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Physiological response to pruning severity in *Eucalyptus regnans* plantations

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Abstract The photosynthetic response to pruning was measured in two *Eucalyptus regnans* stands, aged 2 and 3 years, located in areas of high productivity on the coast of the province of Arauco, Chile. Variables such as rates of CO_2 assimilation and stomatal conductance were measured in three ages of foliage on trees with different pruning severity treatments, which corresponded to the removal of 0 % (control), 30, 50 and 70 % of live crown length. The 2-year-old stand measurements were performed at the time of pruning and 6, 10, 14 and 18 weeks later, and the 3-year stand, 5, 9, 18 and 28 weeks after pruning. In both trials, significant differences were found between the foliage ages for all instances of measurement showing the mature foliage the highest values up to 30 % higher than old foliage. There were also significant differences between pruning severity treatments in both trials in which, in general, the highest values of CO_2 assimilation were observed among the highest pruning severity treatments with values up to 40 % higher than the unpruned trees.

Keywords Photosynthesis · Stomatal conductance · Pruning severity · Compensatory response to pruning

Introduction

All over the world there is an increasing social pressure on protecting natural forests which were the principal source of solid wood, for that reason wood producers are looking for

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Eucalyptus plantations as an alternative to produce high value timber (Donnelly et al. 2003; Flynn 2003; Sedjo 1999; Wardlaw et al. 2003).

Obtaining high-value wood products requires maximizing timber production free of knots and other defects. Senescence processes and ejection branch occlusion control the formation of knots and other defects associated with the timber (Montagu et al. 2003). Because many species of Eucalyptus do not naturally lose basal branches quickly enough for solid-wood production, producing defect-free wood from them requires pruning. However, this activity could affect the rate of growth of trees. Severe pruning carried out at a young age helps minimize the size of the defective cylinder yet involves a significant reduction in the leaf area, a growth-related variable since it determines the tree's ability to absorb carbon, the basic element to make photosynthesis and to produce carbohydrates (Pinkard and Beadle 1998a).

The severity of pruning a tree can bear without reducing its growth rate varies greatly between species. Among the factors that would explain the response, in addition to the quantity of radiation reaching the different parts of the crown and patterns of biomass distribution in the crown, is the intensity of compensatory physiological response to pruning. Trees have the ability to decrease the impact of pruning on growth through physiological responses like changes in resources allocation patterns that favour leaf area development and modify the leaf morphology but principally increasing the assimilation rate of carbon dioxide (CO_2) (Alcorn et al. 2008; Maurin and DesRochers 2013; Pinkard and Beadle 1998a, 2000). Different authors have reported this type of response. Pinkard et al. (1998) reported a 170 % photosynthetic rate increase after pruning in *Eucalyptus nitens*. Increases in photosynthetic capacity were also found in *Acacia melanoxylon* after a pruning that reduced the crown size by 50 % (Medhurst et al. 2006). Another variable that has been measured in response to pruning is the stomatal conductance, which usually presents linear, logarithmic or exponential relationships with photosynthetic capacity (Medrano et al. 2002; Pinkard 2003; Medhurst et al. 2006).

Generally pruning is done at the moment of canopy closure. In that moment the basal area of the crown it's receiving a very little amount of light so photosynthetic rates of these part of the crown are very low (Alcorn et al. 2008; Pinkard and Beadle 2000). The useful radiation to be used by the plant to perform photosynthesis is called the "photosynthetic photon flux density" (PPFD) and its relationship to the photosynthetic capacity can be described as a rectangular hyperbola (Sands 1995).

In Chile, forestation with *Eucalyptus regnans* starts 30 years ago and there are currently more than 1,200 ha of *E. regnans*, a species with high growth rates, exceeding even the species that dominates the production of sawn lumber in Chile, *Pinus radiata* D. Don. These plantations are destined for high-value wood products requiring the implementation of early and severe pruning as part of the forestry management to produce defect-free timber. Although this activity is common in plantations of this species, the definition of pruning schemes is done based on other species due to the limited information that exists on management of *E. regnans* in Chile. In order to maximize the production of *E. regnans* clear wood its necessary to study the impact of pruning on physiological variables that determine the growth rates of these plantations. The aim of this study is to assess the effect of different severities of pruning in physiological variables, in plantations of 2- and 3-year-old *E. regnans*, destined for the production of knot-free wood, located near the coast of Arauco province, Biobío region, Chile.

Materials and methods

Description of the area of study

There were two pruning severity trials established in 2- and 3-year-old *E. regnans* stands, established in 2009 and 2008 respectively. Both stands were established in October, with spacing of 2.5 m within row, and 4 (2009 plantation) and 6 m (2008 plantation) between rows, giving a stocking of 1,000 and 667 stems per ha (sph) respectively. In both cases, mechanical weed control was carried out prior to planting, and fertilizer (60 g/plant of NPK) was applied at the time of establishment. Plants of both trials have the same origin.

Both trials are located on the coast of Arauco Province, Biobío Region, Chile. The climate of the area corresponds to temperate rainforest, with a Mediterranean influence, the average annual rainfall is 1,330 mm, with a dry period of 3–4 months, average annual temperature of 13 °C, with a maximum of 23 °C in January and a minimum of 6 °C in July. The soil of the area corresponds to the order Alfisol, originated from marine terraces (Curanipe series). The soils are clay loam and clay in depth, subangular blocky structure, and very plastic and adhesive. The topography is undulated to broken (CIREN and CORFO 1983).

Experimental design

In the 3-year-old stand, the experiment was carried out with a randomized complete block design with four treatments and three replicates; the experimental unit corresponds to a plot of 81 trees, i.e. nine rows with nine trees per row, two border rows and 25 trees in the nucleus. In the 2-year-old stand, due to its small surface (1 ha approx.), the trial was conducted with a completely randomized design with 15 trees per treatment; the experimental unit corresponds to the tree. In each trial, there were four pruning treatments, involving the removal of 0 % (control), 30, 50 and 70 % of the live crown. Pruning was conducted between September and October 2011. The average characteristics of stands and pruning treatments are given in Tables 1 and 2.

In each trial, CO_2 assimilation rates (A), and stomatal conductance (Gs) were measured in three trees closest to the average basal area tree in each pruning treatment. The measurements were made along the crown, which was split longitudinally into four sections. Measurements in the 3-year-old stand were performed at 5, 12, 19 and 28 weeks after pruning, while in the 2-year-old stand measurements were performed prior to pruning and at 6, 10, 14 and 18 weeks after pruning.

Measurements of leaf gas exchange

The measurements were made using an IRGA (Infra Red Gas Analyzer) CIRAS-1 PP System. In each section of the canopy, a branch facing north was chosen (Pinkard 2003; Pinkard et al. 1998), in which were measured three leaves of each three different ages: old foliage, characterized by a dark green colour, sometimes showing yellowing, brown and thickened petiole and a well-differentiated top from the underside; mature foliage, dark green, fully expanded, with well-developed cuticle and reddish petioles; and new leaves, light green in the process of expansion with the cuticle in development and no differentiation between the top and the underside. In both trials, it was not always possible to find the three ages of foliage in each section of crown. In the 2-year-old stand, only mature

Table 1 State variables of each stand at the time of pruning

Establishment year	Age (years)	N (trees/ha)	DBH (cm)	MDOS (cm)	H (m)	Hlc (m)
2008	3	667	8.9 (2.4)	13.3 (2.2)	8.4 (1.4)	0.20 (0.17)
2009	2	1,000	8.0 (1.0)	12.5 (1.9)	6.5 (0.6)	0.09 (0.08)

Parentheses show the standard deviation of each variable

N number of trees per hectare, *H* total height, *DBH* diameter at breast height, *Hlc* live crown height, *MDOS* maximum diameter over stump

Table 2 Average height of pruning (m) according to treatment in each trial and the description of each treatment

Establishment year	T1			T2			T3		
	Pruning height (m)	Leaf area removed (m^2)	% of total	Pruning height (m)	Leaf area removed (m^2)	% of total	Pruning height (m)	Leaf area removed (m^2)	% of total
2008	2.6	10.7	33.41	4.7	19.84	61.94	6.4	25.68	80.17
2009	2	9.55	56.49	3.1	12.35	73.11	4.6	14.84	87.84
Crown removal percentage	30			50			70		

foliage and new foliage were measured. In all measurements, a CO_2 concentration of 380 ppm was used, which is similar to the one that is naturally observed in the atmosphere (Feely et al. 2004), and a flow of 180 μmol/m^2/s.

Determination of the photosynthetically active photon flux density (PPFD) to be used

In order to determine with which PPFD maximum values of *A* are obtained, in October prior to initiating the measurements of physiological variables in the pruning severity treatments, photosynthetic rates were measured with different PPFD. In these measurements, an external light source and plaques were utilized, which allow the passage of different PPFD; CO_2 assimilation rate was measured in mature leaves of tress without pruning at eight different PPFD (0, 130, 400, 750, 900, 1,200, 1,500 and 2,200 μmol/m^2/s). The used light source provides a maximum of 1,500 μmol/m^2/s therefore the PPFD of 2,200 μmol/m^2/s was achieved by exposing the leaf to direct daylight. Four leaves were measured per PPFD. With the obtained data, a light response curve was adjusted, and the relationship between the rate of CO_2 assimilation and PPFD was determined. The adjusted model corresponds to the one reported by Sands (1995) [model 1].

$$A = \frac{2\alpha \cdot PPFD \cdot A_{\max}}{\alpha \cdot PPFD + A_{\max} + \sqrt{(\alpha \cdot PPFD + A_{\max})^2 - 4\theta\alpha \cdot PPFD \cdot A_{\max}}} - r, \qquad (1)$$

where *A* is the CO_2 assimilation rate, PPFD is the photosynthetically active photon flux density and α, *Amax*, θ and *r* are parameters where α is the apparent quantum efficiency, *Amax* is the maximum CO_2 assimilation rate, θ is a shape parameter and *r* is the dark respiration rate.

Measurement schedule determination

In October, before starting pruning treatments measurements, CO_2 assimilation was measured from 09:00 to 17:00 hours in mature leaves from the bottom of the crown of four trees without pruning, in order to determine how this parameter would vary during the day and to define at what time it was convenient to measure the pruning treatments. This methodology was repeated in December.

Data analysis

Data were examined using repeated measures analysis of variance (ANOVA) and mean separation test to assess differences between pruning treatments (Tukey). In the analysis, the MIXED procedure of SAS statistical software was used (SAS 1990); each trial was analysed separately and in both cases as a split-plot design with repeated measures with a first order autoregressive (AR(1)) covariance structure (Littell et al. 1998) where the treatment factor was assigned to the principal plots and the foliage age to the subplots based in a complete randomized block design with three replicates for the 3 years old stand and a complete randomized design with three replicates for the 2 years old stand. The position within the crown factor (section) was confounded with the pruning treatment. Only for the control trees, which have the four crown sections, differences in photosynthetic rates between sections were analysed.

In the 3-year-old trial, the variation due to the time of measurement was included within blocks by dividing the measurement time into three intervals (10:00–11:30; 11:00–12:30; 12:30–14:00 hours in spring and 09:30–10:30; 10:30–11:30; 11:30–12:30 hours in summer) and measuring all treatments of each block in the same period of time. In the analysis of the 2-year-old stand trial, the time of day on which the measurement was made was used as a covariate.

Results

Light response curve fitting and diurnal variation of the rate of CO_2 assimilation

According to the results of measurements of variation of *A* (photosynthetic rate) during the day, it was determined that measurements should be performed between 09:30 and 14:30 hours. This time range was selected because between those hours, photosynthetic rates of mature leaves in a section of crown remained relatively stable; before 09:30 and after 14:30 hours, photosynthetic rates showed low values (Fig. 1). The maximum *A* changes as the summer progresses: in December, the trees begin to photosynthesize earlier, peaking at around 11:00 hours and there is a decrease in the rate of CO_2 assimilation around noon, while in October the maximum is reached near 01:00 hours (Fig. 1). This maximum displacement is primarily influenced by the water content in the soil, which becomes limiting as the summer progresses.

The model fitted to the light curve was found to be significant ($p < 0.05$). Although with 1,500 μmol/m^2/s has not yet reached maximum values of *A* (Fig. 2), it was decided to use this PPFD for measurement since it is the maximum that light source gave, with 1,500 μmol/m^2/s values close to 85 % of *Amax* are obtained (Table 3).

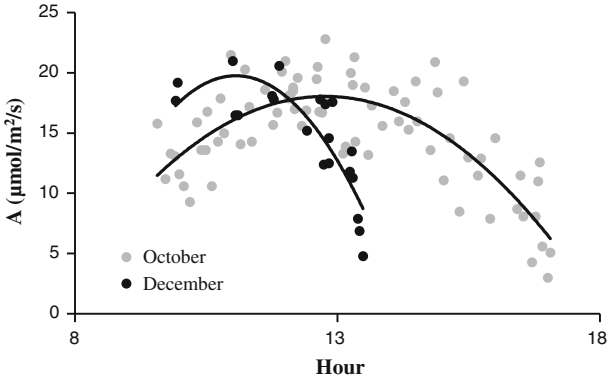

Fig. 1 Diurnal variation of the maximum rate of CO_2 assimilation (*A*) in mature leaves of the lower section of the crown of a 3-year-old *E. regnans*, measured in October 2011 and in late December 2011

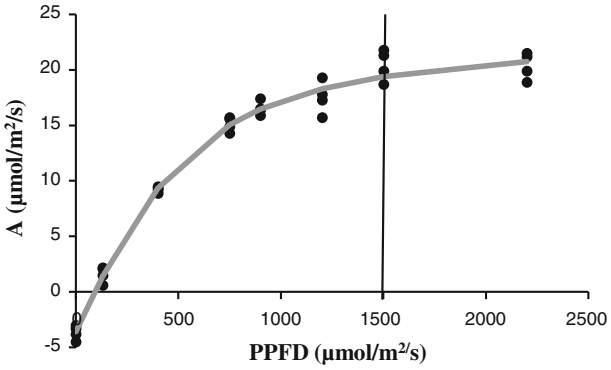

Fig. 2 *A* response curve of mature leaves of the lower section of 3-year-old *E. regnans* trees at different light intensities measured in December 2011 at an average temperature of 22.7 °C. *Vertical line* indicates the light intensity employed in the study

Effect of pruning severity on CO_2 assimilation rates (A) and stomatal conductance (Gs)

The ANOVA in both trials shows significant differences between pruning treatments, foliage ages and time (week). In general, regardless of stand age and intensity of pruning, significant differences ($p < 0.05$) between the different ages of foliage were found (Tables 4, 5). Mature leaves in both trials had the highest CO_2 assimilation rate (*A*), followed by old foliage and recent foliage (Figs. 3, 4). The stomatal conductance behaved in the same way as the CO_2 assimilation rate (Fig. 6a, d). The non significant effect of the interaction treatment × week demonstrate that all pruning treatments has a similar behaviour all over the evaluation period (Tables 4, 5), except for the first measure in the 2 years old stand (Fig. 5), where there was a trend between pruning intensity and photosynthesis rate. The control trees show the lowest values and the 70 % of crown removal treatment shows the highest values of *A* (Figs. 3, 4). In the 2 years old stand significant differences between pruning treatments were found only in the mature foliage.

In both stands, there was a wide variation on the parameters measured over time. Regardless of the pruning treatment and foliage age the highest values for both parameters were found in the first weeks of measurements for both trials, which corresponds to spring (October to December) decreasing towards the last measurements that correspond to the months between January and April (Figs. 3, 4, 5).

Table 3 Results of the model fitting relating the PPFD to CO_2 assimilation rate

Parameter	Estimation	95 % confidence lower limit	95 % confidence upper limit
α	0.0411	0.0301	0.0520
A_{max}	26.9299	23.9984	29.8615
θ	0.7089	0.4492	0.9686
r	3.5674	2.5687	4.5662

Table 4 Repeated measures analysis for photosynthesis rates (*A*) and stomatal conductance (*Gs*) in the 2 years old stand

Effect	*A* (μmol/m^2/s)			*Gs* (mmol/m^2/s)		
	DF	F value	Pr > F	DF	F value	Pr > F
Hour (covariate)	1	1.49	0.2227	1	0.11	0.7377
Treatment	3	6.09	0.0085	3	5.02	0.0433
Foliage age	1	49.28	<.0001	1	11.90	0.0041
Treatment * foliage age	3	3.75	0.0395	3	5.05	0.0170
Week	4	4.63	0.0036	4	13.14	<.0001
Treatment * week	12	1.32	0.2562	12	2.85	0.0133
Foliage age * week	4	4.32	0.0053	4	6.12	0.0008
Treatment * foliage age * week	12	0.86	0.5926	12	1.40	0.2423

Table 5 Repeated measures analysis for photosynthesis rates (*A*) and stomatal conductance (*Gs*) in the 3 years old stand

Effect	*A* (μmol/m^2/s)			*G* (mmol/m^2/s)		
	DF	F value	Pr > F	DF	F value	Pr > F
Treatment	3	5.43	0.0136	3	8.39	0.0002
Foliage age	2	30.93	<.0001	2	7.26	0.0019
Treatment * foliage age	5	1.69	0.1788	5	1.20	0.3277
Week	3	9.66	<.0001	3	31.13	<.0001
Treatment * week	9	0.43	0.9125	9	2.09	0.0490
Foliage age * week	6	3.44	0.0074	6	0.75	0.6128
Treatment * foliage age * week	8	1.03	0.4283	8	0.98	0.4607

In both trials, trees with 70 % crown removal (T3) demonstrated the greatest *A* with rates of up to 40 % higher than the control treatment. In general, the magnitude of the *A* response to pruning was greater in the 2-year-old stand in the mature foliage (Figs. 3, 4). Similar trends were found for stomatal conductance (*Gs*) in both trials, presenting the greatest values for trees with increased pruning severity and the smallest values in the control treatment trees.

There was a trend between the position in the crown and the photosynthetic rate in the control trees of both stands. The lowest values were found in the basal sections (0–30 %)

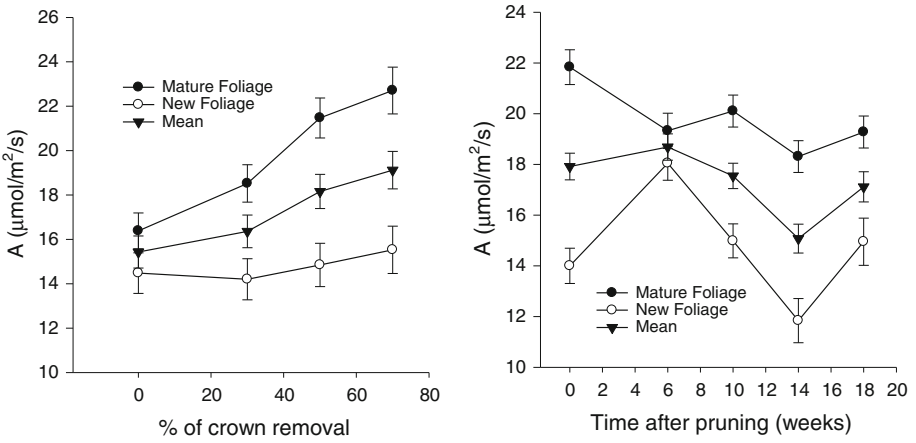

Fig. 3 Photosynthesis rates by pruning treatment (*left*) and time after pruning (*right*) for each foliage age and the mean for the 2 years old stand. *Bars* indicate standard errors

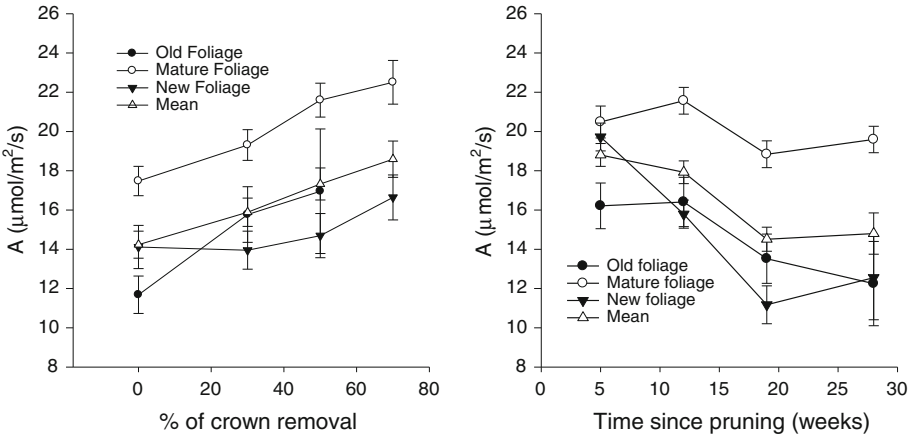

Fig. 4 Photosynthesis rates by pruning treatment (*left*) and time after pruning (*right*) for each foliage age and the mean for the 3 years old stand. *Bars* indicate standard errors

and the highest in the upper sections, but significant differences between sections were found only in the 3 years old stand (Fig. 7).

Discussion

The loss of leaf area due to pruning generate in the tree an unbalance between the capacity of the remaining crown to fix carbon and the demand that permit to maintain the growth rates (Pinkard and Beadle 1998b). For each species in particular site conditions there is an amount of foliage that could be removed without affecting its growth rates either because generally pruning is done at the moment of canopy closure, therefore at this time the basal

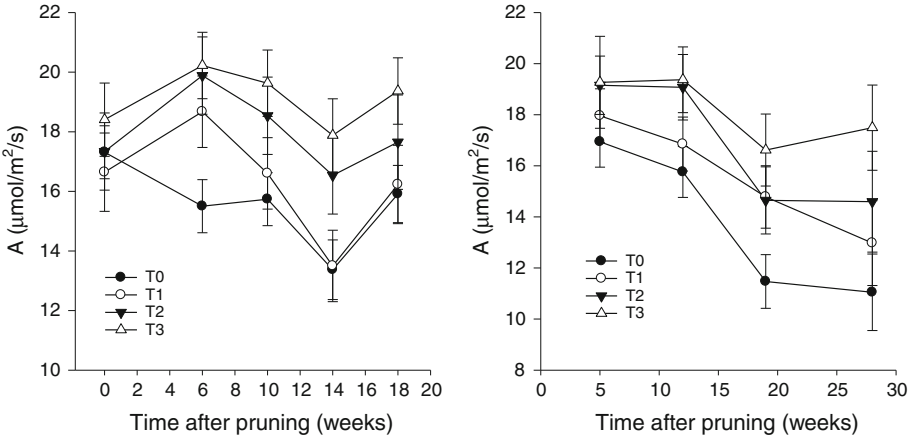

Fig. 5 Photosynthesis rate (*A*) by time for each pruning treatment for the 2 years old stand (*left*) and the 3 years old stand (*right*). *Bars* indicate standard errors

zone of the crown receives a little amount of light and because of that the basal branches, which are removed during the pruning, don't make a great contribution to the whole canopy photosynthesis, as can be observed in the control trees of this study in which the basal zone of the crown presents the lowest values of photosynthetic rates. Moreover the basal zone of the crown has mainly old foliage which receives less radiation, which would result in an incomplete opening of stomata and therefore low values of stomatal conductance; low rates may also be due to a loss of function in old foliage (England and Attiwill 2006). Pinkard et al. (1998) in *E. nitens* found that, in general, the old foliage showed the lowest values of *A*, followed by the newer foliage and then the mature foliage. In *A. melanoxylon*, Medhurst et al. (2006) also found that the recent foliage presented values greater than old foliage. No significant differences between crown sections were found in the 2 years old stand, which can be due to the absent of old foliage in this stand and may indicate that this stand has not reached the canopy closure yet; thus growth rates in this stand are possibly affected by removing an smaller amount of foliage than in the 3 years old stand, because 2 years old stand foliage in the base of the crown it is still contributing to the crown productivity.

Pruning also may change the carbon allocation patterns favouring leaf development and increasing net biomass production (Barry and Pinkard 2012; Reich et al. 1993), but a very important factor that permits to remove some amount of foliage without affecting growth is the compensatory response to pruning. This response is characterized by an increase in the photosynthetic rate of the remaining crown of a pruned tree in contrast to foliage of the same age in an unpruned tree (Nowak and Caldwell 1984). This study shows that pruning a 70 % of the crown of *E. regnans* produces an increase of 40 % in the photosynthetic rates in contrast to the control trees and this effect last even up to 28 week after pruning in the 3 years old stand. In Australia, the effect of pruning on photosynthetic rate (*A*) of some species of *Eucalyptus* has been studied, finding different responses. While Pinkard et al. (1998) found that *E. nitens* increased the photosynthetic rate by 170 % after pruning, Forrester et al. (2012) found only a 19 % increase in the photosynthetic rate 19 weeks after pruning 50 % of the live crown of *E. nitens.* Photosynthetic capacity increases were also found in *A. melanoxylon* after pruning 50 % of its crown (Medhurst et al. 2006). Contrary

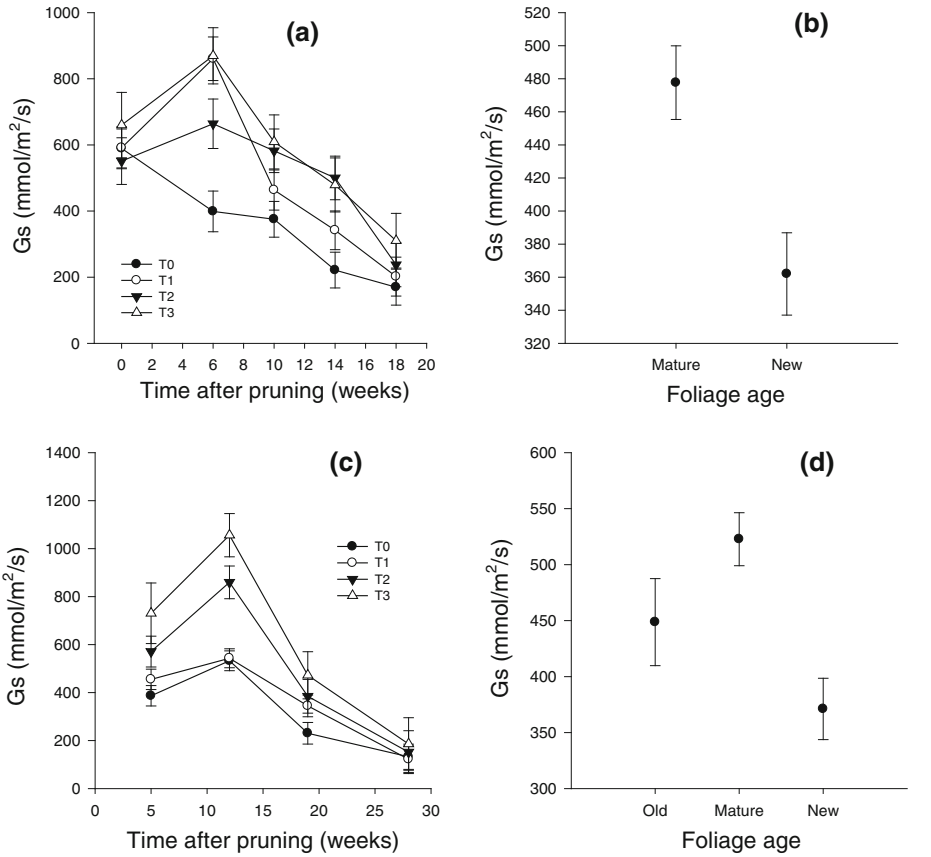

Fig. 6 Stomatal conductance (*Gs*) by week for each pruning treatment for the 2 years old stand (**a**) and the 3 years old stand (**c**); Stomatal conductance by foliage age for each stand (**b**, **d**). *Bars* indicate standard errors

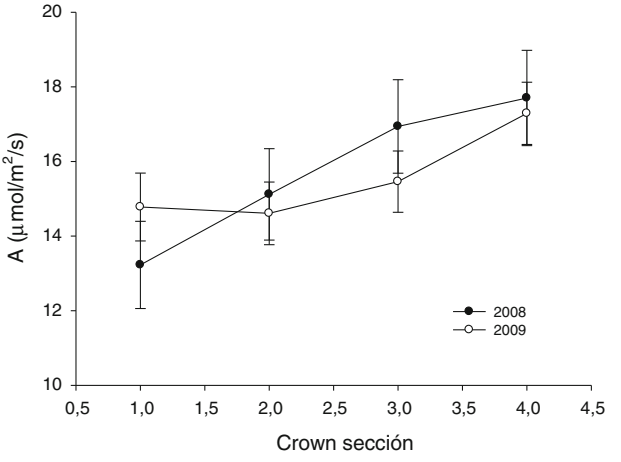

Fig. 7 Photosynthetic rates by crown section for the control trees of both stands. *Bars* indicate standard errors

to what happens in the mentioned species, Alcorn et al. (2008) found that pruning 50 % of live crown of *Eucalyptus pilularis* and *Eucalyptus cloeziana* do not produce increases in CO_2 assimilation rates of up to 13 months after pruning was done. Pinkard et al. (1998) found that younger trees had greater responses to pruning of than older trees, similar to what was found in this study, where the 2-year-old stand produced a response of greater magnitude than the one of 3-year-old stand.

The mechanisms that control the compensatory response to pruning are not clear. Some authors mention the possibility that the increase in photosynthetic rates is related to an increase in foliar N concentration although this hypothesis has been rejected by other studies that doesn't found any relationship between those variables (Pinkard et al. 1998; Turnbull et al. 2007), however it could be due to changes in N partitioning within the cell, e.g. von Caemmerer and Farquhar (1984) found that partial defoliation of *Phaseolus vulgaris* produced an increase in chlorophyll content which might influence the capture of CO_2.

Another theory is that increased photosynthesis is related to an increase in stomatal density of the leaves formed after pruning, which may increase leaf conductance (Maurin and DesRochers 2013; Pinkard and Beadle 1998b). This study shows that there is an effect of pruning on stomatal conductance, as pruning intensity increases stomatal conductance increases. This result was also found in poplar, were stomatal conductance of pruned trees was greater than that of unpruned trees (Maurin and DesRochers 2013). In partial defoliated *Eucalyptus globulus* trees an increase in soil-to-leaf hydraulic conductance was found in associated to an increase in stomatal conductance and transpiration rate per unit of leaf area of the remaining foliage (Quentin et al. 2011) which may be another factor controlling the photosynthetic compensatory response. Changes in hydraulic conductance may be also the reason to the changes in photosynthesis rates along the evaluation period shown in this study, a decrease in soil-to-leaf hydraulic conductance in summer, because of a decrease in the water content of the soil, may be the reason of the lower values of *A,* in all pruning treatments, compared to the values obtained in spring.

Complimentary research on effects of pruning on growth of *E. regnans* it necessary to evaluate how long the compensatory physiological response to pruning maintains on trees and which is the effect on clear wood production.

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References

Alcorn PJ, Bauhus J, Thomas DS, James RN, Smith RGB, Nicotra AB (2008) Photosynthetic response to green crown pruning in young plantation-grown *Eucalyptus pilularis* and *E. cloeziana*. For Ecol Manage 255:3827–3838

Barry KM, Pinkard EA (2012) Growth and photosynthetic responses following defoliation and bud removal in eucalypts. For Ecol Manage 293:9–16

CIREN, CORFO (1983) Ortofotos VIII Región, anexo regional. Santiago, Chile. 17 p

Donnelly R, Flynn R, Shield, ED (2003) The global *Eucalyptus* wood products industry: a progress report on achieving higher value utilization. Dana Publisher, New Zealand. 275p

England J, Attiwill P (2006) Changes in leaf morphology and anatomy with tree age and height in the broadleaved evergreen species, *Eucalyptus regnans* F. Muell. Trees 20(1):79–90

Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. Science 305:362–366

Flynn B (2003) *Eucalyptus*: having an impact on the global solidwood industry. Wood Resources International Report. WRI (www.wri-ltd.com)

Forrester DI, Collopy JJ, Beadle CL, Warren CR, Baker TG (2012) Effect of thinning, pruning and nitrogen fertiliser application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation. For Ecol Manage 266:286–300

Littell RC, Henry PR, Ammerman CB (1998) Statistical analysis of repeated measures data using SAS procedures. J Anim Sci 76:1216–1231

Maurin V, DesRochers A (2013) Physiological and growth responses to pruning season and intensity of hybrid poplar. For Ecol Manage 304:399–406

Medhurst J, Pinkard E, Beadle C, Worledge D (2006) Photosynthetic capacity increases in *Acacia melanoxylon* following form pruning in a two-species plantation. For Ecol Manage 233:250–259

Medrano H, Escalona J, Bota J, Gulías J, Flexas J (2002) Regulation of photosynthesis of C3 plants in response to progressive drought: stomatal conductance as a reference parameter. Ann Bot 89:895–905

Montagu K, Kearney D, Smith R (2003) The biology and silviculture of pruning planted Eucalypts for clear wood production—a review. For Ecol Manage 179:1–13

Nowak RS, Caldwell MM (1984) A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia 61:311–318

Pinkard EA (2003) Physiological and growth responses related to pattern and severity of green pruning in young *Eucalyptus globulus*. For Ecol Manage 182(1):231–245

Pinkard EA, Beadle CL (1998a) Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. New For 15:107–126

Pinkard EA, Beadle CL (1998b) Regulation of photosynthesis in *Eucalyptus nitens* (Deane and Maiden) Maiden following green pruning. Trees 12:366–376

Pinkard EA, Beadle CL (2000) A physiological approach to pruning. Int For Rev 2(4):295–304

Pinkard E, Beadle C, Davidson N, Battaglia M (1998) Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. Trees-Struct Function 12:119–129

Quentin AG, O'Grady AP, Beadle CL, Worledge D, Pinkard EA (2011) Responses of transpiration and canopy conductance to partial defoliation of *Eucalyptus globules* trees. Agric For Meteorol 151(3):356–364

Reich PB, Walters MB, Krause SC (1993) Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. Trees 7:67–77

Sands P (1995) Modelling canopy production. II. From single-leaf photosynthesis parameters to daily canopy photosynthesis. Funct Plant Biol 22:603–614

SAS Institute Inc (1990) SAS/STAT user's guide, version 6. SAS Institute Inc., Cary

Sedjo RA (1999) The potential of high-yield plantation forestry for meeting timber needs. New For 17:339–359

Turnbull TL, Adams MA, Warren CR (2007) Increased photosynthesis following partial defoliation of field-grown *Eucalyptus globulus* seedlings is not caused by increased leaf nitrogen. Tree Physiol 27:1481–1492

von Caemmerer S, Farquhar GD (1984) Effects of partial defoliation, changes of irradiance during growth, short-term water stress and growth at enhanced p(CO2) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. Planta 160:320–329

Wardlaw T, Mohammed CL, Barry KM, Eyles A, Wiseman D, Beadle CL, Battaglia M, Pinkard EA, Kube P (2003) Interdisciplinary approach to the study and management of stem defect in eucalypts. NZ J For Sci 33(3):385–398