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Influences of silvicultural manipulations on above- and belowground biomass accumulations and leaf area in young *Pinus radiata* plantations, at three contrasting sites in Chile

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There is a limited understanding of how resource availability (water + nutrients) interacts with soil physical properties in determining above- and belowground biomass allocation in radiata pine (*Pinus radiata* D. Don) plantations. We studied total above- and belowground biomass accumulation, and belowground biomass allocation (coarse and fine roots) in response to three contrasting silvicultural treatments (soil tillage, weed control and fertilization) applied to three sites of contrasting climate and soil textures in the Central Valley of Chile. At each site, tree growth (aboveground, belowground and total biomass), aboveground:belowground biomass ratio and leaf area index (LAI) were significantly increased by weed control. Weed control produced larger and more consistent responses in growth than subsoiling or fertilization. Weed control appears to ameliorate both water and nutrient limitations. The large differences in growth and biomass accumulation by weed control within sites, were mainly attributed to large differences in soil water availability, and among sites also due to atmospheric water demand differences. A linear relationship was established between LAI and stand growth across sites. The slope of the relationship, stemwood growth efficiency, was different among sites and was related to water and nutrient limitations. Stemwood growth efficiency varied from $2.9\,\mathrm{m^3\,ha^{-1}\,year^{-1}}$ to $7.1\,\mathrm{m^3\,ha^{-1}\,year^{-1}}$ per unit of leaf area, with lower growth efficiencies found on sites with greater water constraints.

Introduction

Our understanding of the mechanisms that control plantation productivity has increased greatly during the last decades.Vose, J.M. *et al.* (1988); Cannell, M.G.R. (1989); Landsberg, J.J. *et al.* (1997); Albaugh, T.J. *et al.* (1998); Waring, R.H. *et al.* (1998); Makela, A. *et al.* (2000) In most temperate environments, biomass production is constrained by water and nutrient limitations that reduce leaf area development and efficiency in converting solar radiation to biomass.Vose, J.M. *et al.* (1988); Linder, S. (1987); Raison, R.J. *et al.* (1992); Carlyle, J.C. (1998); Allen, H.L. (1999) However, mechanisms controlling carbon allocation are not well understood, and little data has been published on how above- and belowground biomass allocation is affected by resource availability in young plantations.Dewar, R. (1997); Zerihun, A. *et al.* (2004) Our current understanding, based on the functional carbon balance model,Brouwer, R. (1983) is that

under conditions of limited soil resource availability, partitioning to the roots will increase.Albaugh, T.J. *et al.* (1998); Gower, S.T. *et al.* (1992); Haynes, B.E. *et al.* (1995); Guo, L.B. *et al.* (2002) Limited resource availability may trigger changes in allometry (more fine roots and less foliage) that result in reduced growth efficiency.Zerihun, A. *et al.* (2004); Gower, S.T. *et al.* (1993) At the same time, the influence of soil physical properties on the ability of trees to access site resources and on tree biomass allocation and productivity are poorly understood. Consequently, process-based models do not quantitatively account for how silvicultural practices affect nutrient availabilityLandsberg, J.J. *et al.* (1996) or how physical and chemical soil properties affect plant growth. The ability to quantify and integrate the interactions among silvicultural manipulations, soil characteristics and environmental effects into current and future modelling efforts may improve our capacity to describe and predict radiata

pine (*Pinus radiata* D. Don.) productivity and improve carbon sequestration estimatesJayawickrama, K.J.S. (2001); Espinosa, M. *et al.* (2005) linking process-based models to silvicultural decisions.

Chile has the largest concentration of radiata pine in the world. Potential productivity modelling efforts show that the large number of soil-climatic environments in Chile create large variation in radiata pine plantation productivity.Flores, F.J. (2004) Considerable work has been completed on young radiata pine examining climatic and nutritional constraints,Hunter, I.R. *et al.* (1984); Turner, J. *et al.* (1985); Schlatter, J.R. *et al.* (1995); Turner, J. *et al.* (2001); Sanchez-Rodriguez, F. *et al.* (2002) silvicultural treatment effects on water and nutrient limitations,Nambiar, E.K.S. *et al.* (1980); Sands, R. *et al.* (1984); Richardson, B. *et al.* (1993); Nambiar, E.K.S. (1995); Rubilar, R.A. (1998); Albaugh, T.J. *et al.* (2004) resource availability effects on leaf area, above- and belowground accumulation and growth efficiencyRaison, R.J. *et al.* (1992); Benson, M.L. *et al.* (1992); Raison, R.J. *et al.* (1992;?) and soil physical properties effects.Sands, R *et al.* (1978); Nambiar, E.K.S. *et al.* (1992); Sheriff, D.W. *et al.* (1995); Zou, C. *et al.* (2000); Constantini, A. *et al.* (2001); Zou, C. *et al.* (2001) However, little research has been completed to determine how above- and belowground biomass is affected by soil and site conditions, and how silvicultural treatments affect these relationships.

To meet these needs, we investigated the effects of silvicultural manipulations designed to ameliorate soil strength, water and nutrient limitations, on the productivity of 3- and 4-year-old radiata pine plantations established across an environmental gradient in the Central Valley of Chile. Our objective was to quantify how silvicultural treatments affected above- and belowground allocation and growth efficiency across a range in soil site conditions.

Materials and methods

Site characteristics

We measured radiata pine growth during the third and fourth growing seasons as part of a larger study examining subsoiling, weed control and fertilization effects at three sites in the Central Valley of Chile (Table 1). The soil types were andesitic-basaltic dry sands (DS), old volcanic ash red clay soils (RC) and recent volcanic ash loamy soils (RV). Monthly meteorological data were available from weather stations within 20 km of each site. Rainfall at the DS, RC and RV sites was 1313, 1194 and 1611 mm year^{-1} in 2002, and 785, 967 and 1240 mm year^{-1} in 2003, respectively. Phenologic year (July to June) rainfall for the DS, RC and RV sites was 972, 972 and 1260 mm for 2002–2003 (third growing season), and 874, 1086 and 1389 mm for 2003–2004 (fourth growing season), respectively. The RV site was a first rotation plantation on a pasture, and the DS and RC sites were second rotation cutovers. Site index (20 years) and productivity estimates (24 years) were 14.9 m and 7.8 m^3 ha^{-1} year^{-1} for the DS site, and 24.4 m and 15.5 m^3 ha^{-1} year^{-1} for the RC site (Forestal Mininco S.A., 2001). At the DS site, herbaceous competition was dominated by *Rumex acetosella* and *Verbascum densiflorum*, and common woody shrubs were *Rubus ulmifolius* and *Baccharis linearis*. At the RC site, herbaceous competition was dominated by *Hypericum perforatum*, *Rumex acetosella*

and *Plantago lanceolata*, and common woody shrubs were *Rubus ulmifolius* and *Rosa eglanteria*. At the RV site, herbaceous competition was dominated by *Cynodon dactylon*, *Lolium* spp. and *Rumex acetosella* and no woody shrub species were found.

Experimental design

The planned experimental design and treatment applications were the same at each site. However, soil tillage treatments were applied prior to plot establishment because of logistical issues related to the timing of tillage operations. The tillage main plots were randomly applied at each site and no bias was observed in plots established in different tilled areas, consequently we completed the analysis as a split-plot design with whole plots testing soil tillage effects (S0 = shovel planting, S1 = subsoiling + bedding + shovel planting). Whole plots were arranged in four blocks, and a factorial combination of weed control (W0 = site preparation treatment, W1 = site preparation treatment + 2-year banded) and fertilization (F0 = boron at establishment, F1 = nitrogen, phosphorus and boron at establishment + nitrogen, phosphorus, potassium and boron after 2 years) were installed in each block as subplots. Treatment plots were 0.4 ha with an internal measurement plot of 0.09–0.12 ha that included 100 trees plot^{-1} and all of these trees were measurement trees.

Tillage treatments were applied February–March 2000. Tillage was shovel planting alone or shovel planting combined with 80 cm deep subsoiling and bedding (20 cm bed height). In May and June 2000, a broadcast vegetation control treatment (glyphosate 2 kg ha^{-1} + atrazine 3 kg ha^{-1} + galactic surfactant 1 ml l^{-1}) was applied by backpack sprayers before planting. The glyphosate was Roundup Max with 48.7 per cent glyphosate (*N*-(phosphonomethyl) glycine) from Moviagro S.A. in Chile. The atrazine was Atrazine 90 WG with 90 per cent p/p dispersed granules of atrazine (2-chloro-4 ethylamino-6-isopropylamino-s-triazine) from ANASAC in Chile. Galactic is a blend of organosilicone and nonionic surfactants designed to improve herbicide performance. Bareroot 1–0 (1–0 indicates 1 year in the seed bed and 0 years in the transplant bed before planting to the field) radiata pine cuttings of one full-sib family were planted at each site (Table 1) in June and July 2000. The DS site was planted at a 4.0 × 2.0 m spacing (1250 trees ha^{-1}) and the RV and RC sites were planted at a 2.0 × 5.0 m spacing (1000 trees ha^{-1}). In September and October 2000, weed control treatments were applied by hand as glyphosate 2 kg ha^{-1} + atrazine 3 kg ha^{-1} + galactic surfactant 1 ml l^{-1}) in a 2 m wide band centred on the planting row. The planted pines were sheltered from the spray. A second chemical weed control treatment was applied in September and October 2001 using the same chemicals, rates, and application method. All trees received 1.5 g plant^{-1} of elemental boron applied in September 2000. Trees in the fertilized plots also received 29.5, 32.4 and 1.5 g plant^{-1} of elemental nitrogen, phosphorus and boron, respectively, applied at the same time (September 2000). Fertilized trees received a second application with 29.5, 32.4, 25.0 and 3.0 g plant^{-1} of elemental nitrogen, phosphorus, potassium and boron, respectively, in September 2002. In September 2000, fertilizer was applied around each cutting; in September 2002, fertilizers were applied in the planting

Table 1 Site and stand information for the three sites examined in this study

Site name	Recent volcanic ash (RV)	Dry sands (DS)	Red clay (RC)
Latitude and longitude	39° 4′ 40″ S	37° 10′ 40″ S	37° 50′ 43″ S
	72° 24′ 23″ W	72° 15′ 47″ W	72° 20′ 5″ W
Mean annual temperature (°C)	10.7	13.7	13.3
Mean annual rainfall (mm year^{-1})	2180	1160	1100
Geology	Recent volcanic ash	Volcanic sands	Red clay – old volcanic ash
Soil taxonomic name	Medial, mesic typic haploxerands	Fragmental, thermic dystric xerorthents	Very fine, mixed, thermic typic rhodoxeralfs
Drainage	Well	Somewhat excessively well	Well
Family genotype	MP31	IF24	MP31

row band. Total nutrient additions for the F1 treatments on the RC and RV sites were 59.0, 64.8, 25.0 and 4.5 kg ha^{-1} for nitrogen, phosphorus, potassium and boron, respectively. Additions at the DS site were 73.7, 81.0, 31.3 and 5.6 kg ha^{-1} for nitrogen, phosphorus, potassium and boron, respectively.

Growth measurements

Tree height and diameter (at breast height, 1.35 m) were measured on all measurement trees in the winter (July–August) after the third and fourth growing seasons.

Biomass measurements

In August and September 2004, biomass measurements of foliage, branch, stem and coarse and fine root were completed on the S0F0W0, S0F1W1 and S1F1W1 treatments corresponding to a low (LIT), medium (MIT) and high (HIT) intensity treatment level, respectively. These treatments were selected to provide a range in tree size across treatment to facilitate regression equation development for the biomass equations described later in this section. In addition, these treatments allowed examination of weed control effects on aboveground biomass at each site and allowed us to determine if the site preparation treatment caused any belowground changes given that no aboveground effects were observed for site preparation treatment. We sampled the range of tree sizes at each site and treatment based on the year 3 measurements.

Aboveground biomass

Twelve trees (four trees in each of the three treatments) were selected at DS and RC sites, and 10 trees were selected at the RV site. Trees were cut at the ground line and divided into stem and branches. Starting at 10 cm above ground level, stem discs were cut from the bole every 1 m at the DS and RC sites, and every 2 m at the RV site. Green weights of stem discs and bole sections were recorded in the field. Stem discs were dried at 70°C to a constant weight. The average ratio of dry mass to fresh mass of the discs from either end of each stem section was used to estimate the dry mass of the stem section. All stem disc and bole section

dry weights were summed for each tree. We measured branch diameter and distance from the tree top for all branches on each felled tree. We selected between 6 and 28 branches per tree across the range of branch diameters and relative distance from the tree top found on the felled trees. Foliage and branch tissues were separated for each sampled branch and dried at 70°C to a constant weight. We developed a relationship between branch or foliage biomass and relative distance from the top and branch diameter from the sampled branches and then used the relationship to estimate branch or foliage biomass for the other branches. These estimates were summed by tree to estimate total tree branch and foliage biomass.

Belowground biomass estimates

We excavated 1 × 1 × 1 m soil pits centred on the felled trees to estimate coarse (>2 mm diameter) and fine root (≤2 mm diameter) biomass. We had a fixed amount of resources (time and labour) at each site and continued excavating pits until we exhausted our resources. The order of excavation difficulty was RV > RC > DS, so we were able to excavate more pits at the DS site compared with the RC site and more pits at the RC site compared with the RV site. Consequently, we sampled 1, 2 and 3 trees per treatment at the RV, RC and DS sites, respectively. Pits were excavated in 0.2 m layers. Fine roots were sampled by hammering six randomly distributed cores (5 cm diameter × 7.5 cm height) into the top of each layer before excavation. At the DS site, fine roots were removed from the core by hand using tweezers after sieving the soil through a 0.5 mm mesh colander. At the RC site, the core was washed through a 0.5 mm mesh colander over a pan filled with water and then through a 0.2 mm mesh colander. Roots were captured in the colanders or floating in the pan. At the RV site, a combination of sieving and washing procedures was applied based on soil–root adherence related with clay content of the sample. Coarse roots were removed from the soil by sieving each layer through a 5 mm mesh screen. Coarse roots were washed to remove soil particles. Roots were kept cool in the field and transported to the laboratory where they were maintained at 4°C until

Table 2 Statistical significance (P-value < 0.05)[1] of soil tillage, fertilization and weed control and their interactions for 4 year height (H), diameter (DBH), basal area (BA), survival (SURV), standing volume (VOL) and volume growth in year 4 (VOLINC) for *Pinus radiata* at three sites (DS – dry sandy soil, RC – red clay soil, RV – recent volcanic ash soil) in Chile

	H	DBH	BA*	SURV*	VOL*	VOLINC*
Effects	DS site					
Soil tillage (S)	**0.0178**	0.4001	**0.0371**	**0.0033**	0.0737	0.1833
S × F	0.0876	0.1320	0.1474	0.2619	0.7408	0.8736
S × W	0.1420	0.1265	0.3894	**<0.0001**	0.6826	0.6435
Fertilization (F)	**0.0047**	**0.0002**	**0.0003**	0.1487	0.1015	0.3762
Weed control (W)	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
F × W	0.3158	0.0782	**0.0080**	0.4160	0.4672	0.6274
S × F × W	0.7088	0.9670	0.6911	0.6785	0.3556	0.6736
Effects	RC site					
Soil tillage (S)	0.9986	0.8285	0.6760	0.1861	0.9324	0.9970
S × F	0.5804	0.4258	0.3875	**0.0397**	0.5022	0.3226
S × W	0.2070	0.1393	0.2392	0.4396	0.1102	0.1449
Fertilization (F)	0.2114	**0.0055**	**0.0091**	0.6575	**0.0073**	**0.0033**
Weed control (W)	**<0.0001**	**<0.0001**	**<0.0001**	0.0785	**<0.0001**	**<0.0001**
F × W	0.6929	0.6985	0.4053	0.3159	0.9444	0.9015
S × F × W	0.6007	0.5081	0.4098	0.6575	0.5269	0.5236
Effects	RV site					
Soil tillage (S)	**0.0157**	0.1521	**0.0323**	0.9182	**0.0415**	**<0.0001**
S × F	0.9718	0.5584	0.9928	0.5296	0.8198	0.5818
S × W	0.1223	0.0545	0.3365	0.0901	0.1346	0.4011
Fertilization (F)	**0.0161**	0.8888	0.5250	0.1947	0.1210	**0.0208**
Weed control (W)	**<0.0001**	**<0.0001**	**<0.0001**	**0.0321**	**<0.0001**	**<0.0001**
F × W	0.0738	**0.0319**	0.1285	0.5674	0.1348	0.5156
S × F × W	0.3634	0.2990	0.4948	0.2502	0.5343	0.8477

*Analyses were performed on transformed data using square root and logarithmic transformations to correct for heterocedasticity of basal area, survival, volume and volume increment estimates.
[1]Bold numbers indicate a P-value < 0.05.

further processing. Roots were oven-dried to a constant weight at 70°C.

Leaf area

Foliage was separated from each branch and separated by year produced and branch order. Fifteen to 20 fascicles were randomly chosen from each year and branch order for specific leaf area determination. After selection, the fascicles were refrigerated at $<1^\circ$C until processed. Projected leaf area of each sample was estimated using an optical projection system (AT Delta-T Devices Ltd.). The samples were then oven-dried, weighed and specific leaf area was calculated by dividing projected area estimates by sample dry weight. The remaining foliage was oven-dried at 70°C to a constant weight. Leaf area estimates for a whole branch were obtained by multiplying specific leaf area by foliage dry weight for each foliage year-branch order class.

Data analyses

Cumulative and growth measurements

Individual stem volume was estimated using a function developed for young and intermediate radiata pine stands by Forestal

Mininco S.A.:

$$
\begin{aligned}
\text{VOL} = (&-0.00214 + 0.0000295 \times \text{DBH}^2 + 0.001349 \\
&\times \text{DBH}^2 \times \text{H}) \times (1 - 0.044974 \\
&\times (91.56081 \times \text{DBH}^{-2.528804}))
\end{aligned}
\tag{1}
$$

where VOL is individual tree volume ($\text{m}^3 \text{ tree}^{-1}$), DBH is diameter at breast height (cm) and H is tree height (m). Volume increment was calculated subtracting 2003 from 2004 individual tree volume estimates.

Stand biomass and allocation of production

We developed site- and treatment-specific regression equations to estimate individual tree foliage, branch, stem, coarse root and fine root mass and leaf area from diameter at breast height.Rubilar, R.A. *et al.* (2010) We used the equations to estimate tree biomass; summed tree data by plot and scaled to a hectare basis. The tree leaf area data were summed by plot and divided by 10000 to estimate leaf area index (LAI). Total biomass was the sum of above- and belowground components. Given that we identified site- and treatment-specific individual tree biomass

equations, we limited our biomass analysis to treatments where we completed the biomass harvests.

Stand LAI, foliage mass and growth relationships

We investigated relationships among LAI and incremental growth at the stand level using a linear regression approach to test site and treatment effects on the slope coefficients.Albaugh, T.J. *et al.* (1998) In this case the population of interest is radiata pine in Chile; these models omitted block and whole-plot effects. The full model was as follows:

$$\ln(Y_{ij}) = a + b_i \times Z_i + c \times \ln(X_{ij}) + d_i \times Z_i \times ln(X_{ij}) + \varepsilon_{ij}, \tag{2}$$

where Y_{ij} is volume increment $(\text{m}^3 \, \text{ha}^{-1} \, \text{year}^{-1})$ and X_{ij} is LAI $(\text{m}^2 \, \text{m}^{-2})$ or foliage mass $(\text{kg} \, \text{ha}^{-1})$ for the jth plot and i^{th} site-treatment combination; Z_i is an indicator variable for the ith site-treatment combination with values of $1 = $ DS-LIT, $2 = $ DS-MIT and HIT, $3 = $ RC-LIT, $4 = $ RC-MIT and HIT, $5 = $ PC-LIT, $6 = $ PC-MIT and HIT; ε_{ij} is the error of the model; j is $1, \ldots n_i$ plot in the ith site-treatment combination; a, b_i, c and d_i are parameters to be estimated. If no difference in slope was found, the interaction term was dropped and a reduced model was used to test for intercept differences between regression equations:

$$\ln(Y_{ij}) = a + b_i \times Z_i + c \times \ln(X_{ij}) + \varepsilon_{ij}, \tag{3}$$

where all variables in equation (3) are the same as those in equation (2). If the slopes or intercepts were different, independent regression equations were generated for sites and/or treatments using the following equation:

$$\ln(Y_{ij}) = a + b_i \times \ln(X_{ij}) + \varepsilon_{ij}, \tag{4}$$

again where all variables in equation (4) are the same as those in equation (2). Regression models were selected using R^2 values, residual analyses, variance inflation factors and Mallow's Cp statistics.Rawlings, J.O. *et al.* (2001) All significance tests were at the $P < 0.05$ level.

Stand growth and biomass analysis of variance analyses

A mixed model considering block and whole plots as random effects was used for analyzing the split-plot experimental design for all growth parameters:

$$y_{ijkl} = \mu + r_k + \alpha_i + w_{ik} + \beta_j + \delta_l + (\alpha\beta)_{ij} + (\alpha\delta)_{il} + (\beta\delta)_{jl}$$
$$+ (\alpha\beta\delta)_{ijl} + \varepsilon_{ijkl}, \tag{5}$$

where:

y_{ijkl} is dependent variable (height, DBH, basal area, survival, volume, volume increment and LAI plot mean);
μ is the overall mean;
r_k is the kth block effect assumed iid $N(0, \sigma_r^2)$;
α_i is the effect of the ith level of tillage;

w_{ik} is the whole-plot error effect, assumed iid $N(0, \sigma_w^2)$;
β_j is the effect of the jth level of fertilization;
δ_l is the effect of the lth level of weed control;
$(\alpha\beta)_{ij}$ is the ijth soil tillage $\times$ fertilization interaction effect;
$(\alpha\delta)_{il}$ is the ilth soil tillage $\times$ weed control interaction effect;
$(\beta\delta)_{jl}$ is the jlth fertilization $\times$ weed control interaction effect;
$(\alpha\beta\delta)_{ijl}$ is the ijlth soil tillage $\times$ fertilization $\times$ weed control interaction effect;
ε_{ijkl} is the split-plot error effect, assumed iid $N(0, \sigma^2)$;
w_{ik} and ε_{ijkl} are assumed to be independent of one another.

Statistical analyses were performed using SAS software version 9.1 modules PROC GLM, and PROC MIXED using the Satterthwaite degrees of freedom option.SAS Institute (2002) Graphical analyses were performed using JMP (version 5.1.2).SAS Institute (2002) To reduce the heterocedasticity of the data, a square root transformation was used for basal area and survival, and a logarithmic transformation applied to volume.Steel, R.G. *et al.* (1980)

Results

Cumulative and growth measurements

Weed control significantly increased year 4 height (17–45 per cent), diameter at breast height (12–62 per cent), basal area (28–200 per cent), volume (40–277 per cent), volume increment (28–300 per cent) and survival (3–32 per cent) at all sites (Tables 2 and 3). Fertilization significantly increased height (33 per cent), diameter (45 per cent) and basal area (68 per cent) at the DS site; diameter (40 per cent), basal area (56 per cent), volume (52 per cent) and volume increment (54 per cent) at the RS site; height (21 per cent) and volume increment (16 per cent) at the RV site (Tables 2 and 3). Soil tillage had no significant effects at the RC site, whereas it significantly increased height (5 per cent), basal area (17 per cent) and survival (13 per cent) at the DS site and significantly decreased height (6 per cent), basal area (9 per cent) and volume (12 per cent) at the RV site. An interaction was detected between fertilization and weed control at the RV site, where diameter was reduced 5 per cent when fertilizer was applied without weed control whereas diameter increased 17 per cent when fertilizer was applied with weed control. At the DS site, basal area increased 300 per cent when weed control and fertilization were applied together, compared with a 0 per cent response when fertilizer was applied alone. At the DS site, a soil tillage by weed control interaction was observed for survival, with gains of 24 and 32 per cent, when soil tillage was applied with and without weed control, respectively.

Stand biomass and allocation of production

Within site, the largest responses to treatments were observed at the DS site where stem biomass in the S1F1W1 treatment was 250 per cent greater than that found in the control treatment (Table 4). The lowest responses were at the RV site where stem biomass gains in the S1F1W1 was 33 per cent. In the control

Table 3 Four-year treatment means and standard errors of height (H), diameter (DBH), basal area (BA), survival (SURV), volume (VOL) and volume increment (VOLINC) for *Pinus radiata* at three sites (DS – dry sands, RC – red clay, RV – recent volcanic ash) in Chile

Treatment	DS site						RC site						RV site					
	H (m)	DBH (mm)	BA (m² ha⁻¹)	SURV (%)	VOL (m³ ha⁻¹)	VOL INC (m³ ha⁻¹ year⁻¹)	H (m)	DBH (mm)	BA (m² ha⁻¹)	SURV (%)	VOL (m³ ha⁻¹)	VOL INC (m³ ha⁻¹ year⁻¹)	H (m)	DBH (mm)	BA (m² ha⁻¹)	SURV (%)	VOL (m³ ha⁻¹)	VOL INC (m³ ha⁻¹ year⁻¹)
Control	2.24	26	0.6	75	1.3	0.9	3.39	42	1.5	99	4.3	3.7	5.81	103	7.9	92	23.0	17.4
S	2.22	24	0.6	93	2.1	1.6	3.52	44	1.7	99	4.7	3.9	5.22	94	6.8	95	18.3	13.8
S + F	2.42	29	0.8	92	2.0	1.5	3.62	50	2.1	100	5.7	4.9	4.94	91	6.3	94	16.9	12.7
S + W	3.31	43	2.0	99	5.7	4.3	4.52	61	3.1	100	9.3	6.8	6.57	116	9.7	89	30.1	18.8
F	2.28	28	0.6	68	1.9	1.4	3.48	47	2.0	98	5.2	4.5	5.41	98	7.2	92	20.2	15.4
W	3.20	42	1.8	99	4.9	3.6	4.76	68	3.8	100	11.4	8.3	6.76	115	10.1	95	32.3	22.2
F + W	3.32	48	2.4	98	6.0	4.4	4.82	72	4.2	100	12.5	9.1	6.78	121	10.5	89	32.7	20.6
S + F + W	3.67	52	2.9	100	7.6	5.3	4.80	71	4.3	100	12.6	9.4	6.44	117	9.7	89	29.6	18.1
Standard errors of differences between means																		
S	1.05	2.46	1.07	4.48	1.12	1.18	1.13	12.2	1.27	1.35	1.07	1.07	1.07	4.06	1.21	3.32	1.04	1.03
S × W, S × F	1.06	3.67	1.11	5.47	1.18	1.27	1.15	16.4	1.32	1.65	1.10	1.09	1.09	6.05	1.27	4.48	1.05	1.05
F × W	1.06	3.67	1.11	4.95	1.18	1.27	1.15	16.4	1.32	1.65	1.10	1.09	1.09	5.47	1.26	4.48	1.05	1.05
F, W	1.05	2.46	1.07	3.32	1.12	1.18	1.12	12.2	1.26	1.35	1.07	1.07	1.07	3.67	1.19	3.00	1.03	1.03
S × F × W	1.08	5.47	1.15	9.03	1.26	1.40	1.19	33.1	1.42	2.01	1.14	1.14	1.13	11.02	1.39	8.17	1.07	1.07

Treatments are subsoiling (S), fertilization (F) and weed control (W). The standard errors examining differences between two means were calculated using transformed data. Here the standard errors are shown in the original scale; however, there is a bias when transforming the standard errors back to original scale.

treatment, total biomass at the RC site was 1.8 times greater than at the DS site; whereas at the RV site, total biomass was 7 times greater than at the DS site. For the S1F1W1 treatment at the RC site, total biomass was 1.3 times greater than at the DS site; whereas at the RV site, it was 2.7 times greater than at the DS site. Fine root mass at the RC site was 0.7 to 0.9 of the fine root mass at the DS site, whereas at the RV site, it was 1.6–4.0 times the fine root mass at the DS site (Table 4). Across sites the above:belowground ratios showed an increasing trend in the order of DS ≤ RC < RV. Proportional production of above- and belowground stand biomass components (foliage, branches, stem, coarse roots and fine roots) varied among sites and treatments (Figure 1). Across sites, a larger proportion of fine roots was observed at the DS site and the lowest proportion of coarse roots was observed at the RV site (Figure 1).

Stand LAI, foliage mass and growth relationships

A positive linear relationship was found between stem volume increment and LAI for a given site (Figure 2A). These relationships indicated that from 80 to 97 per cent of variation in volume growth could be predicted from LAI. However, large differences in the slope of this relationship (growth efficiency) were observed among sites and treatments when forcing the intercepts through zero, emulating a light-use efficiency relationshipGrace, J.C. *et al.* (1987) (Table 5, Figure 2A). Practical differences among the LAI and volume increment equations indicated that similar slopes were observed between the RC and RV sites (6.1 *vs* 7.1). Contrastingly, a smaller slope was observed at the DS site (2.9). Differences in slope estimates across sites indicated that for a LAI value of 2, volume increment among sites would differ by 7 m³ ha⁻¹ year⁻¹, suggesting large differences in growth efficiency in these environments. Similar relationships were observed for total biomass and LAI (Figure 2B).

Discussion

Cumulative and growth measurements

Across all sites, the weed control effects on all cumulative growth variables were larger than the responses to tillage and fertilization. Comparing year 3 (Albaugh *et al.*,Albaugh, T.J. *et al.* (2004)) and year 4 analyses, fertilization effects on diameter and height have been maintained at the DS site. Major changes in response were due to fertilizer effects on diameter at the RC site, tillage and fertilizer effects on height at the RV site and fertilizer by weed control interaction effects on diameter at the RV site. Previous studies in radiata pine have shown that early weed control results in large tree growth responses when severe nutrient limitations do not exist.Gerding, V.R. *et al.* (1991); Woods, P. (1992); Toro, J. (1995); Kogan, M. (2002) Weed control effects on survival at the DS and RV site may be related to reductions in competition for water, nutrients and light, increased rooting volume, removal of allelopathic limitations, or some combination of these.Kogan, M. (2002); Nambiar, E.K.S. (1984) The large rainfall gradient (1100–2180 mm) among sites also suggests that the large weed control effects were associated with increased soil

Table 4 Four-year treatment means of above and belowground biomass accumulation by component, above and belowground biomass ratio and LAI at each site

	Foliage (kg ha^{-1})	Branches (kg ha^{-1})	Stem (kg ha^{-1})	Coarse Roots (kg ha^{-1})	Fine Roots (kg ha^{-1})	Above (kg ha^{-1})	Below (kg ha^{-1})	Ratio	Total Biomass (kg ha^{-1})	LAI (m^2 m^{-2})
Treatment means	**DS Site**									
Control	934	748	985	1578	165	2667	1743	1.53	4411	0.51
F × W	2807	2549	2901	3125	452	8257	3578	2.31	11835	1.66
S × F × W	3221	2982	3457	5190	512	9659	5702	1.69	15362	1.93
	RC Site									
Control	1923	1159	1874	3034	109	4955	3142	1.57	8097	0.64
F × W	3281	3683	5509	5497	337	12474	5834	2.14	18308	1.3
S × F × W	3289	3690	5531	6836	338	12510	7174	1.73	19685	1.3
	RV Site									
Control	6041	7682	8581	7943	665	22303	8608	2.59	30911	2.37
F × W	7984	13686	12328	9253	909	33999	10162	3.35	44161	3.13
S × F × W	7457	12374	11373	8878	843	31204	9721	3.21	40926	2.93

Treatments were subsoiling (S), fertilization (F) and weed control (W). Sites were dry sands (DS), red clay (RC) and recent volcanic ash (RV).

water availability.Nambiar, E.K.S. *et al.* (1980); Gholz, H.L. *et al.* (1994)

Our results support the synergistic effect of weed control and fertilization described at year 3 by Albaugh *et al.*Albaugh, T.J. *et al.* (2004) for this experiment. However, the small responses to nutrient additions suggest that inherent nutrient availability meets plant nutrient demands on these sites. A lack of response to early fertilization of second rotations sites may be expected,

Figure 1 Biomass allocation for *Pinus radiata* where no treatment (control); fertilization and weed control; soil tillage, fertilization and weed control were applied in Chile on three sites: (a) dry sands, (b) red clay soils and (c) recent volcanic ash soils.
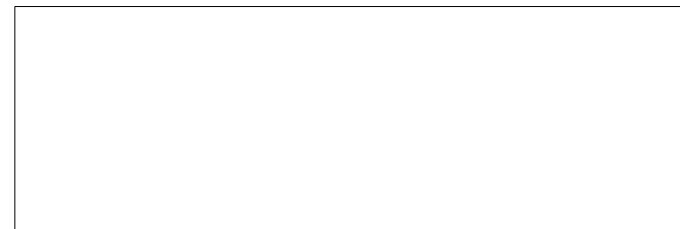

Figure 2 Current annual increment (a) and total biomass (b) *vs* LAI for *Pinus radiata* in Chile on three sites: (▲) dry sands, (□) red clay soils and (●) recent volcanic ash soils.

considering the high soil nutrient supply generated by the decomposition of residues after harvesting,Kimmins, J.P. (1997) and the low demand of young plantations.Allen, H.L. *et al.* (1990); Smethurst, P.J. *et al.* (1990); Fife, D.N. *et al.* (1997) The former pasture at the RV site is characterized by high native soil fertility. The observed negative responses to fertilization, tillage and fertilization by tillage interaction at the RV site may be attributed to weed competition that developed with the added nutrientsGent, J.A. *et al.* (1986) or propagation of weeds in plots receiving site preparation. The small growth responses to the tillage treatments across sites may be attributed to soil structure, the presence of root channels on second rotation sites and low soil strength at the RV site former pasture.Sands, R *et al.* (1978); Sheriff, D.W. *et al.* (1995); Gautam, M.N.K. *et al.* (2003) However, an indirect weed control effect on woody vegetation by tillage may have improved survival at the DS site.

Stand biomass and allocation of production

Empirical data analyses,Schlatter, J.R. *et al.* (1995); Jackson, D.S. *et al.* (1974) highly controlled experimentsRaison, R.J. *et al.* (1992); Benson, M.L. *et al.* (1992); Cromer, R.N. *et al.* (1983) and model simulationsFlores, F.J. (2004); Sands, P.J. *et al.* (2000) have all indicated that radiata pine productivity is highly constrained by water availability. The large responses to weed control and small changes with added nutrients at each site suggest that water availability may be the main reason for the differences in productivity and total biomass accumulation across sites. Weed control effects ranked DS > RC > RV, whereas ambient rainfall ranked RV > RC > DS indicating the relative importance of water limitations across the sites. Nevertheless, the weed control by fertilizer interaction (positive fertilizer response when weed control applied) at the DS site, and the positive fertilizer effects at the RC site, suggest that some nutrient limitations exist at these sites. At the same time, weed control may have had an additional effect by increasing nutrient availability or allowing tree

Table 5 Regression equations comparison between LAI (m^2 m^{-2}) and volume increment ($m^3\,ha^{-1}\,year^{-1}$)

Contrast	Full model	Reduced model
	Homogeneity of slopes (P-value)	Homogeneity of intercepts (P-value)
DS-LIT *vs* MIT & HIT	0.2766	<0.0001
RC-LIT *vs* MIT & HIT	0.2370	0.0119
RV-LIT *vs* MIT & HIT	0.0459	0.1829
DS-MIT & HIT *vs* RC-LIT	0.0143	<0.0001
RC-MIT & HIT *vs* RV-LIT	0.4210	0.9831

Site and treatment silvicultural intensity effects on slope and intercepts (Models (2) and (3)).

Tested models:

(a) Full model: $\ln(Y_{ij}) = a + b \times Z_i + c \times \ln(X_{ij}) + d \times Z_i \times \ln(X_{ij}) + \varepsilon_{ij}$

(b) Reduced model: $\ln(Y_{ij}) = a + b \times Z_i + c \times \ln(X_{ij}) + \varepsilon_{ij}$,

where, X_{ij} is LAI and Y_{ij} is volume increment of the jth plot at the i site-treatment combination.

Z_i indicator variable value at the ith site-treatment combination with values: 1 = DS-LIT, 2 = DS-MIT & HIT, 3 = RC-LIT, 4 = RC-MIT & HIT, 5 = RV-LIT, 6 = RV-MIT & HIT. DS = dry sand site; RC = red clay site; RV = recent volcanic ash site; LIT, MIT and HIT are low, medium and high intensity of silviculture treatment, respectively.

ε_{ij} is the error of the model.

$i = 1$–6 site-treatment combination.

$J = 1, \ldots n_i$ plot in the ith site-treatment combination.

crops access to limited nutrients. Comparing the same treatments across site, it appears the magnitude of differences in total aboveground biomass component and coarse root mass decreased with increasing intensity of silviculture. At the same time, tree size is also increasing with increasing silvicultural intensity. Root:stem ratio changes with changing stem diameter where the root:stem ratio increased in small trees (up to ∼10 cm DBH)Ovington, J.D. (1957); Adegbidi, H.G. *et al.* (2002) and then decreased as the DBH increased beyond 10 cm.Ovington, J.D. (1957); Albaugh, T.J. *et al.* (2006) Soil water holding capacity of the DS and RC soils differs by more than 10-fold (data not shown) and there is close agreement between the differences in water holding capacity and differences in total biomass accumulations on the controls and weed control treatments. The combination of these factors likely contributes to the observed responses. However, given there is overlap in tree sizes at the two sites and the magnitude of difference in water holding capacity, water holding capacity differences are likely to be the more influential factor. Consequently, these results suggest that the manipulation of site resources by silvicultural treatments has effectively reduced the environmental constraints on tree growth or has provided preferential access to site resources.Albaugh, T.J. *et al.* (2004)

Lower productivity for a similar LAI was observed at the DS site compared with the RC site. Trade-offs between maintenance of foliage and tree growth in water-limited environments have been suggested.Warren, C.R. *et al.* (2000) In fact, greater foliage longevity was observed in the DS compared with the RC sites.Kirongo, B.B. *et al.* (2002)

Negative responses to fertilization in aboveground growth observed at the DS and RV sites is in agreement with previously reported reductions in growth and aboveground biomass with fertilization but without weed control of radiata pine.Toro, J. (1995); Kogan, M. (2002); Nambiar, E.K.S. (1990) Previous detailed work conducted in an older stand on a water-limited site (annual rainfall 700 mm year^{-1}) in northern Chile found that foliage mass was not affected by repeated annual fertilization.Rodriguez, R. *et al.* (2003) The lack of tree growth or foliage mass response suggests that the limiting growth factor at this site was not applied.Flores, F.J. (2004); Albaugh, T.J. *et al.* (2004) Alternatively, fertilization may have disproportionately benefited the competing vegetation that permitted the competition to grow faster and deplete resources like water and light at the expense of the crop pine trees.

Given the soil textural conditions, a larger effect of tillage was expected at the RC site but not at the DS site with its loose structured sandy soil. A lack of large responses to tillage, across soil textural classes, has been observed before and has been attributed to improved soil structure or remnant root channels from previous stands.Carlson, C.A. *et al.* (2006) Soil preparation may have affected biomass allocation at the DS site increasing our estimates of belowground biomass. This response is not surprising, as roots are known to follow the path of least penetration resistance in the soil. More compacted soils have been found in second rotation sites previously planted with *P. radiata* stands,Sands, R *et al.* (1978); Sheriff, D.W. *et al.* (1995) which is the case of the DS and RC sites.

Taking into account differences in biomass components between the DS and RC sites, fine roots showed the largest differences between sites (4 *vs* 2 per cent). Increased allocation to belowground components, and specifically to fine roots, has been suggested as one of the major mechanisms for trees to improve their ability to capture scarce site resources under nutrient and water deficient conditions.Albaugh, T.J. *et al.* (1998); Dewar, R. (1997); Nadelhoffer, K.J. *et al.* (1992) Fine root production has one of the highest respiratory costs, reducing net primary productivity.Keyes, M.R. *et al.* (1981); Marshall, J.D. *et al.* (1985); Ryan, M.G. *et al.* (1996) Differences in soil temperature may also accelerate fine root turnover and become a compensation mechanism for plant growth.Marshall, J.D. *et al.* (1985) Undoubtedly, large differences in specific heat and conductivity of dark sands and clay textures may favour a temperature effect on fine root production. In addition, genetic differences may account for differences in carbon balance between sites and treatments.Snowdon, P. (1985); Li, B.L. *et al.* (1991)

Belowground growth increased at the expense of the aboveground components under conditions of reduced resource availability (water and nutrients). The same was observed within sites when comparing weed control treatments that effectively increased resource availability. However, our ratio and belowground estimates need to be interpreted with caution, because a preferential root growth pattern may have occurred at the DS site in response to subsoiling treatments. This would have increased our belowground estimates when sampling $1\,m^3$ soil volumes centred in the line of site-prepared soil.

Stand LAI, foliage mass and growth relationships

LAI, an index of photosynthetic area intercepting radiation,Landsberg, J.J. *et al.* (2011) determined stand volume growth across sites. The strong linear relationship with the volume increment was expected given similar results reported for radiata pine in Australia and New Zealand.Linder, S. (1987); Raison, R.J. *et al.* (1992); Grace, J.C. *et al.* (1987) Similar strong relationships have been found for others species in a variety of environments.Vose, J.M. *et al.* (1988); Cannell, M.G.R. (1989); Linder, S. (1987) Large responses to weed control and small responses to fertilizers, suggest that water availability may be the primary factor limiting foliage production, LAI and productivity at our sites (Figure 2A,2B). Water availability and water stress have been shown to strongly affect radiata pine foliage production and longevity, as well as photosynthesis, carbon fixation, and, ultimately, tree growth.Raison, R.J. *et al.* (1992); Benecke, U. (1980) Similar responses have been reported for nutrient additions in loblolly (*Pinus taeda* L.) pine in the southeastern United States.Albaugh, T.J. *et al.* (1998); Colbert, S.R. *et al.* (1990); Vose, J.M. *et al.* (1991)

Changes in the slope of the relationship between LAI and growth indicate large differences in growth efficiency at our sites. Similar results have been reported for radiata pine and other species.Linder, S. (1987); Teskey, R.O. *et al.* (1987); Jokela, E.J. *et al.* (2004); Albaugh, T.J. *et al.* (2004) In other studies, increases in growth efficiency for radiata pine have been obtained with increases in water and nutrient availability.Raison, R.J. *et al.* (1992); Linder, S. *et al.* (1987) Stope *et al.*Stape, J.L. *et al.* (2004) found that water supply and demand (vapor pressure deficit) played a large role in the growth efficiency of eucalyptus plantations in Brazil by affecting carbon allocation and reducing stemwood production efficiency. Similar results have been found for other species in water-limited environments.Linder, S. *et al.* (1987) Albaugh *et al.*,Albaugh, T.J. *et al.* (2004) in a long-term nutrient × water experiment with loblolly pine, found increases in growth efficiency caused only by nutrient additions. However, given the rainfall regime of the area (~1200 mm year^{-1}, well distributed throughout the year), water limitations at this site were sporadic compared with chronic nutrient limitations at our DS site. The Sampson and AllenSampson, D.A. *et al.* (1999) model for loblolly pine in the southeastern United States suggested considerable differences in growth efficiency across the region. However, the authors concluded that despite growth efficiency differences across environments, differences in LAI accounted for the largest variation in productivity on a regional scale. Our results for the DS and RC sites do not suggest that LAI alone accounts for productivity differences on a regional scale without considering soil-site conditions. Jokela *et al.*Jokela, E.J. *et al.* (2004) presented a comprehensive report of seven experiments in loblolly pine plantations including irrigation, weed control and fertilization across the southeastern United States. They concluded that growth efficiency changes were related to nutrient availability across sites. Allen *et al.*Allen, H.L. *et al.* (2005) suggested that water limitations were less important in influencing leaf area than were nutrients, due to leaf area being developed in the spring when high soil water availability exists. However, they indicated that the typical low water availability during the summer

together with increased evapotranspiration constrained growth efficiency. This would likely explain the large differences in growth efficiency between the DS and RC sites sustaining similar foliage mass.

The growth efficiency reductions at higher levels of leaf area have been attributed to higher respiration costs of a larger foliage mass.Teskey, R.O. *et al.* (1987); Vose, J.M. (1988); Maier, C.A. *et al.* (2004) At the RV site, our data suggest increased variability in growth efficiency at levels of LAI greater than two. Jokela *et al.*Jokela, E.J. *et al.* (2004) also showed increased variation and reduction in growth efficiency for LAI greater than three. Our growth efficiency estimates suggest increased variation, but not productivity declines; at the RV site the LAI was around three. Stand density differences among sites are not likely to account for the large differences observed in LAI, volume or volume increment responses. The lowest productivity and lowest LAI levels were observed at the DS site with 250 more trees per hectare compared with the RC and RV sites. Differences in growth efficiency have been associated with genetic material and its interaction with nutrition.Li, B.L. *et al.* (1991); Teskey, R.O. *et al.* (1987); Allen, H.L. *et al.* (2005) That a different genotype was planted at the DS site may account for the lower growth efficiency at this site. However proportionally, the lack of genetic × environment interactions at the genotype level and volume gains in the order of 10–30 per cent are not likely to be the only explanation for our observed differences in productivity among sites.Allen, H.L. *et al.* (2005); McKeand, S.E. *et al.* (2003)

Our results suggest that large differences in growth efficiency in Chile may be driven by differences in soil water availability and moisture constraints. Previous potential productivity modelling efforts using 3PG in ChileFlores, F.J. (2004) also suggest that water availability constraints may be responsible for variation in stand productivity. Our empirical estimates at each site agree with model outputs obtained by Flores and AllenFlores, F.J. (2004) after a linear reduction in LAI from 4.0 (model assumption) to our empirical values. For example, the model-predicted $32 \, \text{m}^3 \, \text{ha}^{-1} \, \text{year}^{-1}$ for a 2000 mm rainfall site were slightly higher than RV estimates. The simulations from Flores and AllenFlores, F.J. (2004) used a LAI of 4.0, whereas our maximum observed LAI was 3.0, modelled productivity at the RV site would be 75 per cent of potential productivity or $24 \, \text{m}^3 \, \text{ha}^{-1} \, \text{year}^{-1}$. The same approach indicated a good agreement with the RC site but not for the DS site estimates. Estimates of potential productivity and LAI relationships for the DS site differ from model estimates even when the lowest level of soil water holding capacity is considered. This emphasizes the importance of our experiment for understanding how soil-site characteristics influence site productivity and for producing valuable data to validate and calibrate models estimates. Climatic factors such as air temperature and vapor pressure deficit need to be considered as drivers of evapotranspiration,Whitehead, D. *et al.* (1983) and therefore plantation use of available soil water.

The large differences in current productivity among our sites, and the large response to silvicultural treatments at each site suggest that manipulation of site resources to improve current productivity of radiata pine plantations is possible. If site-specific water limitations are ameliorated by irrigation, by using genetic material with higher water use efficiency, by thinning regimes to reduce evapotranspiration and interceptionHuber, A. *et al.*

(2001) or by reduced soil evaporation, then gains in productivity may be expected. Economic analyses have indicated that such investments may become financially attractive.Sands, P.J. *et al.* (2000)

Conclusions

At each site, above- and belowground tree growth, total biomass, above:belowground biomass ratio and LAI increased largely due to weed control. The magnitude of differences in total aboveground mass and coarse root mass decreased with increasing silvicultural intensity across sites. The large gradient of tree growth and biomass accumulation among sites, and within sites varying by response to weed control, was attributed to large differences in soil water availability and potential water stress differences among sites. A linear relationship was established between LAI and stand growth across sites. Differences in the slope of the relationship between LAI and stand growth (stemwood growth efficiency) were related to water and nutrient limitations.

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