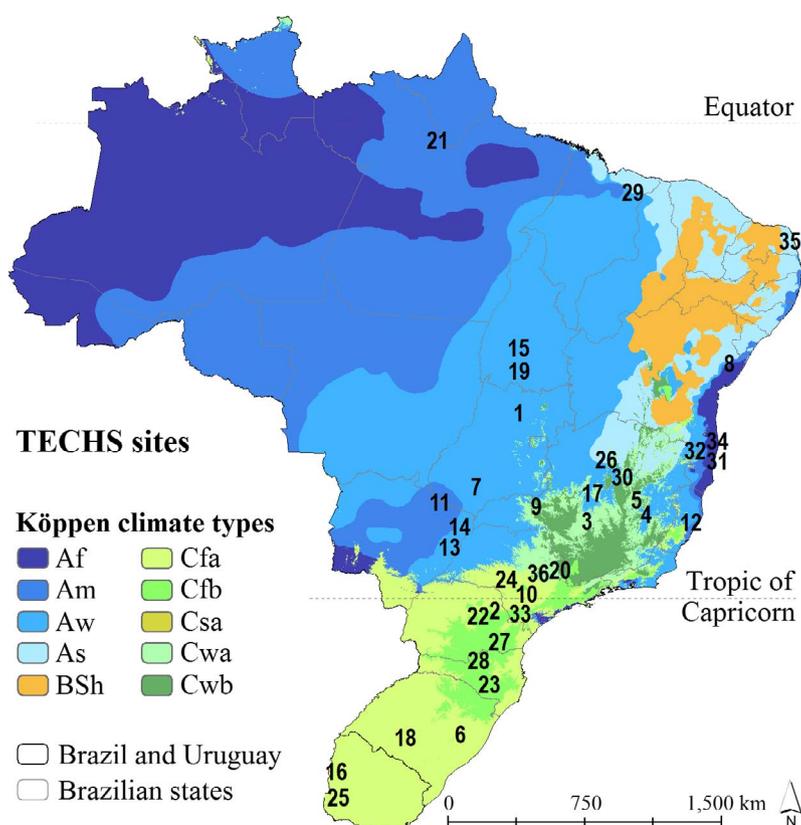


Fig. 3. Location and climate classification of all 36 of the TECHS sites across a 3500 km geographic gradient (climate types from Alvares et al., 2013a,b).

based on the lowest AICc (Akaike's Information Criterion corrected for small sample size) adjusted for small sample sizes.

3. Results

The weather patterns across the TECHS sites were generally typical of long-term climate patterns, with no extreme droughts or excessive rains. The TECHS sites and clones showed a wide range of leaf area and growth, as expected. Fig. 6 illustrates the response of two clones to the environmental conditions across 3 sites. Clone A1 was most productive at Site 22, producing $34 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ of stemwood, with the light intercepted by a leaf area index of 3.8. Clone A1 produced about the same LAI on sites 20 and 30, but growth was only 19 and $22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$. The large difference in stem production across the sites related not to leaf area and light interception, but to the efficiency of producing wood per unit of light intercepted. Similar to Clone A1, Clone C3 was the most productive at site 22 ($46 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ with a LAI of 3.0), but produced about the same stemwood as Clone A1 on Sites 20 and 30, despite 33% lower LAI. The lack of a difference in stem production in this case resulted from a higher LAI and efficiency of light use at Site 20 for Clone 3. Differences in leaf assimilation and respiration, carbon allocation and local herbivory rates can influence light use efficiency, and future research will estimate the influences of these factors.

The environmental gradient across the Tropical region led to a 5-fold range in stem production ($9\text{--}45 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, site averages for all clones within each site, Fig. 7). The variation across sites was not as large for the Subtropical region, differing only about 2-fold (19 and $44 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). The production of the best and worst clone differed by a factor of 2 or more for both the Tropical and Subtropical regions. The grand average of all clones within the Tropical region (21 Mg ha^{-1}

yr^{-1}) was 25% lower than Subtropical region ($28 \text{ Mg ha}^{-1} \text{ yr}^{-1}$). Within each site, stemwood production of the clones differed between the more productive tropical sites and the subtropical sites.

The productivity of each clone varied substantially across sites (Fig. 8). Clone P7 (planted only in the Tropical region) showed relatively low variation in production, indicating a limited ability to reach high growth rates even on favorable sites. Clones H8 and B2 were the most variable across sites in the Tropical region, achieving high growth rates on the best sites, but much less on poorer sites. The clones planted only in the Subtropical sites showed generally less variation across sites than those in the Tropical region. Within the Tropical region variation was lowest for the poorest sites (Fig. 7), perhaps indicating a single overriding factor such as water supply strongly limited the expression of genotypic differences. The plastic clones that were planted in both regions showed high variation in the Tropical region, similar to the Tropical-only clones (Fig. 8). The potential growth of *Eucalyptus* at each site may be indexed better by the production of the best clones. The average growth of the three fastest-growing clones (at each site) averaged about $1.5\text{--}4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ ($3\text{--}8 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$) more than the average for all clones ($22 \text{ Mg ha}^{-1} \text{ yr}^{-1}$).

These patterns of production for the clones across sites are also illustrated in Fig. 9, where the clones are ranked for each region. Plastic Clone A1 was a top performer overall for the Tropical region (ranked as the best performer for the greatest number of sites), but A1 ranked near the middle for the Subtropical region. Plastic Clone C3 was near the bottom for performance on Tropical region, but did better than the other three plastic clones in the Subtropical region. The regional pattern of production for Clone C3 may relate to the distribution of a gall-wasp (absent from some of the Tropical sites and from the Subtropical region).

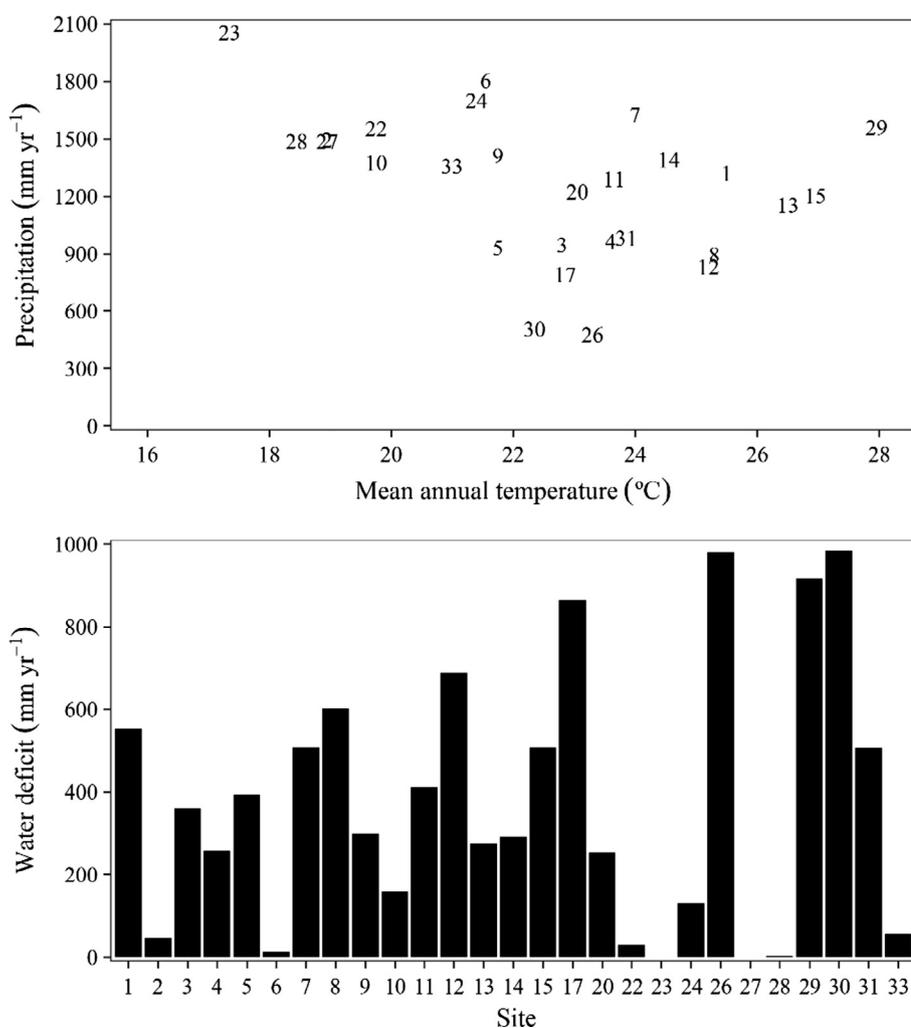


Fig. 4. The average annual precipitation for the TECHS sites spanned a fourfold range, along with a 10 °C temperature range (upper graph). The combination of water supply and temperature provided estimated water deficits (lower graph) of 0–1000 mm yr⁻¹ (based on temperature, precipitation, and water holding capacity of soil in each site).

Across sites the annual rainfall from year 2 to 3 ranged from 500 to 2000 mm, and mean annual temperature ranged from 17 to 27 °C. The average growth of clones across all sites showed linear relationships with both temperature and precipitation. An increase of precipitation of 100 mm yr⁻¹ was associated with a 1.51 Mg ha⁻¹ yr⁻¹ ($r^2 = 0.21$, $P = 0.03$) increase in stemwood production across all clones, and 1.79 Mg ha⁻¹ yr⁻¹ ($r^2 = 0.28$, $P = 0.01$) when considering only the 3 best clones for each site. An increase of 1 °C in mean annual temperature was associated with a decline in stemwood production of 2.9 Mg ha⁻¹ yr⁻¹ for all clones and for the three best clones ($r^2 = 0.35$, $P < 0.01$).

The geographic patterns in precipitation and temperature were not independent. Hotter sites were generally drier, with precipitation decreasing by an average of 78 mm yr⁻¹ for 1 °C increase in mean annual temperature ($r^2 = 0.27$, $P = 0.01$). Simple correlations with production as a function of temperature had about the same AICc (within 1 unit) as the more complex relationship with both temperature and precipitation. The pattern of growth with precipitation alone was weaker (AICc about 4 units higher) than when both precipitation and temperature were included. The apparent response of production to precipitation was substantially lower when temperature was also included as an independent variable, declining to an increase of only 0.43 Mg ha⁻¹ yr⁻¹ with an increase of 100 mm of precipitation (Fig. 10). The apparent influence of temperature on production was similar when examined in relation to temperature and precipitation

(2.5 Mg ha⁻¹ yr⁻¹ for a 1 °C change in temperature) as it was with temperature alone.

The influence of temperature and precipitation may be combined into a single variable of a water deficit, incorporating the energy available to evaporate water, and the supply of water based on precipitation and soil water-holding capacity (Table 1). Condensing these influences into the single variable of water deficit lowered the AICc (by about 4 units) and raised the r^2 (from 0.37 to 0.45) for predicting stem production relative to using temperature and precipitation as independent variables, highlighting that temperature and water together with soil physical drainage properties influences clone adaptation and performance.

Clones varied strongly in responsiveness to differences in climate across sites. The clone with the highest average growth across the Tropical sites (Clone D4) showed very high growth at cooler Tropical sites, and a linear response to precipitation (Fig. 10). In contrast, the best-growing plastic clone (across both regions, A1) showed a relatively large plateau of growth, declining at all extremes. Interestingly, the different curvilinear responses of individual clones led to the overall linear pattern in the upper part of Fig. 10(A and B) when multiple clones were averaged together.

In the spacing experiment, the trees planted at the widest spacing showed the highest individual tree growth (Fig. 11). All clones showed declining individual tree size as distance to neighbors declined, though some were notably more sensitive than others. The influence of

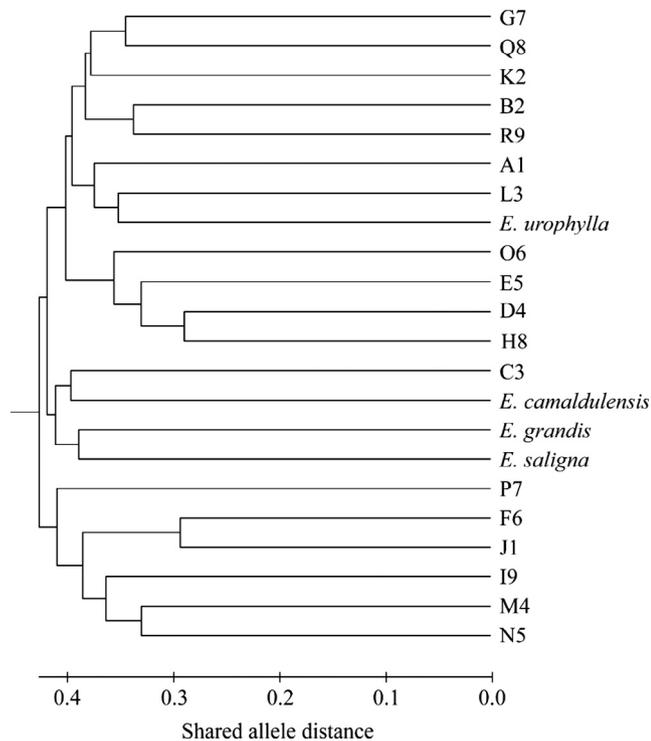


Fig. 5. TECHS clones came from two main genetic pools of the *Eucalyptus* genera: (i) Section Maidenaria (clones F6, J1, I9, M4 and N5 of *E. dunnii* or *E. benthamii*); and (ii) Sections Transversaria and Exsertaria (all the others clones and the 4 seedlot species).

neighbors was much stronger for the Tropical sites than for the cooler and wetter Subtropical sites, based on the average response of all clones within each site. The individual tree patterns can be extrapolated to a plot scale based on the area available to each tree. The plot-level production increased somewhat for each clone with increasing density of tree spacing, but the pattern differed strongly among the clones. When all clones are averaged within each site, the Subtropical sites showed the strongest plot-level response to density of tree spacing. This results from a weaker effect of spacing on individual tree growth (Fig. 11B), allowing the number of trees to then have a larger overall effect on plot-level growth (Fig. 11C).

4. Discussion

The broad range of climate, soils, and genotypes in the TECHS project provided a strong platform for evaluating patterns of stem production. Three findings were especially intriguing. The range of precipitation across the TECHS sites was associated with a threefold range in stemwood growth, about the magnitude of response to temperature. Although both precipitation and temperature showed similar magnitudes of influence on stemwood production, the effect of temperature was statistically stronger. The temperature response was negative, in contrast to typical regional patterns that include changes of species across temperature gradients in the Tropics. For example, Beer et al. (2010) examined the pattern of gross primary production (GPP) as a function of latitude, and found GPP decreased with distance from the Equator as temperatures declined.

The negative effect of warmer temperatures could result from

increasing respiration loss of carbon. Ecosystem respiration generally increases with temperature, with a typical increase of 40% for a 10 °C increase in temperature (Mahecha et al., 2010). However, the TECHS Project stemwood production showed a much steeper response to the geographic temperate gradient, with a 40% decline in stemwood production in response to only a 4 °C increase in temperature. Therefore we suspect that a temperature response of respiration would likely be too small to account for the bulk of the decline in stemwood production.

Perhaps the most relevant examination of possible factors comes from Aspinwall et al. (2016), with an examination of long-term and short-term temperature responses of *Eucalyptus tereticornis* grown under controlled conditions. They found strong declines in both photosynthetic capacity (at saturating levels of CO₂) and nighttime respiration of leaves with increasing temperatures. Taking 20 °C as a baseline, increasing temperature to 24 °C lowered photosynthetic capacity by 17% and nighttime respiration by 29%. An increase of 4 °C across the TECHS site was associated with a notably larger reduction in stemwood production, so these mechanisms may not be sufficient to explain the TECHS pattern. Overall, the TECHS Project shows that direct assessment of tree ecophysiology and carbon partitioning will be needed to explain the strong decline we observed in stem production with increasing temperature across the geographic gradient, as found by Stape et al. (2008) and Ryan et al. (2010).

A second major point is that the TECHS pattern of production in response to precipitation (about 1.5 Mg ha⁻¹ yr⁻¹ for each increase of 100 mm yr⁻¹ in precipitation) was similar to trends reported for inventory plots across geographic gradients in eastern Brazil (Fig. 12). Stape et al. (2004) estimated an increase of 2.2 Mg ha⁻¹ yr⁻¹ for each 100 mm yr⁻¹ increase in precipitation (Fig. 12) across 14 sites in northern Bahia. A database with thousands of operational inventory plots also showed a similar response to increasing precipitation in southern Bahia, northern Espírito Santo, and eastern Minas Gerais, where an increase of 100 mm yr⁻¹ was associated with increased production of 2.4 Mg ha⁻¹ yr⁻¹ on drier sites (about 1000 mm yr⁻¹ mean annual precipitation) and 1.5 Mg ha⁻¹ yr⁻¹ on wetter sites (about 1500 mm yr⁻¹; (J.L. Stape, unpublished data).

As noted above, these apparent effects of increasing precipitation may be confounded with changes in temperature across geographic gradients. Any influence of temperature may be excluded by testing response to either additions or removals of water within sites. Irrigation treatments in *Eucalyptus* plantations in Brazil have shown about 0.66 Mg ha⁻¹ yr⁻¹ additional stemwood production for each 100 mm of irrigation water (Stape et al. 2010). This irrigation was close to the TECHS value of 0.43 Mg ha⁻¹ yr⁻¹ for each 100 mm increase in rainfall across sites (when the effect of temperature was included). A relatively modest response of stemwood production to water supply was also evident in a rainfall removal experiment in São Paulo. Removal of 37% of throughfall beneath *Eucalyptus* trees had little effect on forest production, though tree nutrition (particularly potassium supply) and deep-soil drawdown of stored water were also important (Christina et al., 2015, Laclau, 2016).

A third major point is that the TECHS Project indicated that the overall patterns of stem production varied as strongly among clones within sites as across the geographic gradient of sites. As illustrated in Fig. 6, the clones differed greatly in the deployment of leaf area, and in the ability of leaves to grow wood. The clones also differed strongly in response to temperature and precipitation (Fig. 10). On-going studies are examining some of the processes that underlie these patterns. The wide range of responses among clones to the geographic gradient in the TECHS study demonstrates opportunities for matching genotypes, and even genes, to sites. We anticipate that on-going investigation of genetic markers among the clones in this study may relate to the degree of

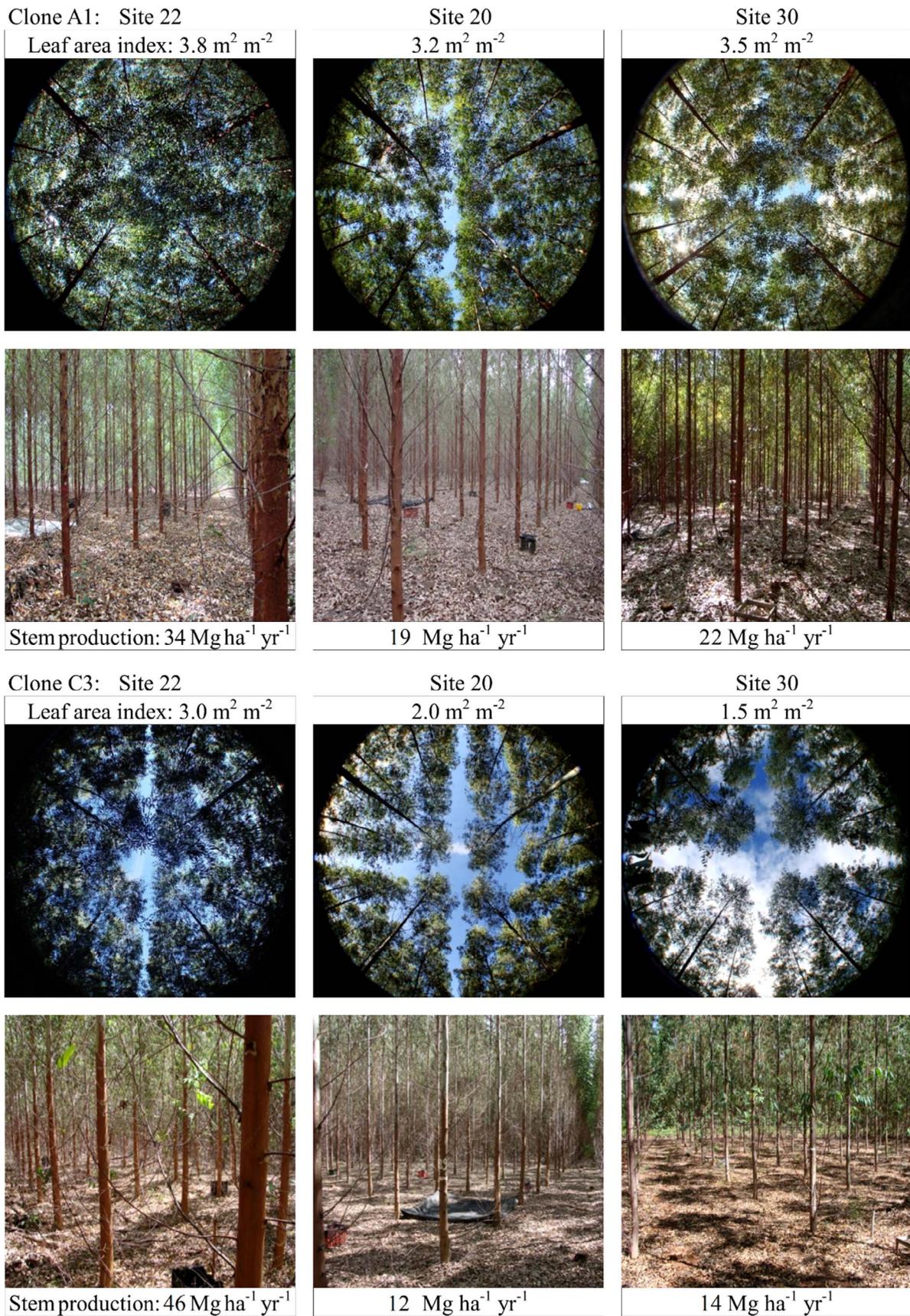


Fig. 6. Leaf area and stem production showed strong interactions across sites at 24 months of age, as illustrated by clones A1 and C3 at 3 sites. Leaf area of Clone A1 varied little across sites (upper), even though stem production differed substantially. The leaf area of Clone C3 changed more strongly across sites, in concert with stem production (bottom).

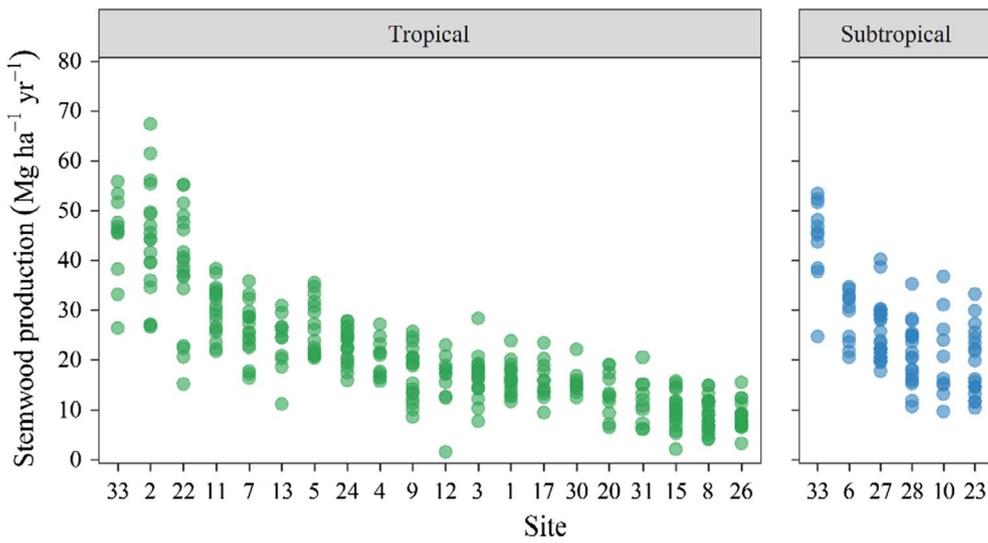


Fig. 7. The stem production varied by more than 50% among clones within sites, for both Tropical and Subtropical regions (each circle represents one clone in each site). The average production varied by about 5-fold across Tropical sites, in contrast to a 2-fold range among Subtropical sites. Sites are sorted by decreasing productivity.

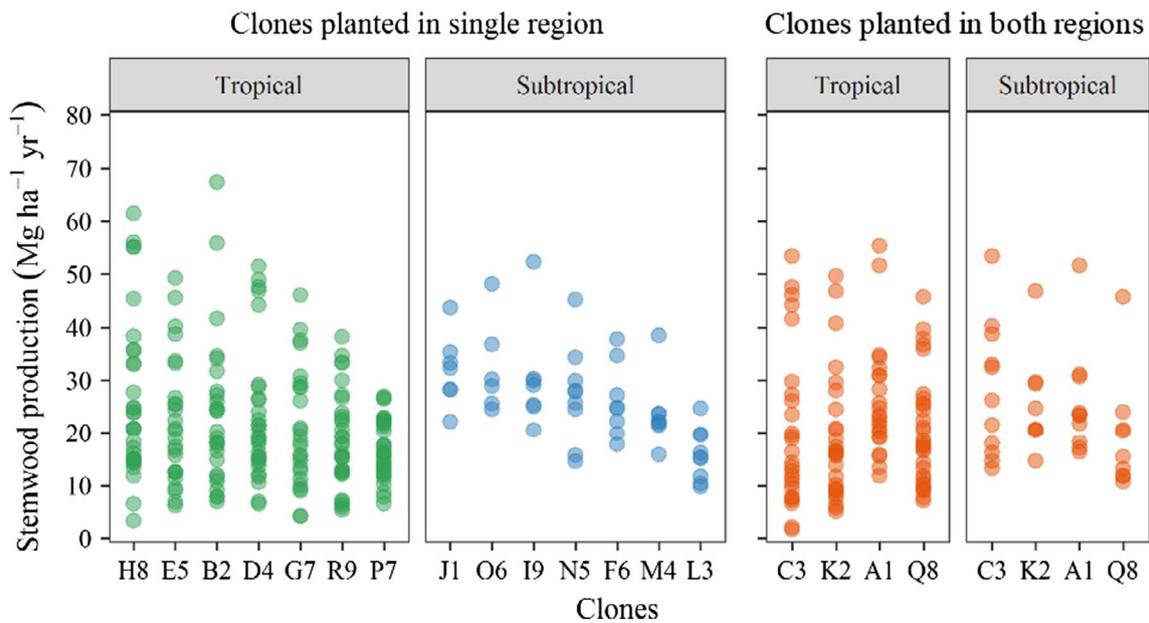


Fig. 8. The performance of each clone varied by 2- to 6-fold across sites. Among the Tropical clones, more productive clones tended to show greater responsiveness to site conditions, but this trend was not apparent in the Subtropical clones (perhaps owing to less environmental variation). Four clones were planted across sites in both regions, with similar growth patterns between regions.

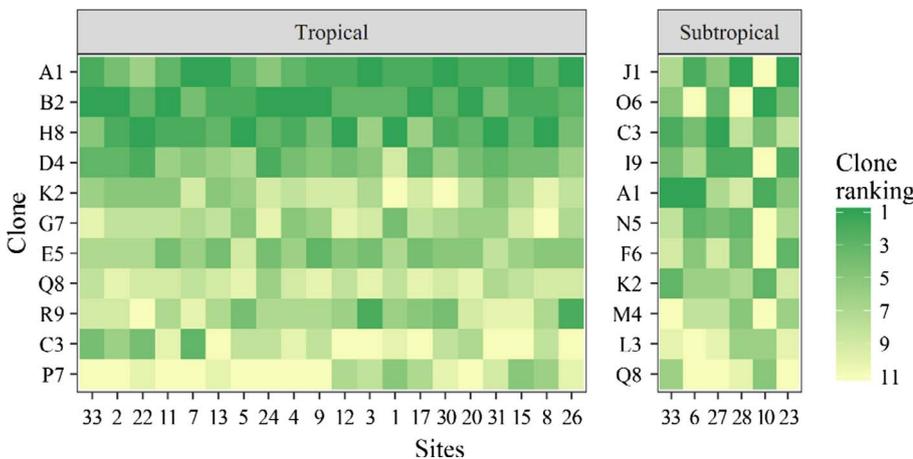


Fig. 9. Some clones, such as A1, were among the top performers across a broad range of sites, whereas others were top performers only in a few sites. Clones (from top to bottom) and sites (from left to right) are sorted by increasing productivity.

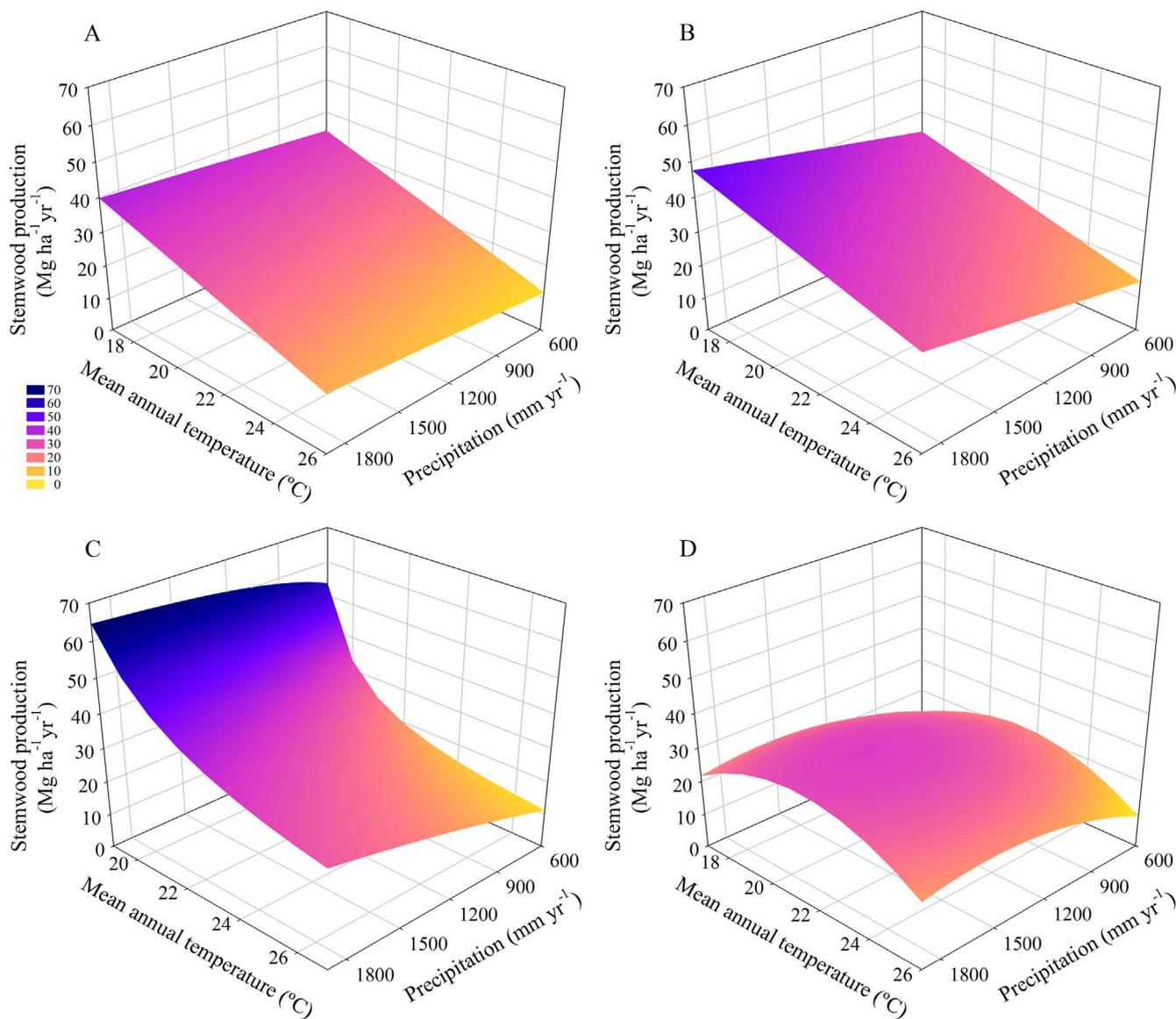


Fig. 10. The average stemwood production of all clones across all sites increased linearly with precipitation and decreasing temperature (A, $r^2 = 0.37$). Not all clones grew well at all sites, and the response surface for the three fastest-growing clones at each site (B, $r^2 = 0.41$) averaged about $3\text{--}8\text{ m}^3\text{ ha}^{-1}\text{ yr}^{-1}$ (greater differences for wetter and hotter sites) more than the average of all clones. The responses of individual clones was curvilinear; the clone with the highest average growth for tropical sites was especially sensitive to temperature (C, Clone D4 B2, $r^2 = 0.70$), whereas the best plastic clone showed a broad optimum for both temperature and precipitation. (D, Clone A1, $r^2 = 0.29$).

sensitivity to environmental factors, which is fundamental for selection of clones for operational planting, and parameterizing process-based models.

Finally, these results have value for understanding how the future supply of wood from intensively managed plantations of *Eucalyptus* would likely shift in response to changing management and climate. For example, changes in land value for growing *Eucalyptus* and other potential crops may shift the geography of land available for *Eucalyptus* silviculture. The TECHS Project results indicate that a shift to slightly warmer sites might lead to as great a reduction in growth as a shift to slightly drier sites. Changes in future climates within sites may alter both temperature and precipitation, and again changes in temperature

appear to have strong potential to lower *Eucalyptus* production, especially for dryer landscapes. These tentative conclusions may be revised after results are available for the full rotation and the within-site water removal treatments. A full evaluation of the herbivory associated with exotic pests and diseases will also be important. The breadth of available genes and genotypes in future breeding programs may also shift this balance between the sensitivity of intensively managed plantations of *Eucalyptus* to temperature and precipitation.

Acknowledgements

The TECHS Project depended on the contributions of more than 150

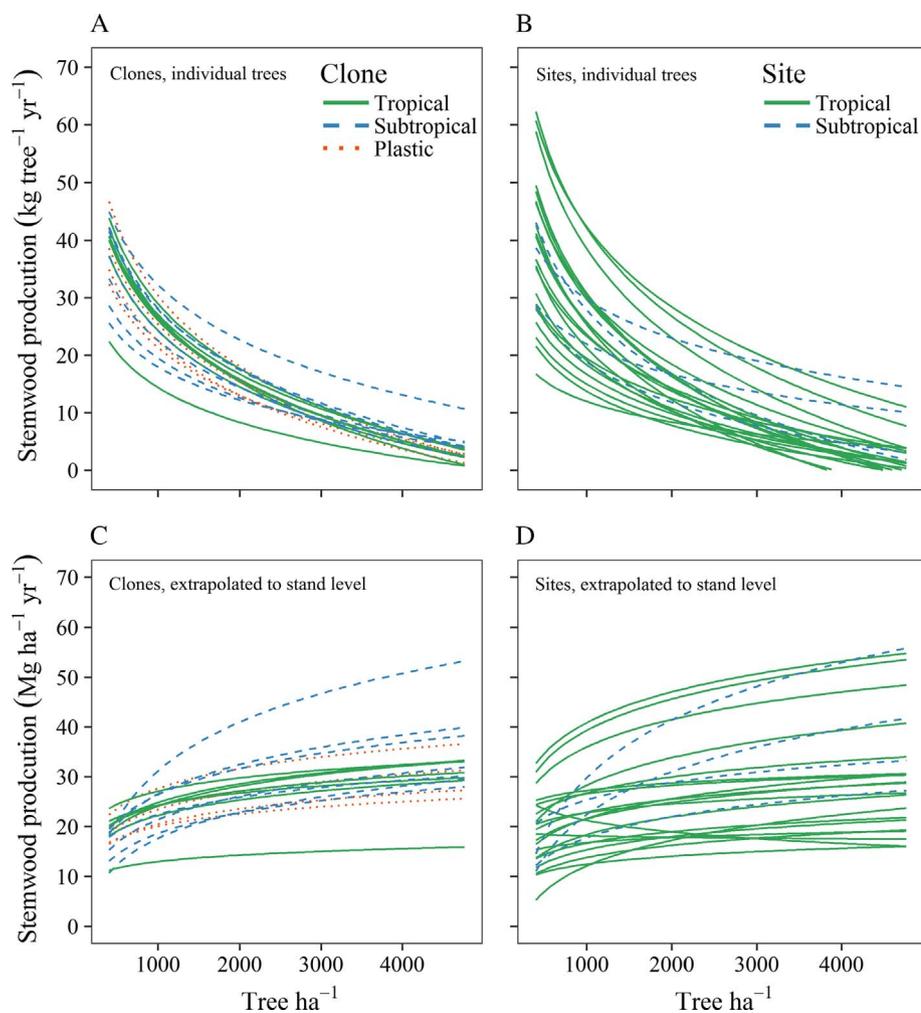


Fig. 11. The production of individual trees declined with increasing density of trees per hectare, when examined as clones across sites (A), and averages of all clones within sites (B). Extrapolation to a plot level showed that faster growing clones showed a stronger increase in relation to density (steeper slopes in C). Plot-level extrapolation of production across all clones generally showed increasing production with density, with stronger responses for subtropical sites (D).

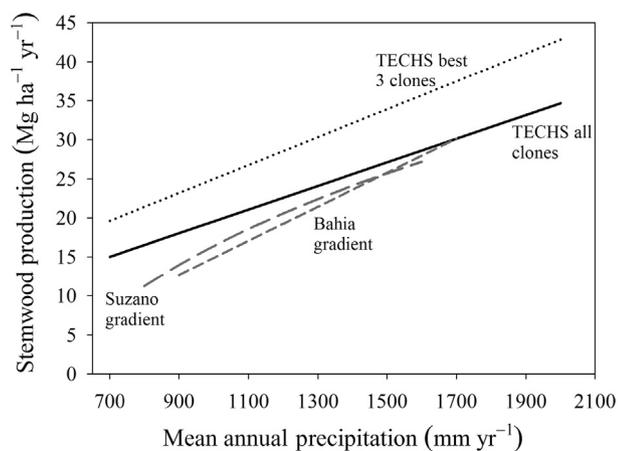


Fig. 12. The pattern of stemwood production with precipitation was similar to the pattern across a geographic gradient of 14 sites in northern Bahia (Stape et al., 2004) and across hundreds of inventory plots in southern Bahia, eastern Minas Gerais, and northern Espírito Santo (J.L. Stape, unpublished data). The TECHS lines are for the year of peak production of the rotation, and the others are lower because they are mean annual production for the entire rotation.

people from 26 companies, and we thank them all for their contributions to the Project. The project was funded by the following 26 companies, with a main researcher: Anglo American (Andre Machado), Arauco (Rodrigo Coutinho), Arborgen (Gabriela Bassa), ArcelorMittal (Roosevelt Almado), Cenibra (Fernando Leite), CMPC (Elias Araujo), Comigo (Ubirajara Oliveira), Copener (Jacyr Alves), Duratex (Raul Chaves), Eldorado (Vinicius Silva), Fazenda Campo Bom (Jacqueline Pirez), Fibria (Rodolfo Loos), Florestal Itaquari (Admir Mora), Forestal Oriental (Ricardo Methol), Gerdau (Francisco Gomes), GMR (Paulo Leite), International Paper (Cristiane Lemos), Jari (Katia Silva), Klabin (James Stahl), Lwarcel (Marcela Capoani), Montes del Plata (Alejandro Gonzalez), Plantar (David Fernandes), Rigesa (Ricardo Paim), Suzano (Luiz Fabiano), Vallourec (Helder Andrade) and Veracel (Helton Lourenço). Fundamental assistance was provided for many aspects of the project by Luiz Barrichelo, Dario Grattaplagia, Mike Ryan, Eduardo Mattos, Robert Hubbard, Rodrigo Hakamada, Aurelio Aguiar, Leandro de Siqueira, Gleison dos Santos and João Flavio Silva. The project also received support from these universities and institutes: University of Sao Paulo - Brazil, Sao Paulo State University – Brazil, Federal University of Lavras – Brazil, Federal University of Rio Grande do Norte – Brazil, Colorado State University – USA, North Carolina State University – USA, USDA Forest Service, CNPq – Brazil and Fapesp – Brazil.

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