

Available online at www.sciencedirect.com



Forest Ecology and Management

Forest Ecology and Management 255 (2008) 365-373

Review

www.elsevier.com/locate/foreco

## The effect of pruning and thinning on above ground aerial biomass of *Eucalyptus nitens* (Deane & Maiden) Maiden

F. Muñoz<sup>a,\*</sup>, R. Rubilar<sup>a</sup>, M. Espinosa<sup>a</sup>, J. Cancino<sup>a</sup>, J. Toro<sup>a</sup>, M. Herrera<sup>b</sup>

<sup>a</sup> Facultad de Ciencias Forestales, Universidad de Concepción, Casilla 160-C, Concepción, Chile <sup>b</sup> Escuela Técnica Superior de Ingenieros Agrónomos y de Montes, Universidad de Córdoba, Apdo. 3048, Córdoba, Spain Bospivad 20 December 2005, received in revised form & Sentember 2007, eccepted 24 Sentember 2007.

Received 20 December 2005; received in revised form 8 September 2007; accepted 24 September 2007

## Abstract

There has been an increasing interest in Chile and Australia in using *Eucalyptus nitens* (Deane & Maiden) Maiden fast growing plantations for sawntimber production. We investigated the effects of pruning and thinning treatments, applied at age 6 years, on the growth and aboveground biomass accumulation of a 15-year-old *E. nitens* plantation located in the coastal Arauco-Central Chile. Pruning treatments did not affect growth or aboveground biomass. Lowest stocking thinning treatment (400 trees ha<sup>-1</sup>) doubled average individual tree aboveground biomass with 762 kg tree<sup>-1</sup>, but reduced stand mean aboveground biomass productivity by 31% (22.2 t ha<sup>-1</sup> year<sup>-1</sup>). The highest stocking thinning treatment (1100 trees ha<sup>-1</sup>) accumulated 342 kg tree<sup>-1</sup> and grew 29.1 t ha<sup>-1</sup> year<sup>-1</sup>. Crown biomass was concentrated in the central and lower sections regardless of thinning treatment. Allometric models, used to estimate crown biomass based on ln(dbh<sup>2</sup>) as a predictor variable, resulted in determination coefficients (*R*<sup>2</sup>) of 0.74, 0.63, and 0.80 for leaf, twig, and branch biomass components, respectively. Stem components (wood and bark biomass) were estimated using ln(dbh<sup>2</sup>h) as predictor variable, resulted in *R*<sup>2</sup> of 0.94 for wood and 0.80 for bark. Thinning increased individual tree average stem, crown, and total biomass. No differences in biomass and wood accumulation were found between 800 and 1100 trees ha<sup>-1</sup> stockings. Reduced live crown length and average height were found for the 1100 trees ha<sup>-1</sup> stocking, suggesting a negative effect of stocking on live crown length. © 2007 Elsevier B.V. All rights reserved.

Keywords: Eucalyptus nitens; Aboveground biomass; Allometric equations; Eucalyptus plantations

#### Contents

1.	Introduction	. 366
2.	Methodology	. 366
	2.1. Site characteristics	. 366
	2.2. Stand characteristics, experimental design, and tree measurements	. 366
	2.3. Data analysis	. 367
3.	Results	
	3.1. Individual tree aboveground biomass	. 367
	3.2. Stand biomass and estimated leaf area	. 368
	3.3. Total height, live crown length, and crown biomass distribution	
	3.4. Allometric models	. 369
4.	Discussion	. 369
	4.1. Individual tree and stand aboveground biomass	. 369
	4.2. Total height, live crown length and crown biomass distribution	
	4.3. Allometric relations	. 371
5.	Conclusions.	
	Acknowledgements	. 371
	References	. 371

\* Corresponding author. Tel.: +56 41 2204679; fax: +56 41 2255164. *E-mail address:* fmunoz@udec.cl (F. Muñoz).

0378-1127/\$ – see front matter  $\odot$  2007 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2007.09.063

#### 1. Introduction

*Eucalyptus nitens* has been extensively planted in Australia, New Zealand, South Africa, and Chile (Cromer, 1996; Knight and Nicholas, 1996; Herbert, 1996; Prado and Toro, 1996; Trincado et al., 2003). This fast growing species has been planted mainly for pulp (Kube and Raymond, 2002; Smethurst et al., 2003; Trincado et al., 2003; Infor, 2004). However, during the last decade, there has been growing interest in the use of *E. nitens* for sawntimber (Gerrand et al., 1997; Pinkard and Battaglia, 2001; Pinkard et al., 2004; Muñoz et al., 2005). *E. nitens*, having little natural pruning ability in plantations, requires a timely removal of green branches for clearwood production (Gerrand et al., 1997; Pinkard, 2002).

Several experiments investigating thinning and pruning intensity have been established in Australia (Gerrand et al., 1997; Pinkard and Beadle, 1998a,b; Pinkard, 2002; Medhurst et al., 2002). Effects of thinning and pruning on individual tree and stand biomass have several implications for carbon capture estimations (Schlegel et al., 2000), estimation of stand nutrient content (Ingerslev and Hallbäcken, 1999; Geldres et al., 2004), development of forest structure models (Caldentey et al., 1992), assignment of silvicultural interventions (Cannell, 1989), and evaluation of forest harvesting effects (Teller, 1988). Results of these experiments indicate that pruning affect aboveground biomass distribution and foliage efficiency. Pruning treatments may cause reductions in individual tree stem diameter growth, especially when a large proportion of the live crown is removed, or conversely when no branches are removed (Pinkard and Beadle, 1998b,c). Minimizing negative impacts of pruning on individual tree and stand growth for clearwood production is critical for determining appropriate pruning regimes for E. nitens (Pinkard et al., 1999; De Moraes et al., 2004).

Changes in leaf area distribution in the crown are also affected by pruning and thinning (Medhurst and Beadle, 2001). Various studies across species have established a good relationship between individual tree leaf area and productivity (Albaugh et al., 1998; Whitehead and Beadle, 2004), and productivity per unit of leaf area is highly dependent on environmental conditions and genotype that affect foliage retention and its efficiency (Smethurst et al., 2003; Rojas, 2005; Rubilar, 2005).

Individual tree growth response to thinning and pruning has been also closely linked to existent or improved site resource availability which allows crown expansion and therefore larger individual tree growth rates (Knight and Nicholas, 1996; Close et al., 2004). Thinning and pruning manipulate light availability but also affect allocation of soil-site available resources to crop trees. Individual tree availability of water and nutrients is affected by reducing foliage interception of rainfall and increasing forest floor decomposition and mineralization (Medhurst et al., 2002). In addition, branch removals may not only cause instantaneous differences in individual tree photosynthetic capacity, but also on nutrients remobilized in the crown (Medhurst and Beadle, 2005). Therefore, pruning and thinning treatments require detailed assessment of the imposed changes in terms of percentage of crown removed, and remaining efficiency of the stand photosynthetic mass at the individual tree and stand level.

Wood properties and tree shape are affected by enhanced crown growing space and following changes in biomass distribution at individual tree level (Pinkard and Neilsen, 2003). Productivity and value of thinned and pruned stands may vary greatly as tree allometry is affected by management effects (Rietz and Smith, 2004). Thinning practices usually result in the increase of individual tree size at expense of stand total volume (Smith et al., 1997).

Several studies have reported aboveground individual tree and stand biomass production for stands of *E. nitens* (Prado and Toro, 1996; Pinkard and Beadle, 1998b). However, less is known about how thinning and pruning treatment combinations affect yield of managed plantations and biomass partitioning (Prado and Toro, 1996; Bartelink, 1998; Medhurst and Beadle, 2000; Rodríguez, 2002). Pinkard and Neilsen (2003), reporting an experiment that investigated initial spacing effects on crown and stand development of *E. nitens* in Australia, found that low stocking did not affected total individual tree biomass but increased partitioning to stem instead of branches.

Biomass studies of *E. nitens* in Chile are scarce and have been only restricted to ages ranging from 4 to 7 years (Aparicio, 2001; Gerding et al., 2002; Muñoz, 2002; Toro, 2002; Geldres et al., 2004). Our study reports the oldest study, established in Chile, investigating the effects of pruning and thinning intensity on the distribution of above ground biomass for a 15-year-old *E. nitens* plantation after harvesting. The objective of our study was to understand how mid rotation thinning and pruning intensity treatments affected individual tree and stand growth, and biomass accumulation at harvesting.

#### 2. Methodology

## 2.1. Site characteristics

The study was established in a 6-year-old stand of *E. nitens* located near Los Alamos ( $37^{\circ}38'$  southern latitude,  $73^{\circ}27'$  western longitude), at approximately 180 m.a.s.l. in the coast of Arauco, Chile. The landform corresponded to marine terrace soils derived from clayey sediments. The area has been extensively eroded after intensive agricultural use (Carrasco and Millán, 1990). Average monthly temperatures range between 23.2 °C in January (mid summer) and 6.0 °C in June (mid winter). Average annual rainfall at the site is 1437 mm with an average of five dry months during the summer (Santibáñez and Uribe, 1993).

## 2.2. Stand characteristics, experimental design, and tree measurements

The plantation was established in the winter of 1989 at a spacing of 2.0 m  $\times$  3.5 m with plants produced from seeds from Toorongo provenance (Victoria, Australia). Average diameter and height of the stand at 6 years old (1995) were 16.2  $\pm$  0.7 cm and 18.3  $\pm$  0.4 m, respectively (Muñoz et al., 2005). Average live crown height before pruning, not

considering isolated non-active green branches, was  $8.1 \pm 0.7$  m. The experiment was established in October 1995 as a complete randomized factorial design with treatments of thinning and pruning applied at three levels each with tree replications. Thinning treatments included 1100 (not thinned), 800 and 400 trees ha<sup>-1</sup> stockings. Pruning treatments included 0 m (no pruning), 3.5 m and 7.0 m height from the ground. Measurement plots had  $324 \text{ m}^2$  (18 m × 18 m) with 5 m buffers on each side. In October 2004, a single tree was randomly selected for biomass assessment from trees in each plot corresponding with the mean diameter class (Pardé, 1980). A summary of the average diameter at breast height (dbh), quadratic mean diameter  $(D_{\sigma})$ , stand density, final sampled single tree dbh, and effective stocking for each thinning treatment is presented in Table 1.

Selected trees for biomass assessments (27 trees total) were measured for dbh, total height (h), and live crown length (LCL). The trees were cut into seven sections of equal length, and stem discs approximately 5 cm thick were obtained from the base of each section and weighed fresh. The crown of each tree was divided in thirds of equal length, and branches of each third were separated into branch, twigs (less than 5 mm diameter), and foliage components, and weighed fresh (green weight). Stem discs and samples of branches, twigs and foliage were oven-dried at 75 °C for 48 h and weighed (dry weight). Wood specific gravity was obtained by relating the dry mass of each stem disc and its green volume using the picnometer method (Blake and Hartge, 1986). The volume of each stem section was calculated multiplying its length by the diameters inside bark at the end of each section using Smalian's formula (Hush et al., 1982). Stem dry mass was calculated based on the volume of wood of each tree section multiplied by the corresponding specific gravity. Dry mass of each crown component (branches, twigs, and foliage) was estimated based on average dry/green mass ratios following the procedure described by Espinosa and Perry (1987).

#### 2.3. Data analysis

Biomass estimation for each component was obtained using a linearized allometric model proposed by Ter-Mikaelian and Korzukhin (1997):

$$\ln(Y) = \ln(a) + b\ln(X),\tag{1}$$

where Y is the dry weight of the aerial component, X is the independent variable (dbh, height, or its transformation), and a and b are coefficients of the model. A single regression equation was fit for each biomass component considering all sampled trees (27 total). Analyses of residuals were performed to evaluate the quality of fit and underlying regression analyses assumptions.

For each plot, stand biomass was obtained summing individual tree estimates using our regression equations for each biomass component, and plot estimates were scaled up to an hectare level. Mean annual increment (MAI) estimates for each plot were obtained dividing stand biomass estimates by harvesting age. Leaf area estimates were obtained using published values of specific leaf area (SLA) (Pinkard and Neilsen, 2003). For the highest stocking thinning treatment (1100 trees ha<sup>-1</sup>) a value of SLA of 4.93 m<sup>2</sup> kg<sup>-1</sup> was used, and of 4.63 m<sup>2</sup> kg<sup>-1</sup> for other treatments.

Analysis of variance (ANOVA) was used to evaluate treatment effects on individual tree biomass and its distribution. Treatment means were compared using Tukey (Steel and Torrie, 1988). All analyses were performed using SAS V6.1 statistical program (SAS Institute, 1985).

Individual tree level results may have been affected by our mean tree sampling method at higher densities. Analyses of diameter distribution for each thinning treatment against sampled diameters showed a deviation of less than 2 cm from the real mean tree (less than 0.5 standard deviations from plot means). Analyses of height distribution for each thinning treatment against sampled trees showed that selected trees were approximately 1.6 m from the real mean tree (less than one standard deviation from plot mean).

## 3. Results

## 3.1. Individual tree aboveground biomass

Biomass accumulation for stemwood, bark, branchwood, foliage and twigs and total amounts estimated at individual tree level are presented in Table 2. Stem biomass (stemwood + bark) accounted for the largest proportion of individual tree aboveground biomass across treatments. Stem biomass ranged between 94.2% for the 400 trees ha<sup>-1</sup> to 96.4% for the 1100 trees ha<sup>-1</sup> stocking. Bark proportion of total biomass ranged between 10.8% for the 400 trees ha<sup>-1</sup> to 9.7% for the

Table 1

Average diameter at breast height (dbh), quadratic mean diameter  $(D_g)$ , average effective stocking, and dbh sampled trees at harvesting, for each thinning and pruning treatment combination (n = 3)

Thinning (trees ha <sup>-1</sup> )	Pruning height (m)	dbh mean (cm)	D <sub>g</sub> (cm)	dbh sampled mean (cm)	Average effective stocking after thinning (trees $ha^{-1}$ )
400	0	33.5	34.1	33.5	432
400	3.5	32.5	33.7	33.1	422
400	7	32.2	33.0	32.8	401
800	0	27.1	28.0	28.0	844
800	3.5	28.2	29.0	29.4	772
800	7	27.7	28.2	27.4	813
1100	0	24.3	25.3	23.4	1121
1100	3.5	24.9	25.7	26.5	1111
1100	7	24.9	25.8	24.6	1142

Table 2

	Dry weight	crown (kg tre	$e^{-1}$ )		Dry weight stem (kg tree $^{-1}$ )			Total (kg tr
	Foliage	Twigs	Branchwood	Total	Stemwood	Bark	Total	
Thinning								
$400 \text{ trees ha}^{-1}$	16.5 a	4.0 a	23.6 a	44.0 a	635.9 a	82.3 a	718.2 a	762.2 a
$800 \text{ trees ha}^{-1}$	11.4 b	2.0 b	13.9 b	27.3 b	458.9 b	57.4 b	516.3 b	543.6 b
$1100 \text{ trees ha}^{-1}$	4.5 c	1.3 b	6.5 c	12.3 c	296.2 c	33.0 c	329.2 c	341.5 c
Pruning								
0 m	10.6 a	2.3 a	13.7 a	26.6 a	463.3 a	61.0 a	524.3 a	550.9 a
3.5 m	9.3 a	2.8 a	16.3 a	28.3 a	495.8 a	57.1 a	552.9 a	581.2 a
7.0 m	12.4 a	2.3 a	14.1 a	28.7 a	432.0 a	54.6 a	486.6 a	515.3 a
Pr (F)								
Thinning	<0.0001	0.0030	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Pruning	0.1402	0.7169	0.3852	0.7876	0.1030	0.3070	0.1228	0.1367
Thinning $\times$ pruning	0.0318	0.6309	0.2938	0.2300	0.5505	0.0568	0.5034	0.5055

Individual tree biomass distribution according to crown section and thinning and pruning intervention level<sup>a</sup>

<sup>a</sup> Pr (F) probability limit in ANOVA with two factors (significant values in bold). Different letters in each column indicate significant differences (Tukey, p < 0.05).

1100 trees  $ha^{-1}$  stocking (Table 2). Bark biomass was more than twice the biomass accumulated in the crown.

Analyses of variance indicated that thinning but not pruning affected distribution of aboveground biomass of individual trees except for foliage (Table 2). An interaction was observed between pruning intensity and thinning (p < 0.0318), however interaction effects were very small compared to thinning effects on foliage biomass.

Higher stemwood, bark, and total individual tree aboveground biomass were observed at the 400 trees ha<sup>-1</sup> and 800 trees ha<sup>-1</sup> stockings. Biomass of crown components (foliage, twigs, and branchwood) increased with thinning intensity (Table 2). For foliage biomass this effect reduced the foliage proportion of individual tree total biomass from 2.2% for the 400 trees ha<sup>-1</sup> to 1.3% for the 1100 tress ha<sup>-1</sup> stocking. Similar to foliage biomass, branchwood biomass also diminished from 3.1 to 1.9% of individual tree total biomass for the same treatments.

## 3.2. Stand biomass and estimated leaf area

Stand total biomass ranged between 303 t  $ha^{-1}$  to 450 t  $ha^{-1}$ and stem biomass (stemwood + bark) ranged from 283 t  $ha^{-1}$  to 427 t ha<sup>-1</sup> (Table 3). The highest stand and stem biomass was observed for the 1100 trees ha<sup>-1</sup> stocking with averages of  $437 \pm 10$  t ha<sup>-1</sup> and  $415 \pm 9$  t ha<sup>-1</sup>, respectively. The lowest stand and total biomass values were recorded for the 400 trees ha<sup>-1</sup> stocking with averages of  $333 \pm 21$  t ha<sup>-1</sup> for the stand and  $310 \pm 19$  t ha<sup>-1</sup> for stem biomass. No differences in stand biomass were observed among pruning treatments at each stocking (Table 3).

 $xg tree^{-1}$ )

Branch biomass (branches + twigs) ranged from 12.4 to 15.1 t ha<sup>-1</sup> and foliage biomass ranged from 8.1 to 10.3 t ha<sup>-1</sup> (Table 3). No significant differences in branch or foliage biomass were observed among stocking treatments with averages of  $13.8 \pm 0.8$  t ha<sup>-1</sup> for branches and  $8.9 \pm 0.7$  t ha<sup>-1</sup> for foliage.

Largest average biomass mean annual increment (MAI) was found for the 1100 tress ha<sup>-1</sup> (29.1  $\pm$  0.6 t ha<sup>-1</sup> year<sup>-1</sup>), followed by the 800 trees ha<sup>-1</sup> (27.2  $\pm$  0.6 t ha<sup>-1</sup> year<sup>-1</sup>) and the 400 trees ha<sup>-1</sup> stocking (22.2  $\pm$  1.4 t ha<sup>-1</sup> year<sup>-1</sup>). The MAI for stem biomass for all treatments ranged from 18.9 to 28.5 t ha<sup>-1</sup> year<sup>-1</sup> (Table 3).

Leaf area estimates ranged from 3.8 to  $4.7 \text{ m}^2 \text{ m}^{-2}$  with no differences among thinning treatments or pruning levels (Table 3).

Table 3

Effect of thinning and	pruning treatments on stand	above ground biomass (	quantity and distribution <sup>a</sup>

Treatments		Dry weight crown (t $ha^{-1}$ )				Dry weight stem (t $ha^{-1}$ )			Total	Leaf area	MAI
Thinning (tree ha <sup>-1</sup> )	Pruning (m)	Foliage	Twigs	Branchwood	Total	Stemwood	Bark	Total	(t ha <sup>-1</sup> )	$(m^2 m^{-2})$	$(t ha^{-1} year^{-1})$
400	0	9.5 a	1.7 a	12.6 a	23.9 a	288.5 abc	37.8 ab	326 abc	350 ab	4.4 a	23.3 ab
400	3.5	10.3 a	1.7 a	13.4 a	25.4 a	283.4 ab	37.8 ab	321 ab	347 ab	4.7 a	23.1 ab
400	7	8.2 a	1.5 a	10.9 a	20.5 a	250.1 a	32.6 a	283 a	303 a	3.8 a	20.2 a
800	0	9.2 a	1.9 a	12.4 a	23.5 a	349.0 bcd	43.1 ab	392 bcd	416 bc	4.3 a	27.7 bc
800	3.5	9.4 a	1.9 a	12.7 a	24.0 a	346.3 bcd	43.1 ab	390 bcd	413 bc	4.4 a	27.6 bc
800	7	8.1 a	1.8 a	11.1 a	21.0 a	334.3 cd	40.7 ab	375 bcd	396 abc	3.8 a	26.4 abc
1100	0	8.3 a	1.8 a	11.4 a	21.5 a	362.2 cd	43.2 ab	405 bcd	427 bc	4.1 a	28.5 bc
1100	3.5	8.2 a	1.9 a	11.3 a	21.4 a	368.1 d	43.8 b	412 cd	433 bc	4.0 a	28.9 bc
1100	7	8.8 a	1.9 a	12.1 a	22.8 a	381.6 d	45.6 b	427 d	450 c	4.3 a	30.0 c

<sup>a</sup> Different letters in each column indicate significant differences (Tukey, p < 0.05). MAI: Mean annual increment of stem biomass (wood).

Table 4
Biomass distribution of the crown according to section and treatment <sup>a</sup>

Treatments		Tree height (m)	ht (m) Live crown length (m)		Dry weight crown (kg tree $^{-1}$ )		
Thinning (tree ha <sup>-1</sup> )	Pruning (m)			Upper	Middle	Lower	
400	0	37.1 abc	12.6 ab	4.8 a	21.3 a	17.1 ab	
400	3.5	39.0 a	12.1 ab	7.5 a	17.3 a	13.8 ab	
400	7	35.9 abc	14.5 a	7.4 a	19.4 a	23.4 a	
800	0	37.9 ab	12.3 ab	4.8 a	12.2 ab	9.0 bc	
800	3.5	37.6 ab	13.3 ab	8.1 a	12.1 ab	11.6 bc	
800	7	35.0 abc	14.5 a	5.4 a	13.1 ab	5.7 bc	
1100	0	32.0 bc	8.7 bc	2.3 a	4.3 b	3.9 c	
1100	3.5	35.0 abc	9.9 abc	2.9 a	6.7 b	4.9 c	
1100	7	31.3 c	6.4 c	1.7 a	5.0 b	5.2 c	

<sup>a</sup> Different letters in each column indicate significant differences (Tukey, p < 0.05).

## 3.3. Total height, live crown length, and crown biomass distribution

Average tree height diminished for the 1100 trees ha<sup>-1</sup> stocking; however no significant differences were found for pruning treatments (Table 4). Average LCL diminished at the 1100 trees ha<sup>-1</sup> stocking with an average of  $8.3 \pm 1.5$  m, and was longer at the 800 trees ha<sup>-1</sup> (13.4  $\pm$  0.9 m) and the 400 trees ha<sup>-1</sup> stockings (13.1  $\pm$  1.0 m).

Distribution of crown biomass components was not homogeneous. Crown biomass across treatments had an average of 17.9% for the upper, 44.4% for the middle, and 37.7% for the lower section of the crown. Crown biomass was different at different stockings. Larger crown biomass at the middle and lower sections was estimated for the 400 trees  $ha^{-1}$ and the 800 trees  $ha^{-1}$  stockings (Table 4), and no differences in total crown biomass accumulation were observed between these treatments for these crown sections. Proportion of live crown length from total tree height averaged  $0.35 \pm 0.04$  for the 400 trees ha<sup>-1</sup>,  $0.36 \pm 0.04$  for the 800 trees ha<sup>-1</sup>, and  $0.25 \pm 0.03$  for the 1100 tress ha<sup>-1</sup> stocking.

The leaf/branch biomass ratios were 0.69 for the 1100 trees  $ha^{-1}$  and 0.70 kg kg<sup>-1</sup> for the 400 trees  $ha^{-1}$ stocking. In both cases, the leaf/branch ratio was greater in the upper section with values of 0.82 and 1.08 kg kg<sup>-1</sup>, and lower at the base with values of 0.52 and 0.50 kg  $kg^{-1}$  for the same stockings.

## 3.4. Allometric models

The allometric models indicated a good correlation of the independent variables dbh<sup>2</sup> and dbh<sup>2</sup>h with the aboveground biomass components. The coefficient of determination  $(R^2)$ ranged between 0.63 for the twig model and 0.95 for total dry weight (Table 5).

Crown biomass components were best estimated using diameter  $\ln(dbh^2)$ . Coefficients of determination ( $R^2$ ) were 0.63, 0.74, and 0.80 for the twig, leaf, and branch regressions, respectively (Table 5). Stem components (wood and bark) were best estimated using both diameter and height  $\ln(dbh^2h)$  with  $R^2$ of 0.94 and 0.80 for the wood and bark regressions, respectively.

### 4. Discussion

## 4.1. Individual tree and stand aboveground biomass

Similar to our 15-year-old E. nitens stand, Monteiro and Pereira (1990) found that between 85 and 90% of the above ground biomass in adult E. globulus plantations was concentrated in stemwood and bark, and the proportion of bark with respect to the stem biomass ranged 9-12%. Bark biomass accumulations are important in *Eucalyptus* plantations and may export more than 50% of total aboveground Ca and Mg at harvesting (Attiwill, 1980; Turner and Lambert, 1983; Grove et al., 1996; Laclau et al., 2000). Foliage biomass of individual trees accounted for less than 3%. Foliage and branch biomass accumulations were small, given the continuous increase in accumulation of stem biomass at older ages instead of crown components that are more ephemeral (Satoo and Madgwick, 1982; Grove et al., 1996; Rubilar, 2002).

In our study individual tree and stand aboveground biomass was strongly affected by stocking. Pinkard and Neilsen (2003), in a spacing trial for E. nitens in Australia, found that initial stocking did not affect individual tree total aboveground biomass at age 7. However, a large proportion of biomass was partitioned to stem instead of branches at higher densities, with an associated increase in individual tree diameter. In our study, stem production of individual trees decreased due to increased

Allometric functions for aerial biomass components (kg)<sup>a</sup>

Allometric function <sup>b</sup>	$R^2$	Se
$\ln(dwf) = -12.060 + 2.1307 \ln (dbh^2)$	0.74	0.3489
$\ln(dwt) = -10.167 + 1.6295 \ln (dbh^2)$	0.63	0.3377
$\ln(dwb) = -11.0755 + 2.033 \ln (dbh^2)$	0.80	0.2815
$\ln(dww) = -4.5592 + 1.0374 \ln (dbh^2h)$	0.94	0.0886
$\ln(dwba) = -8.3290 + 1.1987 \ln (dbh^2h)$	0.80	0.2056
$\ln(dwto) = -4.8233 + 1.0793 \ln (dbh^2h)$	0.95	0.0824

<sup>a</sup> dwf: dry weight foliage, dwt: dry weight twigs, dwb: dry weight branches, dww: dry weight wood, dwba: dry weight bark, dwto: dry weight total, ln: natural logarithm, dbh: diameter at breast height (1.30 m) (cm), h: total height (m), Se: standard error,  $R^2$ : coefficient of determination. The unit of component dry weight is kg.

All the coefficients are significant (p < 0.05).

competition in the stand (Satoo and Madgwick, 1982; Bernardo et al., 1998; Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003). Several studies investigating spacing effects and their implications for thinning at harvesting for E. nitens, have concluded that total production of wood increases as stocking increases (Gerrand et al., 1997; Bernardo et al., 1998; Pinkard and Neilsen, 2003). Stand wood production has been also observed to decline at high stocking levels (Satoo and Madgwick, 1982; Smith et al., 1997). Our study showed no differences in stand biomass production for the 1100 and 800 trees  $ha^{-1}$  stocking treatments. Despite that no mortality was observed at the highest stocking (1100 trees  $ha^{-1}$ ), the treatment reduced significantly individual tree growth. Considering harvesting costs and wood quality, the 800 trees  $ha^{-1}$ stocking treatment at this site would allow for greater value and maximum economical return for sawntimber production objectives.

Bernardo et al. (1998) found no change in partitioning to branches at 41 months since establishment in a spacing study investigating several Eucalyptus species ranging from 833 to 2222 trees  $ha^{-1}$ . However, branch biomass accounted for 24% of the total in a 7-year-old E. nitens stands with a stocking of 500 trees ha<sup>-1</sup> and for 20% in a 1667 trees ha<sup>-1</sup> stand, respectively (Pinkard and Neilsen, 2003). Our results showed smaller partitioning to branches at higher stockings in agreement with previous results (Niemisto, 1995; Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003). Differences in results suggest ontogenetic differences in response to changes in growth space. Effects on branch biomass may be complex and are linked to history, age, and stocking of the stand (Satoo and Madgwick, 1982). Lower biomass allocated to branches at higher stockings may improve wood quality for sawntimber or structural purposes (Satoo and Madgwick, 1982; Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003), avoiding processing problems of trees with larger branches at lower stockings and volume down-grading (Wardlaw and Neilsen, 1999).

Thinning intensity affected the percentage of individual tree foliage biomass participation of total biomass. In terms of foliage partitioning, our results differ from Pinkard and Neilsen (2003) and agreed partially with Bernardo et al. (1998), who found lower individual tree partition to foliage as stocking increased, and a linear pattern of stand leaf area index across spacing for young plantations. At our trial, reductions in individual tree foliage biomass were only associated to the highest stocking treatment. Given that all treatments showed the same leaf area index, shorter live crown lengths found at higher stockings suggest that light availability constraints may have created a negative balance for carbon acquisition at lower crown positions at higher stockings (Pinkard et al., 1999).

Pinkard and Neilsen (2003) found a spacing effect in *E.* nitens leaf area with a plateau above 833 trees ha<sup>-1</sup>. Our stand is older compared to stands evaluated by Bernardo et al. (1998) and Pinkard and Neilsen (2003) allowing complete stand leaf area development since thinning or pruning. A leaf area value of 4 has been proposed by Pinkard et al. (1999) as an optimum for *E. nitens* plantations across ages. In our 15-year-old trial, estimated leaf area was close to the proposed optimum, suggesting no nutrient or water limitations at this site (Jarvis and Leverenz, 1983; Albaugh et al., 1998). In Tasmania optimal conditions for eucalypt sawlog production have been suggested for sites with higher than 1000 mm of rainfall and good fertility (Gerrand et al., 1997). Accordingly, our site is well above in rainfall to present water availability limitations, and soils are considered of high fertility to maintain the observed leaf area levels (Bennett et al., 1997; Smethurst et al., 2003, 2004; Wiseman et al., 2006).

Our results show that pruning had no effect on the total amount or biomass distribution. Live branch pruning has been found to decrease stem growth (Shepherd, 1986; Pinkard et al., 2004), and especially in *E. nitens*, when a large proportion (>50%) of the live crown is removed (Pinkard and Beadle, 1998c; Pinkard and Neilsen, 2003; Pinkard et al., 2004; Wiseman et al., 2006). In our study pruning treatments were very conservative for the age of the stand and equivalent to less than 40% of crown removal. Several studies with different species have found that pruning effects are related with the opportunity and intensity of its application (Sutton, 1985; Maclaren, 1993; Pinkard et al., 2004; Wiseman et al., 2006). First pruning of E. nitens green branches should be applied around age 3 ( $\sim$ 7 m height) on sites of high productivity (before crown closure) to avoid degrading of timber quality (Gerrand et al., 1997; Mohammed et al., 2000; Wiseman et al., 2006). Considering that pruning in this study was applied when the plantation was 6 years old, removal of branches that have died or were dying had no effects on tree growth (Pinkard et al., 2004).

Stemwood biomass mean annual increment (MAI) for the lowest and intermediate stockings were higher than values obtained in Tasmania by Pinkard and Neilsen (2003) in a 7-yearold *E. nitens* stand (23.9 t  $ha^{-1}$  year<sup>-1</sup>) and higher than the range reported by Monteiro and Pereira (1990), for E. globulus located in the central coast of Portugal (16–24 t  $ha^{-1}$  year<sup>-1</sup>). Similarities between biomass values for different stockings have also been reported by Pinkard and Neilsen (2003), who determined that biomass MAI ranged from 23.9 to 23.6 t  $ha^{-1}$  year<sup>-1</sup> for stockings of 833 to 1010 trees  $ha^{-1}$ , respectively. Our results suggest that thinning treatments have affected the rates of growth of the stands. Differences in allocation patterns to branches may explain these responses (Niemisto, 1995; Neilsen and Gerrand, 1999; Pinkard and Neilsen, 2003). However, no large differences in branch and foliage biomass components were observed in our stands (Table 3). Belowground components may affect these relationships also (Cannell and Dewar, 1994; Misra et al., 1998a,b; Moroni et al., 2003).

# 4.2. Total height, live crown length and crown biomass distribution

Negative effects of stocking on stand height have been rarely observed in *Pinus* or *Eucalyptus* stocking experiments. However, negative effects on mean tree height have been observed on highly stocked pine stands, especially when trees are under high competition for nutrient or water resources (Harms and Langdon, 1976; DeBell et al., 1989; Neilsen and Gerrand, 1999; Medhurst et al., 2002). In our study we observed reductions in live crown length associated with lower mean tree height, and lower foliage biomass at middle and lower crown positions, for the highest stocking (1100 tree ha<sup>-1</sup>). Reductions in tree height and foliage biomass may suggest nutritional or water limitations at this stocking treatment (Smethurst et al., 2003, 2004; Wiseman et al., 2006). However, no differences in total biomass and leaf area at the highest stocking (1100 tree ha<sup>-1</sup>), suggest that light availability conditions may have affected tree height development.

Pinkard and Neilsen (2003) found in 7-year *E. nitens* plantations a proportion of live crown length of 65 and 49% for stockings of 500 and 1667 trees ha<sup>-1</sup>, respectively. Our results showed similar effects of stocking on the proportion of live crown length from total height. However, for our 15-year-old stand, differences between lower stockings (400 and 800 trees ha<sup>-1</sup>) and the highest stocking (1100 tree ha<sup>-1</sup>) were only of 10%.

Light crown environment and foliage photosynthetic efficiency may be affected by its relative distribution in the upper, middle and lower sections of the crown. Pinkard et al. (2004) found that E. nitens mature foliage C assimilation is higher compared to other Eucalyptus species. Medhurst and Beadle (2005) also found an increase in C assimilation after thinning in lower and mid crown positions in old and mature foliage. Improvements in light conditions have been found to increase lower crown leaf area development (Brix and Mitchell, 1983; Medhurst and Beadle, 2001). Improved tree growth at the lower stockings (400 and 800 trees  $ha^{-1}$ ) may be triggered by large foliage biomass accumulations of mature foliage in the lower and middle crown sections compared to higher stockings. Therefore, larger stand growth at the intermediate stocking  $(800 \text{ trees ha}^{-1})$  seems to be a result of a combination of improved physiological mechanisms for individual tree growth, larger leaf area, and high stocking.

Branch biomass accumulation followed foliage biomass distribution in our stand. Our results differed from Medhurst and Beadle (2001), who indicate that the proportion of branches at each crown section was similar in thinned and non-thinned trees. In the same study, Medhurst and Beadle (2001) indicated that branch biomass across treatments averaged 16% in the lower third, 32% in the middle third, and 52% in the upper third of the crown. Contrastingly, our study found larger branch and foliage biomass at lower and mid-crown positions.

A higher leaf/branch ratio indicates that a lower proportion of photosynthetic production may be needed to maintain the supporting structure of the foliage. Our values are in the range indicate for *Pseudotsuga menziesii* with values of 0.90 and 0.79 kg kg<sup>-1</sup> for stockings of 1030 and 690 trees ha<sup>-1</sup>, respectively (Espinosa and Perry, 1987); for *Pinus radiata* with 0.62 kg kg<sup>-1</sup> at a stocking of 489 trees ha<sup>-1</sup> (Rodríguez, 2002); and for *E. nitens* with 0.50 and 0.55 kg kg<sup>-1</sup> for stockings of 500 trees ha<sup>-1</sup> (Pinkard and Neilsen, 2003).

## 4.3. Allometric relations

There is large variability in biomass equation estimates for *Eucalyptus* species. Madgwick et al. (1991) using equations derived from New Zealand trials underestimated wood of South

African *E. nitens* studies by 20–30% and bark by 30–40%. This suggest that site specific equations are required to estimate more effectively *E. nitens* biomass (Bernardo et al., 1998), or that taper effects on biomass estimates should be taken into account (Gerrand et al., 1997; Pinkard et al., 2004). More variation is commonly found for allometric models for branches and foliage (Madgwick et al., 1991). Branches and foliage are more ephemeral tissues compared to stemwood and therefore more susceptible to annual and biannual changes affecting allometric relationships (Rubilar et al., 2005).

Pinkard and Neilsen (2003) concluded that allometric relationships in *E. nitens* can be used to estimate leaf area, aboveground biomass and its components, and crown length, irrespective of plantation spacing. Similar results were found by Medhurst et al. (1999) for a wide variety of sites, ages, and thinning. Our results for older stand ages agree with previous findings, suggesting that estimates of biomass and leaf area are sustained across thinning treatments. As discussed before, the underlying mechanisms affecting leaf area production are water and nutritional limitations that remain the same across thinning treatments therefore no effects would be expected on allometric relationships.

### 5. Conclusions

Thinning increased average stem, crown and total biomass of individual trees. Pruning did not have an effect on aboveground biomass suggesting that late pruning would not affect individual tree growth. There is a need to understand how early or late pruning may affect wood quality and stem form. Given the large differences in crown architecture of clonal material, new experiments should focus attention to investigate silvicultural treatments interactions with genotypes of defined crown characteristics. Stand leaf area, productivity, and biomass accumulation was not different between 800 and 1100 trees ha<sup>-1</sup> at harvesting. Maximum biomass and wood accumulation was reached at both 1100 and 800 trees ha<sup>-1</sup> stockings. However, higher stand value and reduced harvesting costs may be obtained at stockings close to 800 trees ha<sup>-1</sup> for sites of high fertility and reduced water limitations.

## Acknowledgements

The authors are grateful to two anonymous reviewers and the editor for valuable comments and suggestions on the manuscripts. Also the authors thank to Dr. Lee Allen, Forest Nutrition Cooperative at North Carolina State University, USA. We would like to thank Bosques Arauco S.A. for providing support for this experiment.

## References

- Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf-area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. 44, 317–328.
- Aparicio, J., 2001. Rendimiento y Biomasa de Eucalyptus nitens con alternativas nutricionales para una silvicultura sustentable en un suelo rojo

arcilloso. Master's thesis in Science, Universidad Austral de Chile. Valdivia, Chile, 234 pp.

- Attiwill, P.M., 1980. Nutrient cycling in a *Eucalyptus oblique* (L'Herit) forest. IV Nutrient uptake and nutrient return. Aust. J. Bot. 28, 199–222.
- Bartelink, H., 1998. A model of dry matter partitioning in trees. Tree Physiol. 18, 91–101.
- Bennett, L.T., Weston, C.J., Attiwill, P.M., 1997. Biomass, nutrient content and growth response to fertilisers of six-year-old *Eucalyptus globulus* plantations at three contrasting sites in Gippsland, Victoria. Aust. J. Bot. 45, 103– 121.
- Bernardo, A., Reis, M., Reis, G., Harrison, R., Firme, D., 1998. Effect of spacing on growth and biomass distribution in *Eucalyptus camaldulensis*, *E. pellita* and *E. urophylla* plantations in southeastern Brazil. For. Ecol. Manage. 104, 1–13.
- Blake, G., Hartge, K., 1986. Picnometer method. In: Klute, A. (Ed.), Methods of Soil Analysis, Part I, Physical and Mineralogical Methods, Agronomy Monograph No. 9, second ed. American Society of Agronomy, Soil Sci. Soc. of America, Madison, WI, USA, pp. 377–382.
- Brix, H., Mitchell, A., 1983. Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area and basal area in Douglas-fir. Can. J. For. Res. 13, 384–389.
- Caldentey, J., Bown, H., Donoso, S., 1992. Estimación de la biomasa total extraída bajo intervenciones silviculturales en bosques naturales de lenga (*Nothofagus pumilio*) en Magallanes. 4° Encuentro científico sobre medio ambiente. CIPMA, Valdivia, Chile, Tomo I, 28 pp.
- Close, D.C., Battaglia, M., Davidson, N.J., Beadle, C.L., 2004. Within-canopy gradients of nitrogen and photosynthetic activity of *Eucalyptus nitens* and *Eucalyptus globulus* in response to nitrogen nutrition. Aust. J. Bot. 52 (1), 133–140.
- Cannell, M., 1989. Physiological basis of wood production: a review. Scand. J. For. Res. 4, 459–490.
- Cannell, M., Dewar, R.C., 1994. Carbon allocation in trees: a review of concepts for modelling. Adv. Ecol. Res. 25, 59–104.
- Carrasco, P., Millán, J., 1990. Proyecto de suelos forestales de la VIII Región. Informe final. Universidad de Concepción, Depto. de Cs. Forestales/Min. de Agricultura. Chillán, Chile, 152 pp.
- Cromer, R.N., 1996. Silviculture of eucalypt plantations in Australia. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Australia, pp. 259–274.
- De Moraes, J.L., Stape, J.L., Laclau, J.P., Smethurst, P., Gava, J.L., 2004. Silvicultural effects on the productivity and wood quality of eucalypt plantations. For. Ecol. Manage. 193, 45–61.
- DeBell, D.S., Harms, W.R., Whitesell, C.D., 1989. Stockability; a major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the southeastern United States. For. Sci. 35 (3), 708–719.
- Espinosa, M., Perry, D., 1987. Distribution and increment of biomass in adjacent young Douglas-fir stands with different early growth rates. Can. J. For. Res. 17, 722–730.
- Geldres, E., Gerding, V., Schlatter, J., 2004. Biomasa de *Eucalyptus nitens* de 4 – 7 años de edad en un rodal de la Décima Región. En: Actas Segundo Congreso Chileno de Ciencias Forestales. Universidad Austral de Chile, Valdivia, Chile. En CD.
- Gerding, V., Schlatter, J., Saavedra, C., 2002. Biomasa de plantaciones de *Eucalyptus nitens* de 5 años en un suelo rojo arcilloso con fertilización, comuna de Fresia, X Región. In: Actas Primer Congreso Chileno de Ciencias Forestales. Universidad de Chile, Santiago, Chile, 8 pp.
- Gerrand, A.M., Neilsen, W.A., Medhurst, J.L., 1997. Thinning and pruning eucalypt plantations for sawlog production in Tasmania. Tasforests 9, 15– 34.
- Grove, T.S., Thomson, B.D., Malajczuk, N., 1996. Nutritional physiology of *Eucalyptus*: uptake, distribution and utilization. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Australia, pp. 77–109.
- Harms, W.R., Langdon, O.G., 1976. Development of loblolly pine in dense stands. For. Sci. 22 (3), 331–337.
- Herbert, M.A., 1996. Fertilizers and eucalypt plantations in South Africa. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Australia, pp. 303–325.

- Hush, B., Miller, C., Beers, T., 1982. Forest Mensuration. Krieger Publishing, New York, USA, p. 402.
- Infor, 2004. Eucalyptus nitens en Chile: Primera monografía. Informe Técnico No 165. Instituto Forestal. Valdivia, Chile, 143 pp.
- Ingerslev, M., Hallbäcken, L., 1999. Above ground biomass and nutrient distribution in a limed and fertilized Norway spruce (*Picea abies*) plantation. Part II. Accumulation of biomass and nutrients. For. Ecol. Manage. 119, 21–38.
- Jarvis, P.G., Leverenz, J., 1983. Productivity of temperate, deciduous and evergreen forest. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), Encyclopedia of Plant Physiology. New Series, vol. 12D. Springer-Verlag, Berlin, pp. 233–280.
- Knight, P.J., Nicholas, I.D., 1996. Eucalypt nutrition: New Zealand experience. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Australia, pp. 275–302.
- Kube, P., Raymond, C., 2002. Breeding to minimize the effects of collapse in *Eucalyptus nitens*. Technical Report 93 Project A5: Wood quality. Cooperative Research Centre for Sustainable Production Forestry, Hobart, Tasmania, Australia, 18 pp.
- Laclau, J.P., Bouillet, J.P., Ranger, J., 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. For. Ecol. Manage. 128 (3), 181–196.
- Maclaren, J., 1993. Radiata pine Grower's Manual. New Zealand Forest Research Institute. FRI Bulletin 184. Rotorua, New Zealand, 140 pp.
- Madgwick, H.A.I., Oliver, G.R., Frederick, D.J., Thompson, D., 1991. Estimating the Dry Weights of *Eucalyptus* Trees-Central North Island. New Zealand Biores. Technol. 37, 111–114.
- Medhurst, J.L., Battaglia, M., Cherry, M.L., Hunt, M.A., White, D.A., Beadle, C.L., 1999. Allometric relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden plantations. Trees 14, 91–101.
- Medhurst, J., Beadle, C., 2000. Thinning for solid wood products in *Eucalyptus nitens* plantations. In: Henderson, L., Waugh, G., Nolan, G., Bennett, P. (Eds.), The Future of Eucalypts for Wood Products. Proceedings of IUFRO Conference, 19–24 March 2000, Launceston, Australia, pp. 343–348.
- Medhurst, J.L., Beadle, C.L., 2001. Crown structure and leaf area index development in thinned and unthinned *Eucalyptus nitens* plantations. Tree Physiol. 21, 989–999.
- Medhurst, J.L., Battaglia, M., Beadle, C.L., 2002. Measured and predicted changes in tree and stand water use following high-intensity thinning of an 8-year-old *Eucalyptus nitens* plantation. Tree Physiol. 22 (11), 775–784.
- Medhurst, J.L., Beadle, C.L., 2005. Photosynthetic capacity and foliar nitrogen distribution in *Eucalyptus nitens* is altered by high-intensity thinning. Tree Physiol. 25 (8), 981–991.
- Misra, R.K., Turnbull, C.R.A., Cromer, R.N., Gibbons, A.K., LaSala, A.V., 1998a. Below- and above-ground growth of *Eucalyptus nitens* in a young plantation: I. Biomass. For. Ecol. Manage. 106, 283–293.
- Misra, R.K., Turnbull, C.R.A., Cromer, R.N., Gibbons, A.K., LaSala, A.V., Ballard, L.M., 1998b. Below- and above-ground growth of *Eucalyptus nitens* in a young plantation: II. Nitrogen and phosphorus. For. Ecol. Manage. 106, 295–306.
- Mohammed, C., Barry, K., Battaglia, M., Beadle, C., Eyles, A., Mollon, A., Pinkard, E., 2000. Pruning-associated stem defects in plantation *E. nitens* and *E. globulus* grown for sawlog and veneer in Tasmania, Australia. In: Henderson, L., Waugh, G., Nolan, G., Bennett, P. (Eds.), The Future of Eucalypts for Wood Products. Proceedings of IUFRO Conference, 19–24 March 2000, Launceston, Australia, pp. 357–364.
- Monteiro, A., Pereira, J., 1990. Impactes ambientais e sócio-económicos do eucaliptal em Portugal. Departamento de Engenharia Florestal. Instituto Superior de Agronomía. Universidad Técnica de Lisboa, 106 pp.
- Moroni, M., Worledge, D., Beadle, C., 2003. Root distribution of *Eucalyptus nitens* and *E. globulus* in irrigated and droughted soil. For. Ecol. Manage. 177, 399–407.
- Muñoz, F., 2002. Balance nutritivo de una plantación de *Eucalyptus nitens* (Deane & Maiden) Maiden de 7 años de edad en suelos ñadi. Memoria de título. Facultad de Ciencias Forestales, Universidad Austral de Chile. Valdivia, Chile, 108 pp.
- Muñoz, F., Espinosa, M., Herrera, M.A., Cancino, J., 2005. Características del crecimiento en diámetro, altura y volumen de una plantación de *Eucalyptus*

*nitens* sometida a tratamientos silvícolas de poda y raleo. Bosque 26 (1), 93–99.

- Neilsen, W.A., Gerrand, A.M., 1999. Growth and branching habit of *Eucalyptus nitens* at different spacing and the effect on final crop selection. For. Ecol. Manage. 123, 217–229.
- Niemisto, P., 1995. Influence of initial spacing and row-to-row distance on the crown and branch properties and taper of silver birch (*Betula pendula*). Scand. J. For. Res. 10, 235–244.
- Pardé, D. R., 1980. Forest biomass. Review article. Forest Products Abstract 41, 343–362.
- Pinkard, E.A., Beadle, C.L., 1998a. Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. Trees 12, 366–376.
- Pinkard, E.A., Beadle, C.L., 1998b. Aboveground biomass partitioning and crown architecture of *Eucalyptus nitens* following green pruning. Can. J. For. Res. 28 (9), 1419–1428.
- Pinkard, E.A., Beadle, C., 1998c. Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. New Forests 15, 107–126.
- Pinkard, E.A., Battaglia, M., Beadle, C.L., Sands, P.J., 1999. Modeling the effect of physiological responses to green pruning on net biomass production of *Eucalyptus nitens*. Tree Physiol. 19 (1), 1–12.
- Pinkard, E.A., Battaglia, M., 2001. Using hybrid models to develop silvicultural prescriptions for *Eucalyptus nitens*. For. Ecol. Manage. 154, 337–345.
- Pinkard, E.A., 2002. Effects of pattern and severity of pruning on growth and branch development of pre-canopy closure *Eucalyptus nitens*. For. Ecol. Manage. 157, 127–230.
- Pinkard, E.A., Neilsen, B., 2003. Crown and stand characteristics of *Eucalyptus nitens* in response to initial spacing: Implications for thinning. For. Ecol. Manage. 172, 215–227.
- Pinkard, E.A., Mohammed, C., Beadle, C.L., Hall, M.F., Worledge, D., Mollon, A., 2004. Growth responses, physiology and decay associated with pruning plantation-grown *Eucalyptus globulus* Labill. and *E. nitens* (Deane and Maiden) Maiden. For. Ecol. Manage. 200, 263–277.
- Prado, J.A., Toro, J.A., 1996. Silviculture of eucalypt plantations in Chile. In: Attiwill, P.M., Adams, M.A. (Eds.), Nutrition of Eucalypts. CSIRO Publishing, Collingwood, Australia, pp. 357–370.
- Rietz, D.N., Smith, C.W., 2004. A preliminary study of aboveground allometric relationships of *Eucalyptus nitens* (Deane and Maiden) plantations in South Africa. ICFR-Bulletin-Series 14/2004, 32 pp.
- Rodríguez, R., 2002. Effects of silvicultural regime on leaf, allometry, growth allocation and productivity in *Pinus radiata* D. Don. Tesis de Doctorado en Ciencias Forestales. Universidad de Concepción. Facultad de Ciencias Forestales. Concepción, Chile, 109 pp.
- Rojas, J.C., 2005. Factors influencing responses of loblolly pine stands to fertilization. Ph.D. Dissertation. Dept. of Forestry, North Carolina State Univ., Raleigh, NC, 147 pp.
- Rubilar, R.A., 2002. Biomass and nutrient accumulation comparison between successive loblolly pine rotations on the Upper Coastal Plain of Alabama. M.Sc. Thesis. Dept. of Forestry, North Carolina State Univ., Raleigh, NC, 190 pp.
- Rubilar, R.A., 2005. Environmental constraints on growth phenology, leaf area display, and above and belowground biomass accumulation of *Pinus radiata*

(D. Don) in Chile. Ph.D. Dissertation. Dept. of Forestry, North Carolina State Univ., Raleigh, NC, 190 pp.

- Rubilar, R.A., Allen, H.L., Kelting, D.L., 2005. Comparison of biomass and nutrient content equations for successive rotations of loblolly pine plantations on an Upper Coastal Plain Site. Biomass Bioenergy 28, 548– 564.
- Santibáñez, F., Uribe, J., 1993. Atlas Agroclimático de Chile, regiones sexta, séptima, octava y novena. Corporación de Fomento. Ministerio de Agricultura. FIA. Santiago, Chile, 99 pp.
- SAS Institute, 1985. SAS/STAT Guide for personal computers. Version 6 Edition. SAS Institute, Inc, Cary, NC, USA, p. 378.
- Satoo, T., Madgwick, H., 1982. Biomass. In: Forest Biomass, Martinus Nijhoff Publishers, Kluwer Boston, USA, Chapter 4, pp. 15–46.
- Schlegel, B., Gayoso, J., Guerra, J., 2000. Medición de la capacidad de captura de carbono en bosques de Chile y promoción en el mercado mundial. Proyecto Fondef D98I1076—Universidad Austral de Chile. Valdivia, Chile, 53 pp.
- Shepherd, K.R., 1986. Plantation Silviculture. Martinus Nijhoff Publishers, Dordrecht, p. 322.
- Smethurst, P., Baillie, C., Cherry, M., Holz, G., 2003. Fertilizer effects on LAI and growth of four *Eucalyptus nitens* plantations. For. Ecol. Manage. 176, 531–542.
- Smethurst, P., Holza, G., Moronia, M., Bailliea, C., 2004. Nitrogen management in *Eucalyptus nitens* plantations. For. Ecol. Manage. 193, 63–80.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture: Applied Forest Ecology, ninth ed. Wiley, p. 537.
- Steel, R., Torrie, J., 1988. Bioestadística: Principios y procedimientos. McGraw-Hill/Interamericana de México, México, p. 622.
- Sutton, W., 1985. Pino radiata: Sus excepcionales perspectivas en el comercio mundial de productos forestales. Publicación Técnica No. 17. Fundación Chile, Departamento Forestal. Santiago, Chile, 32 pp.
- Teller, A., 1988. Biomass, productivity and wood waste evaluation in a spruce (*Picea abies*) forest. Commonwealth Forestry Rev. 67 (2), 129–147.
- Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equation for sixty-five North American tree species. For. Ecol. Manage. 97, 1–24.
- Toro, J., 2002. Acumulación de calcio en plantaciones de Eucalyptus globulus y Eucalyptus nitens. Boletín de la Sociedad Chilena de la Ciencia del Suelo 18, 244–248.
- Trincado, G., Quezada, R., Gadow, K., 2003. A comparison of two stand table projection methods for young *Eucalyptus nitens* (Maiden) plantations in Chile. For. Ecol. Manage. 180, 443–451.
- Turner, J., Lambert, M.J., 1983. Nutrient cycling within a 27 year-old *Euca-lyptus grandis* plantation in New South Wales. For. Ecol. Manage. 6, 155–168.
- Wardlaw, T.J., Neilsen, W.A., 1999. Decay and other defects associated with pruned branches of *Eucalyptus nitens*. Tasforest 11, 40–57.
- Whitehead, D., Beadle, C., 2004. Physiological regulation of productivity and water use in *Eucalyptus*: a review. For. Ecol. Manage. 193, 113– 140.
- Wiseman, D., Smethurst, P., Pinkard, L., Wardlawd, T., Beadle, C., Hall, M., Baillie, C., Mohammed, C., 2006. Pruning and fertiliser effects on branch size and decay in two *Eucalyptus nitens* plantations. For. Ecol. Manage. 225, 123–133.