

Species-site matching in mixed species plantations of native trees in tropical Australia

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Abstract Mixed species plantations using native trees are increasingly being considered for sustainable timber production. Successful application of mixed species forestry systems requires knowledge of the potential spatial interaction between species in order to minimise the chance of dominance and suppression

and to maximise wood production. Here, we examined species performances across 52 experimental plots of tree mixtures established on cleared rainforest land to analyse relationships between the growth of component species and climate and soil conditions. We derived site index (SI) equations for ten priority species to evaluate performance and site preferences. Variation in SI of focus species demonstrated that there are strong species-specific responses to climate and soil variables. The best predictor of tree growth for rainforest species *Elaeocarpus grandis* and *Flindersia brayleyana* was soil type, as trees grew significantly better on well-draining than on poorly drained soil profiles. Both *E. grandis* and *Eucalyptus pellita* showed strong growth response to variation in mean rain days per month. Our study generates understanding of the relative performance of species in mixed species plantations in the Wet Tropics of Australia and improves our ability to predict species growth compatibilities at potential planting sites within the region. Given appropriate species selections and plantation design, mixed plantations of high-value native timber species are capable of sustaining relatively high productivity at a range of sites up to age 10 years, and may offer a feasible approach for large-scale reforestation.

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Introduction

High-value tropical tree species can be difficult to cultivate in monoculture plantations and require species mixtures to improve stem form and to reduce environmental pressures which negatively effect growth (Dordel 2009). Mixed species tree plantations may also provide benefits of product diversification, improved risk management and increased productivity when compared to monocultures (del Rio and Sterba 2009; Potvin and Dutilleul 2009; Amoroso and Turnblom 2006; Forrester et al. 2004). Despite mounting interest in mixed species plantations over the last decade (Chen et al. 2003), trials of mixtures of native timber species in Brazil (Yamada and Gholz 2002), Costa Rica (Montagnini et al. 2003), Thailand (Elliott et al. 2003), Australia (Bristow et al. 2005; Vanclay 2006a) and China (Jian-min et al. 2003) have failed to produce plantation models for adoption by landholders or commercial timber growers on a large scale. Framework native species with the best potential for inclusion in mixtures have been identified for most regions (Bristow et al. 2005; Elliott et al. 2003; Jian-min et al. 2003; Yamada and Gholz 2002) but a lack of successful operational scale demonstrations coupled with adequate financial analysis has impeded the adoption of mixed species systems in industrial plantations (Nichols et al. 2006).

Another impediment hindering the implementation of successful mixed species systems is a lack of knowledge for matching species to site, which is especially relevant for native tropical trees including those of the Wet Tropics region of Australia where species exhibit large variations in performance between sites (Bristow et al. 2005). An understanding of the relative height growth rates of individual species at different site types is an imperative both for selecting an optimum suite of species with high productivities on a particular site and for predicting the height growth compatibilities of species in mixtures (Dickinson et al. 2008). Currently, matching species to sites for mixed plantations is difficult given the state of knowledge for most species in the study region and elsewhere.

Studies documenting mixed species systems with productive advantages over monocultures (Amoroso and Turnblom 2006; del Rio and Sterba 2009; Erickson et al. 2009; Forrester et al. 2004; Potvin and Dutilleul 2009) have attempted to generalise

design characteristics important for success. However, in many situations mixed species systems offer no change, or a reduced productivity compared to monocultures (Cavard et al. 2010; Chen et al. 2003; Erickson et al. 2009; Forrester et al. 2005; Hunt et al. 2006) and it is acknowledged that a mechanistic understanding of the underlying processes is required to enable better predictive ability for situations where mixtures can be successful (Forrester et al. 2005; Manson et al. 2006).

Often the processes determining the success of mixtures involve an increase in, or a more efficient use of resources compared to monocultures through species complementarity. Complementarity often occurs when stratified canopies develop with the less shade-intolerant species overtopping the more shade-tolerant species (Amoroso and Turnblom 2006; Chen et al. 2003; Erickson et al. 2009; Forrester et al. 2005; Manson et al. 2006). The positive effects from species interactions can however be limited to specific ecological contexts, developmental stages (Chen et al. 2003) and planting densities (Amoroso and Turnblom 2006). Reduced productivity in mixtures has often been associated with asymmetric competition between species as plantations develop (Cavard et al. 2010; Hunt et al. 2006; Chen et al. 2003). Whilst studies investigating neighbourhood effects have identified the inter-specific competitive effects in mixtures (Canham et al. 2004; Bristow et al. 2006), others have found the size of neighbours, rather than species identity, as the largest source of variation in individual tree diameter and height (Erickson et al. 2009; Potvin and Dutilleul 2009).

Size-asymmetric competition appears as the dominant structuring factor in both monoculture and mixed species plantations (Potvin and Dutilleul 2009) and only when these competitive effects are minimised, by matching species with compatible height growth and shade tolerances, can the positive interactions of facilitation and complementarity drive mixtures to out-yield monocultures (Forrester et al. 2006). Competition for light is often asymmetrical between species, especially in mixtures that include rainforest trees with different shade tolerances (Erskine et al. 2005). Taller trees can shade smaller trees and size differences are exacerbated between species as smaller species gets suppressed. Designing successful mixtures depends on the ability to predict early height differences developing between species to avoid

species combinations that may develop strongly size-asymmetric competition for light and crown space. Here we extend the understanding of the relative height growth of priority species at different site types in the Wet Tropics region of Australia to improve our ability to predict structural development of mixtures in the region to identify the potential for the development of asymmetrical above-ground competition between species.

The Community Rainforest Reforestation Program (CRRP) of the Wet Tropics of North Queensland, Australia, aimed to establish mixed species tree plantations, featuring primarily rainforest trees, on 1782 ha of small private properties (Bristow et al. 2005). The CRRP was initiated in 1993 in response to the Australian Federal Government calling a cessation to timber harvesting from natural forests in the Wet Tropics of Queensland. The program aimed to create healthy vegetated catchments that maximise wood production, environmental protection and employment in Eastern Australia (Vanclay 2006a). Plantations containing a total of 170 tree species were established along the higher rainfall areas of the coastal lowlands and foothills, and on the tropical upland areas of the Atherton Tablelands. CRRP funding ended in 2000 and many of the broad social and production goals set for the program had not been fulfilled due to limited resources and continually changing circumstances (Vanclay 2006a).

The poor growth and survival of trees in some early CRRP plantations re-invigorated cynicism that growing rainforest timbers other than native Hoop Pine (*Araucaria cunninghamii*) is uneconomic under Queensland conditions because of low growth rates (Russell et al. 1993). However it has also been argued poor early performance of CRRP plantations can be attributed to poor site species matching, insufficient silvicultural knowledge and inadequate nursery stock (Vanclay 2006a).

Permanent measurement plots of CRRP trial sites were monitored several times from 1998 to 2002 and the data collected as a part of this monitoring included diameter at breast height, height, form and depth of green crown. Consecutive measurements of 10 focus tree species in these permanent plots at 52 sites form the basis of the study presented here. Some analysis of CRRP sites has occurred (Bristow et al. 2005; Dickinson et al. 2008; Vanclay 2006a) but there has been limited progress in the understanding of how to

match species to site. General estimates of growth rates of the study species in the Wet Tropics have been predicted using expert opinion (Herbohn et al. 1999; Russell et al. 1993) by obtaining intuitive guesses of species-specific rotation times. A comparison of measured mean annual increment (MAI) in height across rainfall gradients and four soil categories highlighted the importance of matching species to site (Bristow et al. 2005), but did not allow sufficient prediction of productivity for existing plantations or plantations on new sites. We extend the analysis of Bristow et al. (2005) by deriving species' specific site index (SI) curves and including new variables in the analysis that have recently become available.

Most tree growth and yield models currently used for forest management and growth prediction use the concept of SI (Avery and Burkhart 2002; Skovsgaard and Vanclay 2008). SI is a measure of species' specific growth potential at a site, often expressed as the expected dominant height of a plantation at a given age. SI models assume that plantations follow a predictable growth curve that can be represented by a single measure of site quality that is not sensitive to stand density or stand treatment. Tree height growth can indicate site quality reliably if the stand is not too open or dense (Alemdag 1988). Although alternatives have been proposed (e.g., Vanclay and Henry 1988; Vanclay 1989), height-based SI remains one of the preferred methods for assessing site productivity in mixed-species stands (Vanclay 1992), notwithstanding the challenges of estimation. SI equations have been produced for many important temperate forestry species (Alemdag 1988; Brown 2006; Elfving and Kiviste 1997; Wilczynski and Slawomir 2006) but are lacking for most tropical species (Pancel 1993). Here, we aimed to determine SI equations for a selection of Australian tree species at contrasting sites in context of the main variables determining the growth of mixed species tree plantations in tropical Queensland.

Methods

Trials of the Community Rainforest Reforestation Program (CRRP)

The CRRP initiated the planting of more than 1 million trees on 1,782 ha in North Queensland

(Vanclay 2006a). Whilst most plantations contained between 1 and 8 tree species, a total of 170 mostly native species were trialled with species usually being intimately mixed or planted in alternating rows. The initial stocking of these trials generally ranged from 600 to 800 stems ha^{-1} with seedlings supplied from diverse seed sources and nurseries. Pre-planting preparation included deep ripping with a tractor or a bulldozer and herbicide sprayed along planting rows. Post planting weed control was conducted and fertiliser applied to seedlings at or after planting. Ninety ‘permanent measure’ plots were established on a range of sites planted between 1992 and 1997 (Dickinson et al. 2008). Sites for these permanent plots represented a range of soil and rainfall gradients across the region (Bristow et al. 2005; Dickinson et al. 2008). The sample plots in the CRRP plantations were limited to sites that had received adequate weed maintenance during the establishment phase. Plots were randomly located within plantations larger than 2 ha and aimed to include 60 trees, with 6 rows of 10 trees while avoiding the plantation boundary (Erskine et al. 2006). Tree measurements included diameter of stem at breast height over bark (dbh, cm), height (m) and stem form. Individual trees at the permanent plots were measured in 1998, 1999, 2000, 2001 and 2002. The consecutive measurements of 10 focus species in permanent plots at 52 sites form the basis of this study. Site details recorded at time of planting and used in our analysis include slope, aspect and landscape position.

The ten focus species, *Acacia mangium* Willd., *Agathis robusta* F. Muell., *A. cunninghamii* Aiton., *Castanospermum australe* A. Cunn and C Fraser., *Cedrela odorata* L., *Elaeocarpus grandis* F. Muell., *Eucalyptus cloeziana* F. Muell., *Eucalyptus pellita* F. Muell., *Eucalyptus tereticornis* Sm., and *Flindersia brayleyana* F. Muell., were planted in sufficient numbers and at sufficient sites to allow an analysis of species performance (Table 1). All study species are native to Australia with the exception of the exotic *C. odorata*, a popular plantation species in South America. *Acacia mangium*, *A. cunninghamii*, *E. cloeziana*, *E. tereticornis* and *E. pellita* have a successful history in traditional forestry plantations both in Australia and abroad. Four study species were present at a sufficient number of representative sites to allow the study of responses to soil and environmental gradients across the study region (Table 1).

Site index

We used the MATLAB (Mathematical Laboratory) software package to fit the Chapman Richards growth curve (Eq. 1) to the height measurements of the tallest 20 % of individuals of a species.

$$h = h_{\max} (1 - be^{-kt})^c \quad (1)$$

In this form of the Chapman Richards equation, h_{\max} is the maximum h for the species (here, h_{\max} was set at 40 m for all species and had little effect on the curve in the early years), t represents the age of the tree and the coefficients b , k and c determine the shape of the curve and are estimated during curve fitting. The values of the SI curves were extrapolated to age 10 years (Fig. 1), SI_{10} , to allow comparison of SI between sites using a reference age convenient for forest managers.

Site index curves were fitted to height of the tallest 20 % of each species at each site obtained from repeat height measurements from permanent plots within the CRRP trials. Site index curves are usually computed either by using permanent plot data (Elfving and Kiviste 1997) or from stem analysis data (Teshome and Petty 2000). Various models of tropical rainforest obtain growth curves for tree species groups from measurements of permanent plots of multi-aged rainforest (Korning and Henrik 1994; Lieberman et al. 1985; Vanclay 1991, 1994). However it is often noted that the data required to define SI for less well known tree species in even aged plantations is generally lacking as these data sets are often fragmented due to poor record keeping and extend only for short periods at a given site (Lamb et al. 2005; Russell et al. 1993).

The CRRP dataset allows SI to be estimated objectively for those measured at least three times from 1998 to 2002. These plantations were established from 1993 to 1996 and were 4–9 years old at time of measurements. Many species showed varied establishment periods followed by periods of very fast growth and then often phases of slowed growth due to high stocking rates. By fitting curves to growth data from at least three years (typically four date measurements), we aimed to produce reliable estimates of SI. The average r^2 value for SI curves was >0.9 and if the goodness of fit was below 0.8 and data allowed, a small number of obvious outliers were excluded to improve fit. If amended data did not improve the r^2

Table 1 Focus species present at 52 plantation sites were: 1. *Acacia mangium*, 2. *Agathis robusta* 3. *Araucaria cunninghamii*, 4. *Castanospermum australe*, 5. *Cedrela odorata*, 6. *Elaeocarpus grandis*, 7. *E. cloeziana*, 8. *E. pellita*, 9. *E. tereticornis* and 10. *Flindersia brayleyana*

Site	Lat.	Long.	Altitude (m)	Species present										Total	Australian soil order	Rain (mm year ⁻¹)	Ave. Temp (°C)
				1	2	3	4	5	6	7	8	9	10				
1	-21.47	149.20	46	7									20	35	Sodosol	1,440	25.2
2	-21.45	149.25	120									9	6	39	Dermosol	1,390	25.2
3	-21.45	149.21	26		11					6				41	Hydrosol	1,450	24.5
4	-21.23	149.12	21				6		12				8	33	Vertosol	1,390	25.2
5	-21.14	149.11	79								8			35	Sodosol	1,550	25.1
6	-20.98	148.81	36			40			7					57	Sodosol	1,660	25.8
7	-18.97	146.34	37		10		8		12				13	53	Kandosol	2,050	26.7
8	-18.96	146.25	58	10	5						18	16		58	Kandosol	1,960	25.6
9	-18.85	145.80	65				6			10	7		8	38	Kandosol	1,860	26.2
10	-18.82	146.25	22	14							11	18		54	Vertosol	2,050	26.9
11	-18.81	146.25	50				13		15	8			21	57	Tenosol	2,011	26.8
12	-18.80	145.85	83						12		8	18		49	Hydrosol	1,650	25.6
13	-18.80	146.25	681	6						12		17		53	Chromosol	1,130	23.1
14	-18.71	146.05	689	6	10	10						9	12	52	Dermosol	1,210	23.5
15	-18.15	145.83	714				12				10		10	37	Kandosol	1,130	23.5
16	-18.13	145.95	44						20		8		18	49	Chromosol	2,430	26.6
17	-18.12	145.50	25	7	8	7		6		10			8	54	Chromosol	2,210	24.5
18	-17.99	145.90	133			16	8			8	8		13	53	Chromosol	3,800	26.5
19	-17.85	146.02	98	7	6					14	16		8	51	Kandosol	3,960	25.8
20	-17.76	145.90	120		8		9		6		18		12	53	Hydrosol	3,450	23.8
21	-17.64	145.55	277				8	10		6			6	39	Dermosol	1,440	25.2
22	-17.62	145.65	31					9					8	28	Rudosol	4,800	26.4
23	-17.60	145.93	53				10				8			44	Ferrosol	3,820	25.9
24	-17.57	145.50	980		6	8				16	7	8	6	51	Dermosol	1,240	21.9
25	-17.55	145.55	984							24			8	45	Dermosol	2,450	22.1
26	-17.54	145.65	1022	11					6		11			42	Ferrosol	1,080	21.7
27	-17.42	145.70	1052						16				9	38	Dermosol	1,440	21.4
28	-17.34	145.60	760						6		10			41	Ferrosol	1,390	25.2
29	-17.32	145.95	662			8					12		20	45	Ferrosol	3,690	23.8
30	-17.32	145.65	740		6				12		10		8	40	Ferrosol	1,740	22.6
31	-17.32	145.65	730		14	14			10		14			52	Ferrosol	1,540	21.7
32	-17.30	145.73	710				5	8	8				12	37	Ferrosol	2,990	24.5
33	-17.30	145.73	725					11	16					44	Ferrosol	3,000	24.5
34	-17.30	146.03	695					8		7	20	6		49	Ferrosol	1,230	23.1
35	-17.28	145.62	713								26			45	Ferrosol	1,750	22.6
36	-17.22	145.65	766		6	8			6	8	18		6	52	Ferrosol	2,850	26.7
37	-17.25	145.83	719			8				14				36	Ferrosol	2,620	26.2
38	-17.23	145.75	97		8		10	10			16		6	52	Ferrosol	2,030	26.8
39	-17.18	145.75	20								22			45	Ferrosol	2,020	26.8
40	-17.15	145.74	97							14			18	42	Ferrosol	2,170	26.9

Table 1 continued

Site	Lat.	Long.	Altitude (m)	Species present										Total	Australian soil order	Rain (mm year ⁻¹)	Ave. Temp (°C)
				1	2	3	4	5	6	7	8	9	10				
41	-17.06	145.47	352						12	8			12	38	Ferrosol	1,930	26.1
42	-17.01	145.82	425										25	31	Ferrosol	1,190	23.7
43	-16.87	145.62	391						16				16	46	Dermosol	1,350	22.6
44	-16.85	145.75	352									18	17	47	Tenosol	1,720	25.9
45	-16.66	145.32	425		8				9	10			10	43	Dermosol	1,640	26.1
46	-16.63	145.45	429				7		9	12			8	36	Tenosol	2,290	27.6
47	-16.61	145.45	135									20	10	50	Tenosol	2,300	27.6
48	-16.57	145.45	48	11				6	7			12	10	46	Tenosol	2,570	27.9
49	-16.54	145.43	37					9		8				33	Kandosol	2,490	27.4
50	-15.97	145.43	35									12	14	39	Dermosol	1,700	27.6
51	-15.55	145.41	17					8						41	Dermosol	1,720	26.2
52	-15.52	145.25	37					7		9		12		39	Dermosol	1,720	26.2

The number of individuals of each focus species (n) in plantations is presented. If one or more of the trees used to generate site index for a species was measured to be shorter than any of its eight adjacent neighbours, they have potential to bias SI for that species and are noted in *italics*. Rainfall and temperature averages are for the period from time of planting to time of last measurement, (Australian Bureau of Meteorology 2008)

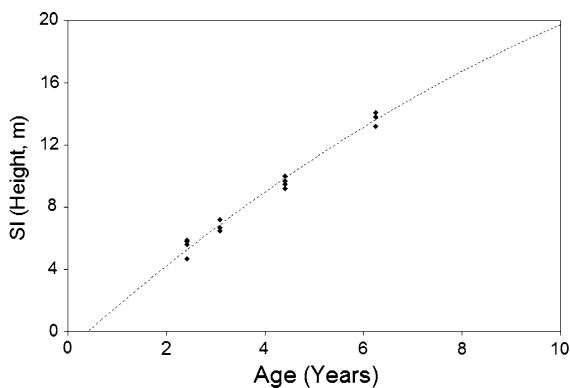


Fig. 1 SI was derived through fitting the Chapman Richards growth curve ($h = h_{\max} (1 - be^{-kt})^c$) to the tallest 20 % of each species at a site. The example fit (dotted line) displayed is for *F. brayleyana* at site 46, the equation derived from this fit was $SI = 40 * (1 - 1.031e^{0.3294t})^{-0.2166}$ which yielded an r^2 value of 0.96 and was used to extrapolate an SI_{10} value of 19.8m

value to be >0.8 , or the data set did not allow the exclusion of a measurement point, species were not included in analysis for the site. From a total of 165 included fits, outliers were removed on 12 occasions.

Across the CRRP plantation sites, there is large variation in species combinations, nursery stock, and plantation design and management regimes. The SI values derived in this study represent the average of the top 20 % of the height values for a species on a

given site. This estimate of performance of the tallest 20 % of trees was used in an effort to better estimate a species' potential on a site, to reduce the effects of weed management, site preparation, stocking, seedling stock and quality and the effects of inter-species interactions in plantations. The focus CRRP plantations ranged from monoculture to mixtures of up to eight species. Here, we assessed the performance of individual species within mixed species plantations, irrespective of the species combinations, by fitting SI curves to the tallest trees of each species. Growth of the tallest 20 % of trees in the experimental plantations represent the potential growth of 100–200 stems ha^{-1} which may be of interest in plantations where trees are thinned to these stocking levels in the final stages of the plantation.

There is potential for the species composition of the different mixtures to bias the estimation of SI if the tallest 20 % of trees for a species are suppressed by other species in a plot. This potential bias was assessed by analysis of the competitive status of trees used in the estimation of SI. Using knowledge of the spatial position of trees in a plot, we identified the relative height of neighbours trees used for estimation of SI. If any of the tallest trees of a species in a plot were overtopped by at least two trees in the eight adjacent positions in the planting grid, they were deemed to

occupy sub-dominant canopy positions and the species was not included in analysis for that site. If any of the trees used to estimate SI were overtopped by only one of their eight possible adjacent neighbours, species were included in SI estimation but were not included during regression analysis (Table 1).

Climate factors

Across the region of CRRP plantations, significant co-variation of soil types, rainfall classes and temperature occurs (Bristow et al. 2005). High rainfall sites with alluvial soils are clustered on the coastal lowlands and experience warmer mean annual temperatures, while lower rainfall metamorphic sites are clustered in the upland areas and have a cooler mean annual temperature (Bristow et al. 2005). This co-variation can confound efforts to identify the effect of any single variable on growth of a species across sites. Despite this constraint, variation in mean annual diameter and height growth of 13 species in the CRRP permanent plots has been attributed to various environmental variables including mean annual rainfall, mean annual temperature and soil nutrient supply (Bristow et al. 2005). Here, we use SI rather than diameter MAI (reported in Bristow et al. 2005) as a representation of a species performance on a site and include more climatic, soil and site variables in regression analysis to explain the variation in SI across environmental gradients. We focus the analysis on four species present on most soil types, *E. cloeziana*, *E. pellita*, *F. brayleyana* and *E. grandis*. The climate variables were obtained over the period of growth (1992–2002) for the 52 study sites by extracting data from an archive of interpolated rainfall and climate surfaces (Australian Bureau of Meteorology 2008). These surfaces were constructed by spatially interpolating available observational data. Climate variables interpolated for the period of growth at our study sites included mean daily temperature, mean daily maximum temperature, mean daily minimum temperature, mean daily minimum temperature of coldest month, mean daily maximum temperature of hottest month, mean monthly precipitation, mean number of rain days per month, mean monthly solar radiation, mean monthly evaporation and mean monthly vapour pressure deficit (Table 2).

Investigating the environmental relationships of rainforest structural and physiognomic characteristics in the Queensland Wet Tropics, Mackey (1993) found

Table 2 Summary of some soil, climate and site variables used in regression analysis

Soil variables (Queensland Combined Digital Soil Map DNR&M 2008)	
(1) Soil order (Australian Soil Classification system)	
(2) Course sand (%)	
(3) Fine sand (%)	
(4) Silt (%)	
(5) Clay (%)	
(6) pH	
(7) Available Water Capacity (AWC) (mm m ⁻¹)	
(8) Available Water Capacity (AWC) (15 bar) (mm m ⁻¹)	
(9) K saturation (mm h ⁻¹)	
(10) Drainage	
(11) EC (μS cm ⁻¹)	
(12) CEC (cmol kg ⁻¹)	
(13) Total <i>n</i> (mg kg ⁻¹)	
(14) Total <i>p</i> (mg kg ⁻¹)	
(15) Exchangeable Ca (mg kg ⁻¹)	
(16) Exchangeable K (mg kg ⁻¹)	
(17) Exchangeable Mg (mg kg ⁻¹)	
(18) Exchangeable Na (mg kg ⁻¹)	
(19) Organic carbon (%)	
(20) Chloride (mg kg ⁻¹)	
(21) Bulk density (g cm ⁻³)	
(22) Course fragment (%)	
(23) Permeability	
(24) Pedality type	
(25) Pedality size	
(26) Texture grade	
Climate variables (Australian Bureau of Meteorology 2008)	
(27) Mean daily average temperature (°C)	
(28) Mean daily maximum temperature (°C)	
(29) Mean daily minimum temperature (°C)	
(30) Mean daily minimum temperature of coldest month (°C)	
(31) Mean daily maximum temperature of the hottest month (°C)	
(32) Average monthly precipitation (cm)	
(33) Average number of rain days per month (days month ⁻¹)	
(34) Driest quarter precipitation (cm)	
(35) Wettest quarter precipitation (cm)	
(36) Mean monthly solar radiation (MJ m ⁻²)	
(37) Mean monthly evaporation (mm day ⁻¹)	
(38) Mean monthly vapour pressure deficit (kpa)	
Site variables (from original site descriptions)	
(39) Slope (°)	
(40) Aspect	
(41) Landscape position	

that a small number of indices proved the best predictors (minimum temperature of the coldest month; maximum temperature of the hottest month; precipitation seasonality; precipitation of driest quarter; nutrient supply index). This refined set of indices best predicted the spatial distribution of rainforest structural types and may not be the best set of indices to predict the variation in growth of rainforest trees in plantations. We investigated the indices identified by Mackey (1993) for their influence on the SI of the focus species here. We included Mackey's key variables in our regression analysis (Table 2).

Soil factors

Soil type strongly influences the productivity of both tree plantations (Costa et al. 2008; Nikles et al. 2008; Turner and Lambert 1998; Turner et al. 1990) and native forests (Vanclay 1989). Here we investigate the productivity of native tree plantations in relation to soil groups.

The Australian Soil Classification system is a categorical scheme with classes defined on the basis of diagnostic horizons or materials and their arrangement in vertical sequence (McKenzie et al. 2004). We analysed the variation in SI of four study species in context of Soil order type as defined by the Australian Soil classification system (Fig. 2). Soil order classifications were obtained for the study sites from the Queensland Digital Combined Soil Map (Department of Natural Resources and Water 2008). The map is in digital vector format derived from detailed regional soil maps with a scale of no more than 1:50,000. This digital soil map also offers over 100 soil parameters at the latitudes and longitudes of our study sites, some of which were used here and are summarised in Table 2. The Queensland Combined Digital Soil Map provides estimates of many soil variables (Table 2), often detailed for five soil horizons. We focused our analysis on the average value of the topsoil (top two horizons) and subsoil layers (bottom three horizons). Soil variables obtained from the Queensland Digital Combined Soil Map (Department of Natural Resources and Water 2008) included clay, silt and sand fractions, pH, Available Water Capacity (AWC, the amount of water that can be stored in soil and be available for plants), saturated hydraulic conductivity (K_{sat}), measures of electrical conductivity (EC, Cation Exchange

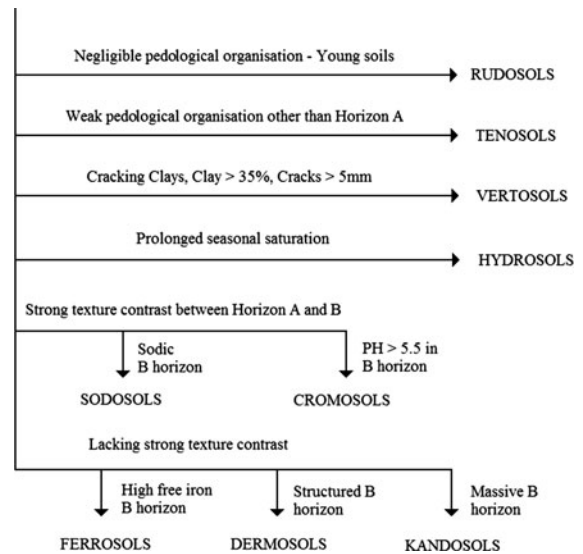


Fig. 2 The classification system for Australian Soil Orders of the CRRP trials sites in this study. Adapted from McKenzie et al. (2004)

Capacity), total n and p , exchangeable Ca, K, Mg and Na, organic carbon, chloride, bulk density and soil type.

Regressions

MATLAB was used to conduct linear regression analysis of more than 26 soil variables and 12 climate variables (Table 2) against SI_{10} for four most common study species, *E. pellita*, *E. cloeziana*, *F. brayleyana* and *E. grandis*. Regressions were conducted to determine least squares fit using the equation $SI_{10} = m \times x + k$, where 'x' is the variable under analysis. The r^2 value, a measure of the goodness of fit of the fit model, and p value were used to measure the significance of association between SI and each environmental variable.

Pearson's correlation coefficient was used to determine a set of independent variables for use as a basis for model development. Variables were included based on the magnitude of the r^2 value and p values resulting from their regression against SI_{10} (r^2 value > 0.15, p value < 0.05) and ease of in field determination. Forward stepwise regression was used to identify the strongest model from combinations of the final set of significant independent variables. The multiple regression model was validated using the

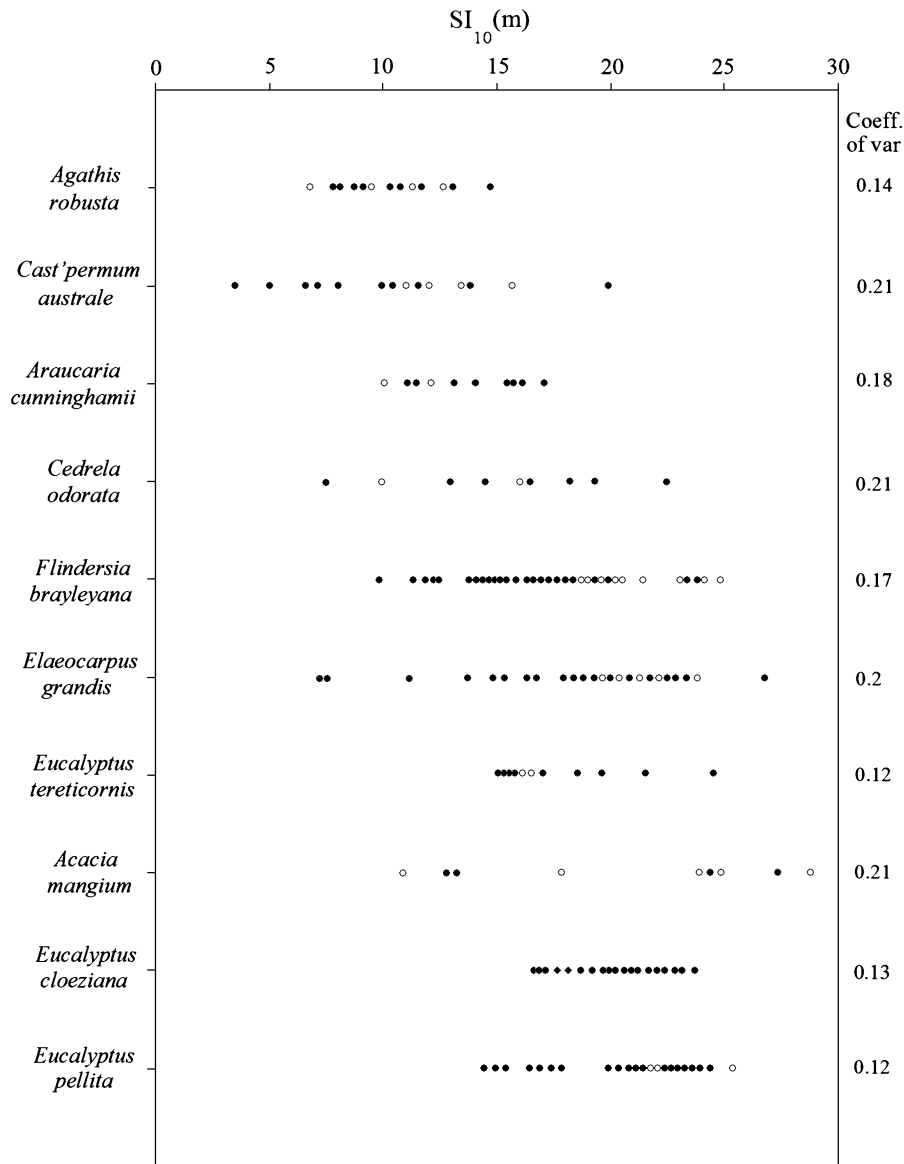


Fig. 3 Site Index values at age 10 years (SI₁₀) for the 10 tree study species at the 52 study sites in North Queensland, species are presented from lowest to highest mean SI. Coefficients of

variation from means SI₁₀ appear at right of rows. Open circles represent Kandosol and Tenosol soil profiles whilst closed circles represent all other soil types

Leave-one-out cross validation procedure and summarising the root mean-square error.

Results

All species showed high variation in SI₁₀ across sites (Fig. 3), with some species exhibiting more deviation from their mean SI₁₀ than others. The relatively high standard coefficient of variation for some species

suggests that species-site matching, obtaining high quality nursery stock and good plantation management is more important for these species than for those with more consistent growth rates. If the coefficient of variation is used as a measure of stability (Fig. 3), the least consistent species is *C. australe* with a coefficient of variation of 0.21, and the most consistent species are *E. cloeziana* and *E. tereticornis*, both with a coefficient of variation of 0.12. There was agreement between species on SI₁₀ among the 52 sites, a

regression of relative SI_{10} (SI_{10}/SI_{10max}) for species at the same sites revealed an r^2 value of 0.41. *A. cunninghamii* disagreed with the consensus of SI of species on numerous sites suggesting an alternate response to site conditions compared with the majority of species.

During analysis, species with their tallest trees in a plot being heavily suppressed by surrounding trees were excluded from analysis. However, SI was estimated using individuals that were overtopped by one of their neighbours on 18 occasions (Table 1). The majority of these cases occurred for slower growing species, seven times for *C. australe*, four for *A. robusta* and on five occasions for *C. odorata* (Table 1). Sub-dominant canopy positions for these trees have potential to negatively effect growth, as a result SI may have been underestimated for a proportion of sites for these slower growing species. Of the faster growing species, at least one of the tallest trees of *F. brayleyana* was overtopped by a neighbour in three plots (two Dermosols and a Ferrosol), and for the tallest *E. grandis* in one plot on a Dermosol, these instances were excluded during regression analysis.

Site index values (SI_{10}) estimated from curves fit to the tallest 20 % of individuals of a species at a site are presented in Fig. 3. Regressions between SI_{10} and

environmental variables at sites for the four species present at greater than 19 sites revealed species growth responses to gradients of climatic, site and soil variables (Table 3). The two more consistent species, *E. cloeziana* and *E. pellita*, showed no significant differences in SI between soil type (Table 3) and were less influenced by environmental variables than the two less consistent species, *F. brayleyana* and *E. grandis* (Table 3). Soil type had the strongest influence on the SI of *E. grandis* and *F. brayleyana* of any variable (Table 3).

The good performance of *F. brayleyana* on Kandosols ($SI_{10} = 21.5 \pm 2.0$ m) and Tenosols (21.1 ± 2.3 m) was significantly different ($p < 0.05$) from the poorer performance on Dermosols (12.9 ± 2.2 m, Table 4). Similarly, strong and poor performances of *E. grandis* on Kandosols (24 ± 4 m) and Dermosols (14.9 ± 1.5 m) respectively, were significantly ($p < 0.05$) different (Table 4).

Responses of *F. brayleyana* and *E. grandis* to soil type may be attributed to the differences in texture and hydraulic characteristics between these soil types (Table 3). Kandosols and Tenosols exhibit a large range of soil conditions but are generally associated with high ratios of sand to clay fraction and high saturated hydraulic conductance (K_{sat}) in the profiles,

Table 3 The soil and climate variables with greatest influence on SI_{10} of four study species, as indicated by r^2 values for simple linear regressions between test variables and SI

	<i>E. cloeziana</i>	<i>E. pellita</i>	<i>F. bray'ana</i>	<i>E. grandis</i>
Soil variables				
Australian soil order	–	–	0.49**	0.41*
Clay fraction (%) in topsoil	–	–	(–)0.27**	(–)0.18*
Clay fraction (%) in subsoil	–	–	(–)0.15*	(–)0.4*
Sand fraction (%) in subsoil	–	–	0.16*	0.72*
Silt fraction (%) in subsoil	–	–	(–)0.16*	–
K_{sat} , in topsoil ($mm\ h^{-1}$)	–	–	0.17*	0.19*
K_{sat} , in subsoil ($mm\ h^{-1}$)	–	–	0.2**	0.22*
AWC in topsoil ($mm\ m^{-1}$)	–	–	(–)0.17*	–
AWC in subsoil ($mm\ m^{-1}$)	–	–	(–)0.16*	–
Climate variables				
Mean rain days per month ($days\ month^{-1}$)	–	0.24*	–	0.28**
Mean daily minimum temperature ($^{\circ}C$)	0.2*	–	–	–

K_{sat} saturated hydraulic conductivity, AWC Available Water Capacity

(–) denotes a negative relationship between study variable and SI

* p value < 0.05; ** p value < 0.01

while Dermosols consistently exhibited a low saturated hydraulic associated with low ratios of sand to clay fraction in their profile.

Regressions of SI against site variables

The variation in SI_{10} of *E. cloeziana* (20.1 ± 3.1 m) was attributed to a positive response to minimum daily temperature ($p < 0.05$, Table 3) while variation in the SI_{10} of *E. pellita* (20.5 ± 3.1 m) showed a positive influence from the mean number of rain days per month ($p < 0.05$, Table 3).

SI_{10} for *F. brayleyana* (17.4 ± 4.3 m) showed a significant response to Australian Soil Order ($p < 0.01$, Table 3). *F. brayleyana* displayed a negative response to clay fraction in the top-soil ($p < 0.05$) and subsoil ($p < 0.05$, Table 3), Available Water Capacity (AWC) in both subsoil and the topsoil ($p < 0.05$) and to silt fraction in the subsoil ($p < 0.05$, Table 3). *Flindersia brayleyana* exhibited a positive response to sand fraction in the subsoil ($p < 0.05$), saturated hydraulic conductance, K_{sat} , in the subsoil ($p < 0.01$) and topsoil ($p < 0.05$) (Table 3).

SI_{10} for *E. grandis* (18.3 ± 5.4 m) showed a significant response to Australian Soil Order ($p < 0.05$, Table 3). *Elaeocarpus grandis* also exhibited a significant positive response to saturated hydraulic conductance, K_{sat} , in the topsoil and subsoil layers ($p < 0.05$, Table 3), sand fraction in the subsoil layer ($p < 0.05$), average number of rain days per month ($p < 0.01$) and mean monthly precipitation ($p < 0.05$, Table 3). *Elaeocarpus grandis* displayed a negative response to clay fraction in the topsoil ($p < 0.05$, Table 3).

We did not observe a correlation between tree size and estimations of soil nutrient levels (N, P, Ca, EC, CEC etc.). The absence of response to these estimations of nutrient availability suggests that soil texture and water interactions are more important factors in determining the performance of our focus species over the first 10 years of growth than the indexes of nutrition estimated for the soil profiles. Initial fertilisation of trees may have overcome early nutrient limitations among sites and since no direct soil measurements were taken from sites, the growth responses to different soil types here may be a result of a combination of the effects from both the soil physical characteristics and levels of soil nutrition left

unaccounted for in this study. It is also acknowledged that the mean monthly values for climate variables interpolated for this study may have been too coarse to identify species responses to differences in rainfall and other climate patterns between sites, weekly or daily climate data may have revealed more significant associations.

The unique responses of the study species to the different variables during regression (Table 3) assist in the development of species profiles and could be used as the basis for the estimation of potential performances on a new site.

Variation in growth exhibited by *E. cloeziana*, *E. pellita*, *F. brayleyana*, and *E. grandis* between biogeographic regions (warm coastal lowlands and cooler upland regions or wet northern and drier southern regions) could be attributed to the general climatic differences between regions. However, our findings suggest that differences in soil types between sites in the different regions may offer a more plausible explanation for the variations observed between regions.

Pearson's correlation coefficients revealed a strong dependency between significant variables associated with soil texture and hydraulic characteristics for *F. brayleyana* and *E. grandis*. The variable with the most significant influence on SI_{10} of *F. brayleyana*, clay fraction of the topsoil, had a Pearson's correlation coefficient >0.8 with clay fraction of subsoil, sand fraction of the subsoil and topsoil, AWC in the subsoil and topsoil and saturated hydraulic conductivity (K_{Sat}) in both layers. Pearson's correlation coefficient also identified high correlation (>0.8) between clay fraction in the topsoil, clay and sand fraction in subsoil and K_{Sat} in both layers for *E. grandis*. The final set of independent variables used as a basis for the development of a multivariate linear regression models consisted of soil order, clay fraction of the topsoil and silt fraction of the subsoil for *F. brayleyana*, and soil order and mean rain days per month for *E. grandis*. The strongest regression model for *F. brayleyana* ($r^2 = 0.56$) included soil order and clay fraction of the topsoil and yielded a root mean-squared error of 2.9 m during Leave-one-out cross-validation. The strongest multiple regression model for *E. grandis* ($r^2 = 0.59$) included soil order and mean rain days per month, and yielded a root mean-square error of 3.4 m during Leave-one-out cross-validation.

Species height compatibilities

The three eucalypts, *E. tereticornis*, *E. cloeziana* and *E. pellita* displayed large heights across all soil types and climatic conditions tested (Fig. 3) and maintained average dominant heights greater than the other study species in most plantation situations (Table 4). Only small height inequalities exist between *E. tereticornis*, *E. cloeziana* and *E. pellita* in mixtures (Table 4) and all seem compatible as upper-canopy species in plantations on most site types.

The slowest growing of the study species, *A. robusta*, *C. australe* and *A. cunninghamii* exhibited consistently lower dominant heights and rarely match the early height growth the *Eucalyptus* species or *F. brayleyana* and *E. grandis* (Table 4).

On average, the SI₁₀ values for *F. brayleyana* and *E. grandis* were 3–4 m lower than those for *E. tereticornis*, *E. cloeziana* and *E. pellita* (Table 4). An exception to this pattern is for species on Kandosols and Tenosols, where mean dominants heights of *F. brayleyana* and *E. grandis* were evenly matched with the dominant heights of the *Eucalyptus* species (Table 4).

Acacia mangium matched heights with the fast growing species at some sites, but was out-performed on others. *Cedrela odorata* also exhibited promising heights on some sites but lagged behind the fastest growing *Eucalyptus* species by an average of 5 m across all sites.

Discussion

Our findings show that with appropriate soil and climate information successful species-site matches are achievable for native trees in plantations in the Australian Wet Tropics.

We reexamined the results of a rainforest reforestation initiative (CRRP) in the context of newly available high-resolution soil information, climate interpolations and SI curves. Derivation of SI curves from successive measurements at sites allowed a more accurate evaluation of potential performance of species than in previous studies. Information regarding soil variables derived from digital soil maps proved effective for determining species-site interactions. These results have relevance for species selection in mixture plantations of native trees and improve predictions of the productivity of study species.

A previous productivity model for rainforest species in the Wet Tropics of Queensland (Nightingale et al. 2008) focused on spatial variations in climate and soil parameters which determine plant available water in the 3-PG forest model (texture and water holding capacity). Our results however, highlight the importance of landscape level changes in soil type and other hydraulic characteristics for accurate productivity estimates of rainforest species in plantation. We analysed 10 focus species with contrasting growth to discern their sensitivity to soil and climate variables

Table 4 SI at age 10 years for study species on different Australian soil classes at CRRP sites

	Dermosol	Ferrosol	Kandosol	Tenosol	Hyd'/Ver'/Rud'	Chro'/Sod'	Average
<i>A. robusta</i>	9.2 ± 1.3 m	10.9 ± 1.5 m	13 m	7 m	11.7 ± 4.5 m	12 m	10.6 m
<i>C. australe</i>	9.2 ± 1.8	7.2 ± 4.7 m	13.8 ± 2.3 m	16.2 ± 5.3 m	11 ± 4.2 m	10.5 m	11.3 m
<i>A. cunn'hamii</i>	13.7 ± 2.5 m	16.2 ± 0.8 m	12 m ± 1.4 m	–	–	10.5 ± 0.7 m	13.1 m
<i>C. odorata</i>	17.2 ± 3.9 m	14.9 ± 6.3 m	10 m	16 m	19 m	–	14.5 m
<i>F. brayleyana</i>	12.9 ± 2.2 m a	17.5 ± 4.7 m	21.5 ± 2 m b	21.1 ± 2.3 m b	17.2 ± 2.9 m	16.8 ± 3 m	17.8 m
<i>E. grandis</i>	14.9 ± 1.5 m c	18.9 ± 5.3 m	24 ± 4 m d	21.7 ± 1 m	13.2 ± 8.5 m	19.5 ± 1.4 m	18.7 m
<i>E. tereticornis</i>	19.2 ± 3.9 m	16 ± 0.1 m	17 m	17.5 m	22 ± 4.2 m	20 m	18.6 m
<i>A. mangium</i>	–	13 m	17 ± 5.3 m	20.3 ± 10.2 m	21.5 ± 4.9 m	–	18 m
<i>E. cloeziana</i>	18.2 ± 4.8 m	21 ± 1 m	22.5 ± 2.1 m	20 ± 0.7 m	–	20.3 ± 1.9 m	20.4 m
<i>E. pellita</i>	16.5 ± 2.1 m	19.9 ± 2.8 m	19.5 ± 4 m	21.8 ± 0.8 m	22 ± 3 m	23.3 ± 2.3 m	20.5 m
Average	14.6 m	15.6 m	17 m	17.9 m	17.2 m	16.6 m	

Hyd' Hydrosol, Ver' Vertosol, Rud' Rudosol, Chro' Chromosol, Sod' Sodosol

Standard deviations from mean SI are displayed. Fields without standard deviations have only one record. Soil types labelled 'a' and 'b' have significantly different (p value < 0.05) SI values for *Flindersia brayleyana*. Soil types labelled 'c' and 'd' have significantly different SI values for *Elaeocarpus grandis*

and identify soil characteristics as a major determinant for the growth of two rainforest species in plantations in the Queensland Wet Tropics. Poor growth rates for some promising species including *F. brayleyana* and *E. grandis* observed in the early years of some trials in North Queensland and a difficulty in identifying the cause of these poor performances, detracted from further investigation into their use in commercial forestry (Russell et al. 1993). The data presented here shows that on suitable sites *F. brayleyana* and *E. grandis* exhibit adequate plantation growth rates that warrant further assessment of their potential in industrial scale mixed species plantations. Both species are high-value cabinet-making timbers with potential for plantation development. *Elaeocarpus grandis* may be used to generate commercial thinnings for early economic return from mixtures and *F. brayleyana* can be grown on a longer rotation and has a high demand in the marketplace as a premier rainforest timber (Glencross and Nichols 2008). Our study also allows for more confident prediction of carbon sequestration and timber production rates of mixtures that include *F. brayleyana* and *E. grandis* and should assist in the design and planning of successful operational scale industrial plantations.

The strong growth responses of *F. brayleyana* and *E. grandis* on different soil types are likely to be a result of the physiological responses to differences in effective rooting depth, texture and drainage characteristics between the preferable Kandosols and Tenosols and less suitable Dermosols and Ferrosols. Poor drainage in soils creates reduced transfer of oxygen to the roots and may impose limitations on growth for some species. The difference in sensitivity to soil type between the two focus *Eucalyptus* species, which had similar growth success on all soils studied, may be a result of the evolutionary adaptation of the two eucalypt species to a broad range of soil types encountered in their large natural distribution in eucalypt forests (Boland et al. 2006). Clarke et al. (2008) describe the general tolerance of *E. cloeziana* and *E. pellita* to varied soils in their natural distributions and suitability to plantations on a wide range of soils within the study region, with growth of *E. cloeziana* limited only by heavy clays and saline conditions and growth of *E. pellita* limited by prolonged water-logging. In contrast, the natural distribution of *F. brayleyana* and *E. grandis* is restricted to rainforests (Boland et al. 2006; Rosetto

et al. 2004) with a smaller range of soil types and *E. grandis* often being restricted to areas near watercourses within their habitat (Rosetto et al. 2004). Our results show that the two eucalypt species have a markedly higher tolerance to soils with high clay fractions and poor drainage than *F. brayleyana* and *E. grandis*. Of the focus species *F. brayleyana* had a unique negative response to AWC (a measure of maximum plant available water) in soil profiles suggesting that soils with a lower capacity to store and make water available to plants may be prerequisite for successful growth of this species.

Multivariate regression models accounted for 36 and 38 % of the variation in SI_{10} away from the mean for *F. brayleyana* and *E. grandis* respectively. These models accounted for less variation in growth than for similar studies of growth of commonly planted species in monoculture plantations in Australia, for example a model for *E. dunnii* based on soil AWC, rainfall and altitude accounted for 62 % of the variation in SI_{10} at 31 sites (Grant et al. 2010), and a soil classification system predicted 75 % of the variation in *P. radiata* wood volume at 181 sites (Turner et al. 1990). A clear difference between our study and the investigations of *E. dunnii* (Grant et al. 2010) and *P. radiata* (Turner et al. 1990) is their direct analysis of soil characteristics, our indirect approach using soil maps constitutes a significant potential source of error as a result of high local variability in soil characteristics, and the relative sparseness of sampling used in the development of the soil maps for the region.

Another major difference between our study and studies of more commonly planted species is the very small sample of trees being used to estimate SI_{10} for species in some plots. The smallest samples of the tallest 20 % of trees of a species at a site constituted only 1–2 trees, significantly less than the 10 individuals available for estimation of SI from similar sized plots in monocultures (Grant et al. 2010). The small number of trees of a species present in some plots makes it less likely that the true growth potential of species was expressed at those sites. The small sample of trees are more likely to have been exposed to negative influences from inter-specific competition, sub-standard nursery stock, poor site-preparation and management, or adverse environmental effects such as wind or insect damage. As a result, the unintended difference in treatments observed between CRRP plots have great potential to influence SI, and efforts to

further sieve out bias from these effects through analysis of records of site preparation, management histories and environmental damage were thwarted by inconsistent record keeping. The confounding effects of inter-specific competition on estimated SI_{10} was reduced through an analysis of the relative height of the neighbours of the tallest trees of a species in a plot and the exclusion of species in which the tallest trees were deemed to occupy suppressed canopy positions. Improved models may be possible if the potential bias from inter-specific competition can be better illuminated through the use of more detailed spatial competition indices (Forrester et al. 2011; Vanclay 2006b). However, for the sake of generality of application, this approach deliberately maintained a methodology that does not include spatial competition indices, as these would be specific to the few datasets in which spatial arrangement and growth histories have been thoroughly documented. The weakness of spatial competition indices is their applicability only to species combinations that have been tested and our approach is specifically designed to overcome this particular limitation. Generally, the CRRP plots were suitable for a coarse analysis of the growth of component species and future mixed-species studies would clearly benefit from larger sample sizes to overcome some of the statistical noise observed in this study. Differences in seed provenances used to produce seedlings planted at CRRP sites may also constitute a source of unexplained variation, significant early growth differences observed between provenances of *E. pellita* (Harwood et al. 1997) highlight the potential for genetic differences between seed sources to influence growth rates.

Many tropical mixed-species plantations are random configurations of species in rows or grids, with little consideration given to future inter-specific competition or plantation management (Dickinson et al. 2008; Erskine et al. 2005). As a result, faster-growing pioneer species can quickly dominate and suppress other species in random intimate mixtures, eventually reducing plantation diversity and productivity (Erskine et al. 2005). To address this problem mixed species designs have produced two main strategies, (1) fast-growing, light demanding species with matching growth rates are planted together and plantations managed as a monocultures block; (2) fast-growing, light demanding species are planted in alternate rows with slower-growing, shade tolerant species

(Dickinson et al. 2008). The latter configuration encourages the development of a stratified canopy (often associated with species complementarity) but complicates thinning, management and harvesting operations, which sometimes needs to be staged. Knowledge of shade-tolerances of the slower growing species is necessary for the stratified canopy approach, and appropriate thinning and management of the upper-canopy species is required to ensure a healthy light environment is maintained for species in sub-dominant positions. Understanding has progressed on the shade tolerances of the study species from observation of performances in a large range of plantation and natural situations. *Acacia mangium* and the three *Eucalyptus* species are considered to be fast growing light demanding species whilst *E. grandis* and *F. brayleyana* are considered to be tolerant of a wide range of light regimes (Thompson et al. 1988, 1992; Kelly et al. 2009).

The results presented in this study enables selection of the most appropriate suite of species for a particular site and prediction of potential asymmetric competition for above ground resources developing between species as the plantation develops.

The strong effect of soil type in determining growth rates of *F. brayleyana* and *E. grandis* highlights the importance of including soil characteristics as major consideration during species-site matching, especially for rainforest trees. The poor performance of *F. brayleyana* and *E. grandis* on Dermosols and some poorly drained Ferrosols suggests a physiological aversion to some of the drainage characteristics of these soils. The reduced vigour and slow height development of *F. brayleyana* and *E. grandis* on some clay rich soils makes them more likely to be suppressed by faster growing species in mixtures on these soils and plantations that combine *F. brayleyana* and *E. grandis* with slower growing species on shallow clays are likely to achieve growth rates unsuitable for production forestry. Further investigations to identify the physiological reasoning for the observed response of *F. brayleyana* and *E. grandis* to some Dermosols and Ferrosols may identify silvicultural opportunities to improve production of these species on shallow clays. If silvicultural systems cannot remove these limitations, mixtures that include *Eucalyptus* species, or longer rotation native species such as *A. cunninghamii* may prove to be more appropriate species selections for these soil profiles.

The consistent height difference of 3–4 m observed between *F. brayleyana* and *E. grandis* and the three *Eucalyptus* species suggests that age 10 years, *F. brayleyana* and *E. grandis* are likely to occupy sub-dominant canopy positions when mixed with the *Eucalyptus* species on most soil profiles. If rainforest species, especially light demanding species such *E. grandis*, are mixed with the three fast growing *Eucalyptus* species on most soil profiles, careful consideration of species configurations and thinning and management goals may be necessary to ensure the slower growing species are not suppressed by the faster growing *Eucalyptus* species. One exception to this competitive pattern is the complementary height development of *F. brayleyana* and *E. grandis* and the three *Eucalyptus* species on Kandosols and Tenosols where all species achieved similar dominant heights, these performances suggesting that it may be appropriate to include *F. brayleyana* and *E. grandis* as a dominant upper-canopy species with other fast growing species in mixtures on these soil types. Best productivity is observed for the *F. brayleyana* and *E. grandis* on Kandosols and Tenosols and mixed plantations on these soil types provide the ideal context for competitive timber production rates for these species.

Cedrela odorata and *A. mangium* exhibited height growth rates competitive with the fastest growing species at some of the CRRP plantations but risk of size-asymmetric competition developing between these species and faster growing species on less suitable sites means caution should be used when considering their inclusion in mixtures. Both *C. odorata* and the *A. mangium* exhibit a large coefficient of variation from mean SI_{10} and a deeper understanding of site preferences of these species may allow them to be more confidently included as upper-canopy species in mixtures on appropriate sites.

Agathis robusta, *C. australe* and *A. cunninghamii* exhibited consistently lower dominant height than other study species. Despite this, *A. cunninghamii* performed relatively strongly on Ferrosols, as did *C. australe* on selected Tenosols, suggesting these species can be productive upper-canopy species on the most suitable of soil profiles.

In summary, our study shows that with appropriate species site matching, native rainforest species can deliver highly competitive growth rates in the Queensland Wet Tropics. SI curves derived in this study allow

for estimation of potential performances up to age 10. Estimates of productivity and prediction of species interactions up to age 20 years and beyond requires re-measurement of CRRP or other older plantations to reliably extend SI curves in maturing plantations. The SI values for the high-value timber species in this study at age 10 years (10–25 m), are favourable when compared to those reported for *Tectona grandis* (Teak) at age 10 of 5–17 m (Nunifi and Murchison 1999; Perez and Kanninen 2005). An increasing global demand for high quality cabinet-wood timber, and a continued depletion of natural stocks, will ensure future demand for forestry systems that include native tropical timber trees.

Mixed species plantations that include the study species have been observed to have higher productivity than monocultures (Erskine et al. 2006; Simpson and Osborne 2006). Appropriately designed mixed species forestry systems should also have advantages of complete site utilisation, reduced disease susceptibility, providing product diversification, and be more readily modified to meet present or future demands of the market or to overcome serious pathogen risks than monocultures (Nichols et al. 2006). Whilst we identify species-site matches, predicting situations where facilitation or complementarity resources use between species will create productivity advantages in mixed species plantations is difficult and must involve study of complicating factors such as canopy light transmission, shade tolerances, nutrition, water availability and root architecture. This study identifies potential detrimental effects of inter-specific asymmetrical competition in mixtures by an examination of the relative heights expected for focus species on a given site. Knowledge generated allows for the more confident design of successful mixed species plantations utilising native tree species in the Wet Tropics region of Australia.

Conclusions

Well-designed mixed species tree plantations have potential to be sustainable production systems. If new mixed tree plantations in the Australian Wet Tropics are designed to be highly productive timber plantations, these models may be adopted on scale, potentially providing a mechanism for the restoration of lost biodiversity in these degraded ecosystems (Lamb et al. 2005).

Several species including *F. brayleyana*, *E. grandis*, *E. cloeziana*, *E. pellita* and *E. tereticornis* have growth rates within mixtures sufficient to satisfy demands of commercial forestry operations given appropriate site selection. While outcomes from the CRRP plantations are promising, it is anticipated that with improved genetic stock and silviculture, growth and wood quality could be further enhanced. Potential productivity gains for these species are promising (Leksono et al. 2008) and selection and breeding programs as well as silvicultural improvement (Nichols et al. 2006) could form the basis of profitable forestry industry based on native mixed species tree plantations.

Further compilation and analysis of plantation data of *A. mangium*, *C. australe*, *C. odorata*, *E. tereticornis*, *A. cunninghamii* and *A. robusta* should clarify their responses to soil types and climate variables and would provide a strong basis for the design of mixed species plantations in the Wet Tropics of Australia.

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