



Patterns of resource use efficiency in relation to intra-specific competition, size of the trees and resource availability in ponderosa pine



Javier Gyenge*, María Elena Fernández

Consejo Nacional de Investigaciones Científicas y Técnicas, CONICET, Argentina Oficina Tandil INTA, EEA Balcarce INTA, Gral. Rodríguez 370 (7000) Tandil, Buenos Aires, Argentina

ARTICLE INFO

Article history:

Received 8 July 2013

Received in revised form 24 September 2013

Accepted 27 September 2013

Available online 26 October 2013

Keywords:

Light use efficiency

Growth efficiency

Nitrogen use efficiency

Water use efficiency

Pinus ponderosa

ABSTRACT

Patterns of resource use efficiency (RUE) in relation to intra-specific competition, size of the trees and resource availability are under debate. Also, the relationship between RUE and growth efficiency (GE) seems to be different depending on the genera studied. We test the following hypotheses: (1) RUE of the stand decreases after canopy closure mainly due to the decrease in RUE of the suppressed trees, (2) RUE increases with the availability of resources and/or stand productivity and, (3) the efficiency of use of water, light and nitrogen are positively correlated each other, and are not correlated with GE. We measured or estimated at tree and plot level, the concentration of ^{13}C in wood as a proxy of intrinsic water use efficiency (iWUE), nitrogen productivity (NP), light use efficiency (LUE) and GE in *Pinus ponderosa* trees growing in two sites in Patagonia, South-America. Within each site, we studied plots with contrasting intra-specific competition due to different plantation density. A decrease in NP and GE at plot level followed canopy closure, with no decrease in LUE or iWUE. In contrast to Hypothesis 1, the decrease in RUE of a stand, when it was observed, was due to a decrease in the efficiency of resource use of the dominant trees. The suppressed trees seem to always have low RUE, independently of canopy closure of the stand. The trend of a positive relation of RUE and resource availability is rather weak as a generalization (in contrast to Hypothesis 2), but it depends on the resource which use efficiency is analyzed. At plot level, NP, iWUE and GE did not present a correlation with stand productivity. Considering iWUE, no positive correlation was observed with tree size, which contrasts with previous findings. On the other hand, clear and positive relationships were observed between GE and NP with tree growth, supporting the hypothesis of higher RUE in those trees which are growing faster within the stand, which in turn are those which are surely accessing to more resources (soil resources and radiation). The third hypothesis stated in this study was not supported by our results. The only significant correlation was that observed between NP and GE, with no correlation at all between iWUE and the other resources use or growth efficiency.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Trees exhibit changes in their resource use efficiency (RUE) during their ontogeny, which are also modulated by resources availabilities mediated by the site characteristics (physical environment) and biotic interactions such as intra-specific competition (Stape et al., 2004; Gyenge et al., 2008; Forrester et al., 2012a,b). By definition RUE is a key component for understanding forest (or other ecosystems) productivity because it quantifies the conversion of captured resources into biomass. Due to changes in resources availabilities, the efficiency of resource use can change across environmental gradients and silvicultural treatments (Binkley et al., 2004).

Some studies have found evidence supporting the idea that resource use efficiency increases as forests increase the rate of

resource use (Binkley et al., 2004; Gyenge et al., 2008) which is related to the access to a higher resource availability (Stape et al., 2004; Fernández and Gyenge, 2009). As a consequence, higher resource availability would result in higher productivity and also in a better (more efficient) conversion of available resources into plant biomass. Stape et al. (2004) found that increased productivity of *Eucalyptus* plantations in Brazil is associated to the simultaneous increases in the use of all main resources (light, water and nitrogen), and that these RUE are also correlated to growth efficiency (GE). This is the amount of biomass produced per unit leaf area (or biomass) of the tree/stand (Waring et al., 1980). Other studies have also documented that GE is correlated with the efficiency of use of different resources (Ryan and Waring, 1992; Binkley et al., 2002; Allen et al., 2005), however, it seems that this is not a universal pattern since a study in ponderosa pine did not find a correlation between GE and WUE (Fernández and Gyenge, 2009).

On the other hand, RUE differences between different size trees of a stand may be a cause (Fernández Tschieder et al., 2012) or a

* Corresponding author. Tel.: +54 2494425311.

E-mail address: javier_gyenge@yahoo.com (J. Gyenge).

consequence (Binkley, 2004) of dominance patterns along stand development (*sensu* Binkley et al., 2002), and it has been proposed that a high differentiation in RUE between trees of a stand – which is related to higher dominance – may be the responsible of stand growth decrease when canopy closures (Binkley et al., 2002; Binkley, 2004). This hypothesis emerged from studies in fast growing *Eucalyptus* stands, in which larger-dominant trees presented much higher RUE and relative growth than smaller-suppressed trees of the stand after canopy closure. However, other studies in *Pinus* species stands have demonstrated that stand growth declines even with very low levels of growth dominance (Fernández Tschieder et al., 2012). Moreover, even when growth dominance was low, WUE differentiation was large between different size trees of a ponderosa pine stand (Fernández and Gyenge, 2009). It is now clear that large differences in dominance patterns do exist between *Eucalyptus* and *Pinus* species (see Fernández et al., 2011), at least from the very few studies in which this process has been documented. And even less are the antecedents from other species and genus. From this background, it appears that in *Pinus* spp species GE is a more related variable to dominance patterns than RUE, which suggests that there is no a clear correlation of both types of efficiencies. At our knowledge, the only study which simultaneously estimated stand productivity, canopy closure, growth dominance and GE differentiation in a *Pinus* species was the study by Fernández Tschieder et al. (2012). However, those authors did not include RUE determinations nor considered the variation in resource availability. In spite of there are several studies in which at least three of these factors were analyzed in other genera, such as *Eucalyptus* (Stape et al., 2004; Forrester et al., 2012a,b), there is still a gap in our knowledge about RUE and GE differences in different size trees of a stand, and how they are related to general resource availability (determined by site quality and competition), particularly in *Pinus* spp, as well as in most of other genera.

In order to provide evidence to increase our understanding of RUE and GE influences on stand development and how resources availability modulates those relationships, we analyzed several variables related to the efficiency of use of nitrogen, light and water, as well as the GE, of different size trees of ponderosa pine stands differing in intra-specific competition level (plantation density, thinning treatments) located in two sites of different general “site quality” in terms of forestry production. We tried to test the following hypotheses: (1) RUE of the stand decreases after canopy closure mainly due to the decrease in RUE of the suppressed trees, (2) RUE increases with the availability of resources and/or stand productivity and, (3) the efficiency of use of water, light and nitrogen are positively correlated between them, and are not correlated with GE.

2. Materials and methods

2.1. Study area and plots characterization

The study was carried out in *Pinus ponderosa* stands planted in two sites, Arroyo del Medio (AM, 41°13'53"S, 71°11'40"W; 1000 m.o.s.l.) and Meliquina Valley (MV, 40°30'S, 71°10'W; 900 m.o.s.l.) in NW Patagonia, Argentina, South-America. The climate of the region is characterized by humid and cold winters and dry and hot summers (with approximately 80% of the annual precipitation registered as rain or snow during autumn, winter and early spring). Both sites showed similar general climatic conditions, but soil depth and texture differ between sites (Table 1), leading to different water holding capacity and soil water deficit levels. AM soil presents a clay pan at approximately 80 cm depth that impedes root growth at deeper soil layers (Table 1). In contrast, soil in MV site is deeper, with more than 2 m depth for roots

exploration. In this regard, Licata et al. (2008) estimated that more than 20% of the water used by *P. ponderosa* in MV site was extracted by deep roots below 1.8 m. According to differences in soil water holding capacity and mean annual precipitation (a difference of about 150 mm per year) between sites, previous studies demonstrated that *P. ponderosa* trees in AM suffer water stress during summer (reaching pre-dawn water potential around -2 MPa; Gyenge et al., 2012), meanwhile in MV site predawn water potential never reaches values down to -1.5 MPa (Gyenge, 2005).

We installed three plots in each of two stands within each site. The size of each plot depended on tree density, and contained at least 15 trees. The stands differed in plantation density and degree of canopy closure due to the different number of trees per unit area and not due to differences in stand age. Stand structure and other sampling (see below) were carried out in winter 2009. High plantation density plots represent forests with full canopy closure (plots numbered #1 to #3 in each site) whereas low plantation density plots (numbered #4 to #6) represent forests without canopy closure (Table 2). Each tree was numbered and mapped, and its diameter at breast high (dbh, cm), diameter at the base of the living crown (dblc, cm) and height (H, m) were measured with a diameter tape and a clinometer.

Reineke stand density index (SDI) was estimated for each plot in order to explore the relationship between RUE and the degree of intra-specific competition. SDI was defined as the equivalent trees per hectare at a quadratic mean diameter (D_g) of 25 cm and a slope of -1.7653 (which represents the maximum density expected for any particular stand diameter computed for ponderosa pine stands in western United States; Cochran, 1992; also see Zhang et al., 2013):

$$SDI = \text{trees ha}^{-1} (D_g 25^{-1})^{1.7653}$$

Four hemispheric images were taken in each plot in order to estimate its leaf area index (LAI, $\text{m}^2 \text{m}^{-2}$) and the intercepted radiation (see below). Each image was analyzed using Gap Light Analyzer (GLA) v.2.0 software (Frazer et al., 1999).

Soil nitrogen content (%N dry weight) was estimated from three soil samples taken at 10 and 50 cm soil depth in each plot (Table 2).

2.2. Resource use efficiency estimation

We determined the relative concentration of the rare isotope ^{13}C ($\delta^{13}\text{C}$, ‰) as a proxy of intrinsic water use efficiency (iWUE) of the trees. The samples were obtained from the last three growth rings (both late- and earlywood, seasons 2006–2007 to 2008–2009) of the three biggest and two smallest trees of each plot and in the trees #2, #4, #6 (the number was randomly assigned to each tree, $n = 8$ trees per plot). The samples were analyzed in an isotope ratio mass spectrometer (Finnigan MAT Delta S, USA) following the methodology of Hoefs and Schidlowski (1967) and Panarello (1987) in the Institute of Geochronology and Isotopic Geology (Instituto de Geocronología y Geología Isotópica, INGEIS, CONICET-University of Buenos Aires, Argentina).

Annual aboveground productivity was estimated as the difference in biomass estimated from the dbh in successive years. Aboveground biomass (gr) of each tree (and then scaled to the plot) was estimated from dbh following Laclau (2003)'s formulas developed for Patagonian ponderosa pine plantations covering site conditions included in this study: $\text{Stem} = 93.648 \text{ dbh}^{2.189}$ $\text{Branch} = 59.769 \text{ dbh}^{1.812}$ $\text{Foliage} = 481.59 \text{ dbh}^{1.002}$

Stem diameter annual growth rate was estimated from the average growth ring width produced in the last three seasons measured in the trees in which $\delta^{13}\text{C}$ was also measured (8 trees per plot). After that, we estimated annual growth of the trees in the

Table 1

Climatic and soil characteristics (average \pm S.D.) of Arroyo del Medio (AM, 41°13'53"S, 71°11'40"W) and Meliquina Valley (MV, 40°30'S, 71°10'W). Climatic data of AM correspond to the period 1981–2006, and those of MV correspond to the period 1978–1999.

Sites	AM	MV
Mean annual precipitation (mm)	840 \pm 195	684 \pm 283
Mean annual temperature (°C)	8.4 \pm 4.0	10.6 \pm 1.5
Mean maximum temperature (°C)	13.5 \pm 5.0	17.1 \pm 0.5
Mean minimum temperature (°C)	3.2 \pm 3.2	4 \pm 2.1
Soil depth (m)	<0.80	>2
Soil texture	Sandy loam with 6% clay, 35% silt and 59% sand	Silty clay loam with 27–40% loam and 20% clay
Water holding capacity (mm)	263.1 (up to 0.80 cm depth)	202 (up to 0.80 cm depth) 382 (up to 150 cm depth)

Table 2

Tree density (trees ha⁻¹), basal area (m² ha⁻¹), average (\pm standard deviation, SD) of the diameter at breast height (dbh, cm), tree height (H, m) and nitrogen soil content (%N) of the six plots (#1 to #6) of *Pinus ponderosa* established in stands located in Arroyo del Medio (AM) and Meliquina Valley (MV) in NW Patagonia, Argentina. Different letters indicate significant differences between plots in each site.

Plot	Tree density	Basal area	dbh	H	%N
AM#1	1333	82.69	27.8 (4.1) B	13.36 (1.49) A	0.16 (0.02)ABC
AM#2	2188	85.36	21.7 (5.1) C	13.31 (2.79) A	0.15 (0.02) BC
AM#3	2200	89.51	22.1 (5.6) C	12.40 (0.69) A	0.12 (0.04) C
Avg. (SD)	1907 (497)	85.9 (3.4)		13.0 (0.5)	
AM#4	798	53.11	28.6 (5.5) AB	13.07 (1.82) A	0.17 (0.02)AB
AM#5	519	41.11	30.8 (7.9) AB	12.84 (1.50) A	0.16 (0.02)A
AM#6	661	66.04	35.1 (6.5) A	12.19 (2.13) A	0.20 (0.02)A
Avg. (SD)	659 (140)	53.4 (12.0)		12.7 (0.5)	
MV#1	1050	65.40	26.4 (9.8) b	13.53 (3.46) a	0.08 (0.03) bc
MV#2	1178	74.20	26.5 (10.4) b	14.02 (3.18) a	0.08 (0.01) c
MV#3	1210	83.43	28.4 (8.7) b	14.43 (2.81) a	0.08 (0.02) bc
Avg. (SD)	1146 (84)	74.3 (9.0)		14.0 (0.5)	
MV#4	284	33.62	38.7 (3.5) a	15.71 (1.75) a	0.14 (0.03) a
MV#5	351	33.40	34.3 (6.2) ab	14.04 (2.38) a	0.10 (0.01) abc
MV#6	320	32.06	35.6 (3.2) ab	14.14 (1.12) a	0.12 (0.02) ab
Avg. (SD)	318 (34)	33.0 (0.8)		14.7 (0.9)	

plots based on the dbh distribution using the values obtained in the measured trees. Ring width was measured with a caliper.

Individual tree and plot growth efficiency (GET and GE_p, respectively) were estimated from stem biomass increment and leaf biomass of the measured trees and then scaled to the plot from the dbh distribution of all trees.

Nitrogen productivity (NP) at the tree and the plot level (NP_t and NP_p, respectively) was calculated as the ratio between aboveground biomass productivity (differences in aboveground biomass between successive years) and N content in the aboveground biomass at the end of the growing period (Finzi et al., 2007). Biomass nitrogen content (%N dry mass) was estimated in three trees per plot (trees #2, #4, #6). For each tree and for each tissue (leaves, cork and wood) we formed a composite sample from samples taken at several tree heights or canopy positions. In the present study NP is considered as a conservative proxy of NUE. NUE is the product of NP and mean residence time (MRT) of N in the tissues (e.g. Aerts and Chapin, 1999; Finzi et al., 2007). Several studies have indicated that PN and MRT display opposite trends (Aerts and Chapin, 1999), resulting in similar NUE even when PN differs between species or environmental conditions. However, in our study case, a longer needle retention of at least two more years, has been observed in pines growing in AM at low plantation density than those at high density (author's unpublished data), suggesting a higher MRT in open canopy plots. According to this, *P. ponderosa* growing at higher plantation density showed a net decrease in leaf area after a marked drought season whereas trees growing at low density presented a net increase in leaf area (Gyenge et al., 2012). Aerts and Chapin (1999) also indicated that MRT depends on leaf life-span divided by the resorption efficiency, which in the case of *P. ponderosa* trees growing in Patagonia presents very low variation across a wide range of ecological conditions (Araujo, 2006). Thus,

MRT directly depends on leaf lifespan. All these observations allow us to propose a lower MRT in *P. ponderosa* growing at high plantation density than in open canopy stands, suggesting that PN and NUE in our study case are positively correlated.

Light use efficiency (LUE) at the plot level was estimated from the estimated aboveground biomass productivity and the absorbed photosynthetic active radiation (APAR). APAR was calculated from the total radiation incident on a tilted or horizontal surface when there is blockage of light from the surrounding topography and overlying forest canopy estimated using Gap Light Analyzer (GLA) v.2.0 for each photography (Frazer et al., 1999) Incident PAR during the main growing season for the pines in the study region (September 2008 to April 2009; Fernández et al., 2012) was measured with a LICOR LI190 sensor of an automatic weather station installed in an open area next to the AM plantation.

3. Results

3.1. N availability and stands productivity

On average, considering the upper soil layers, soil N was higher in AM than in MV (around 0.16 and 0.10, respectively; Table 2) indicating a higher fertility in AM site. However, irrespective of the site the low plantation density (open canopy) plots showed a higher amount of soil N than the high density (close canopy) plots, with higher differences between plots in MV than in AM (Table 2). The %N in leaf, cork and wood were similar in trees growing at different plantation densities within each site. Only leaf and wood N content was significantly different between sites, being higher in AM than in MV trees (1.03 \pm 0.11% and 0.96 \pm 0.09% for leaves and 0.08 \pm 0.02% and 0.06 \pm 0.01% for wood in AM and MV site, respectively).

High plantation density plots had 2.9 and 3.6 times more trees per unit area, and 1.6 and 2.3 times more basal area than the low plantation density plots in AM and MV, respectively (Table 2). Tree height was similar between plots in each site but mean dbh was around 8 cm higher in trees growing at low than at high density plots in both sites (Table 2). Trees in the high density plots of both sites were closed to the maximum value of D_g estimated for *P. ponderosa* in N.W. Patagonia (stand density index, SDI, around 2000, Letourneau F, INTA EEA Bariloche, pers. comm., Fig. 1A). In this regard, SDI of plots AM#2 and #3 were around 1790 and 1870, respectively (Fig. 1A). The LAI of all AM plots was very similar, however, the high density plots in MV showed higher LAI than low density plots in the same site (Fig. 1B).

Annual aboveground productivity of the plots was statistically similar between plantation densities and sites ($P = 0.092$), with a trend of a higher productivity in high density plots within each site. As expected, average annual aboveground production of each individual tree followed the opposite pattern. Trees growing at lower densities showed a higher annual growth than trees at higher densities (around 14 and 5.6 kg tree⁻¹ y⁻¹, respectively; $P = 0.02$, Fig. 1C).

3.2. RUE patterns at tree level

Two way ANOVA applied to wood $\delta^{13}C$ data of each site (factors were plantation density and relative size of the trees) showed significant differences between tree sizes (the smallest and the largest trees of each plot) in both sites, but only a significant difference was observed comparing plantation densities in MV (also the interaction density \times size was significant at this site) (Fig. 2). In both sites, the smallest trees in the high density plots showed more negative values of $\delta^{13}C$ than trees growing at low density plots (Fig. 2). The lowest $\delta^{13}C$ was observed in the smallest trees of the high density plots in MV.

A positive relationship between NPt and GEt with tree size (dbh) was found in both sites (Fig. 3). However, trees with higher dbh in low density plots (plots #4 to #6) showed higher values of both NPt and GEt than trees of similar size growing at high density plots (Fig. 3). In the particular case of AM plots, the smallest trees of both density plots showed similar NPt and GEt. On the other hand, similar NPt and GEt were found comparing trees growing at similar density comparing both sites (Fig. 3).

3.3. RUE patterns at plot level

At the plot level, mean $\delta^{13}C$ of wood was similar between plots with different plantation density or with different soil N ($P > 0.05$, Fig. 4 A and E). Across both studied sites, the relationship between

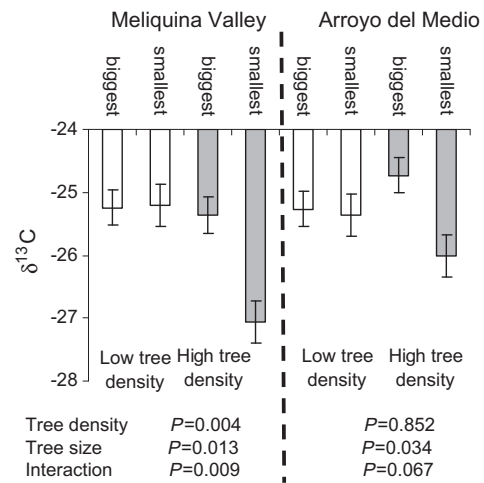


Fig. 2. Relationship between $\delta^{13}C$ in wood rings of the biggest and smallest trees of *Pinus ponderosa* growing in Meliquina Valley and Arroyo del Medio sites (NW Patagonia, Argentina) at two plantation densities.

Npp and GEp with SDI was negative ($P = 0.022$ and 0.006 , respectively, Fig. 4 B and C). In contrast, no relationship was found between LUEp and SDI, but different trajectories were observed between sites, with higher LUE values in AM than in MV (mean \pm SD: 2.3 ± 0.8 and 0.9 ± 0.2 , respectively; Fig. 4 D). On the other hand, the linear relationship between Npp and GEp with soil N was positive with similar slopes but different intercepts between sites. The lower intercept was observed in AM, the more fertile site (Fig. 4 F and G). A non significant relationship was observed between LUEp and soil N within each site, but a positive relationship was found when all data-both sites-were analyzed together (Fig. 4 H).

Considering all studied plots, annual aboveground production only presented a significant and positive relationship with LUE ($r^2 = 0.806$, $p < 0.001$). No relationship was found between aboveground annual productivity and $\delta^{13}C$, Npp or GEp (data not shown).

3.4. Correlation between use efficiency of different resources

In contrast to our hypothesis about the correlation between the efficiency of use of the different resources, and the absence of correlation between RUE and GE, we found no correlation between plots efficiencies of the different resources (the different combinations between LUE, iWUE and NP) (Pearson product moment correlation, $P > 0.05$), and a highly positive correlation between GEp and Npp ($P < 0.001$, $r = 0.982$). As was expected no correlation was observed between GEp and $\delta^{13}C$ and LUE.

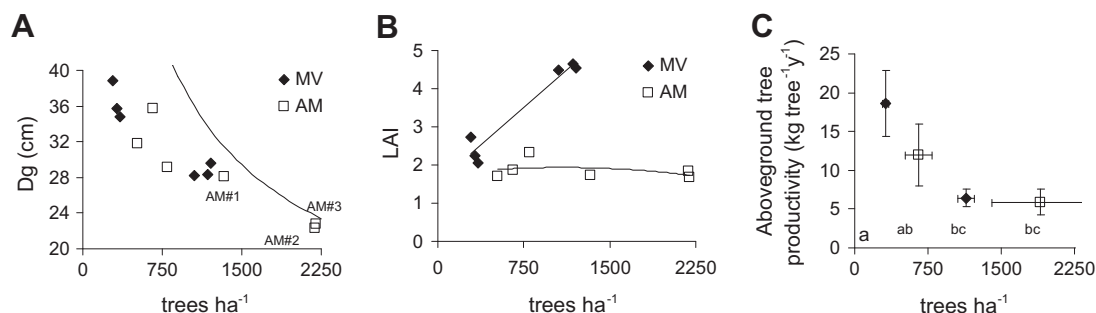


Fig. 1. Relationship between mean quadratic diameter (D_g , cm, A), leaf area index (LAI, m² m⁻², B) and average annual aboveground productivity (kg tree⁻¹ y⁻¹, C) with tree density of six plots of *Pinus ponderosa* growing in Meliquina Valley (MV) and Arroyo del Medio (AM) sites, N.W. Patagonia, Argentina. The line in panel A corresponds to the maximum value of D_g for each density based on a SDI = 2000 (Letourneau F, pers. comm.). Parameters of plots AM#1, #2 and #3, which are the plots closer to that line, are shown in Table 2.

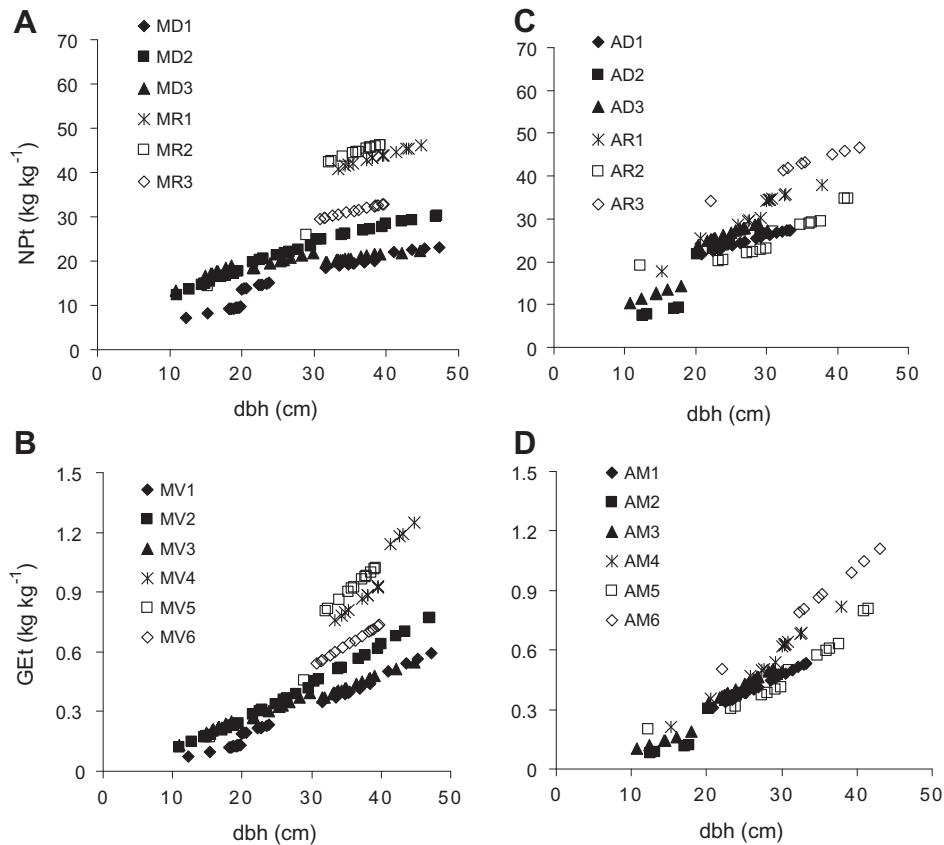


Fig. 3. Relationship between nitrogen use efficiency at the tree level (NPt) and growth efficiency at the tree level (GEt) with diameter at breast height (dbh) of *P. ponderosa* trees growing in Meliquina Valley (MV, panel A and B) and Arroyo del Medio (AM, panel C and D), NW Patagonia, Argentina. Each symbol represent a tree growing at high (plots #1 to #3) and low (#4 to #6) tree density plots.

4. Discussion

Our research was driven by three hypotheses: (1) RUE of the plot decreases after canopy closure, and this is mainly due to the decrease in RUE of suppressed trees, (2) RUE increases with the availability of resources and/or productivity and, (3) RUE of water, light and nitrogen are positively correlated between them, and they are not necessarily correlated with GE. We will discuss below our results at the light of these three hypotheses trying to understand how the efficiency of use of the different resources by the different trees of a stand (different size, different dominance position) may be linked to stand productivity patterns.

Hypothesis 1. RUE and canopy closure.

Different patterns of RUE in relation to canopy closure, in our study represented by high vs low density plots, were observed depending on the resource analyzed. Accordingly with the hypothesis, a decrease in efficiency was associated with canopy closure in relation to nitrogen productivity and growth efficiency. In contrast, no decrease was observed in light or water use efficiency (on the assumption that $\delta^{13}\text{C}$ is correlated with iWUE) in high density plots (Fig. 4 A and D). It is important to note that, in contrast to Binkley's studies (Binkley et al., 2004) relating a decrease in RUE and canopy closure, in our study the differences in canopy openness were due to differences in the number of trees per unit area (tree density) and not due to different ages and stand development. As a consequence, the different observed patterns between those studies and the present study cannot be strictly attributed to differences in species behavior (*Eucalyptus* vs *Pinus* species).

The lower NP and GE estimated in plots with canopy closure compared to open canopy plots were the result of the presence of trees with low dbh and low RUE (see Fig. 3) but also, and in contrast to our hypothesis, due to the lower RUE of the biggest trees in high density plots in comparison with trees of similar size but growing in open canopy plots. This is an important finding of our study suggesting that the decrease in RUE of a stand, when it is observed, is due to a decrease in the efficiency of resource use of the dominant trees of the stand and not due to the decrease in the RUE of suppressed trees. It seems that the small trees have always lower RUE, independently of canopy closure of the stand. It is known that RUE of trees may increase with tree size (Gyenge et al., 2008, Binkley et al., 2013) but our results suggest that this increase could be depressed by intra-specific competition. A similar finding was reported in our previous study (Fernández and Gyenge, 2009) in which we found a general pattern of a higher WUE (estimated from sapflow density of the trees and their stem productivity) in largest trees of the stands in all cases except in a stand with very high competition level (basal area = 80 m²), where largest trees presented a trend of a decreased WUE.

However, caution must be paid in relation to the resource analyzed and the general resources availability in the site. In this regard, iWUE estimated from $\delta^{13}\text{C}$ of wood indicated a decrease in water use efficiency in small trees when canopy closures (as we hypothesized), but this was only observed in one site (MV) and not in the other (AM). Another study in AM site indicated that a lower iWUE may be expected in suppressed trees of high density stands only in particular growing seasons characterized by marked water deficits (Gyenge et al., 2012). Moreover, in contrast to the patterns of use efficiency of water and nitrogen, LUE was not related with canopy closure in neither site (Fig. 4).

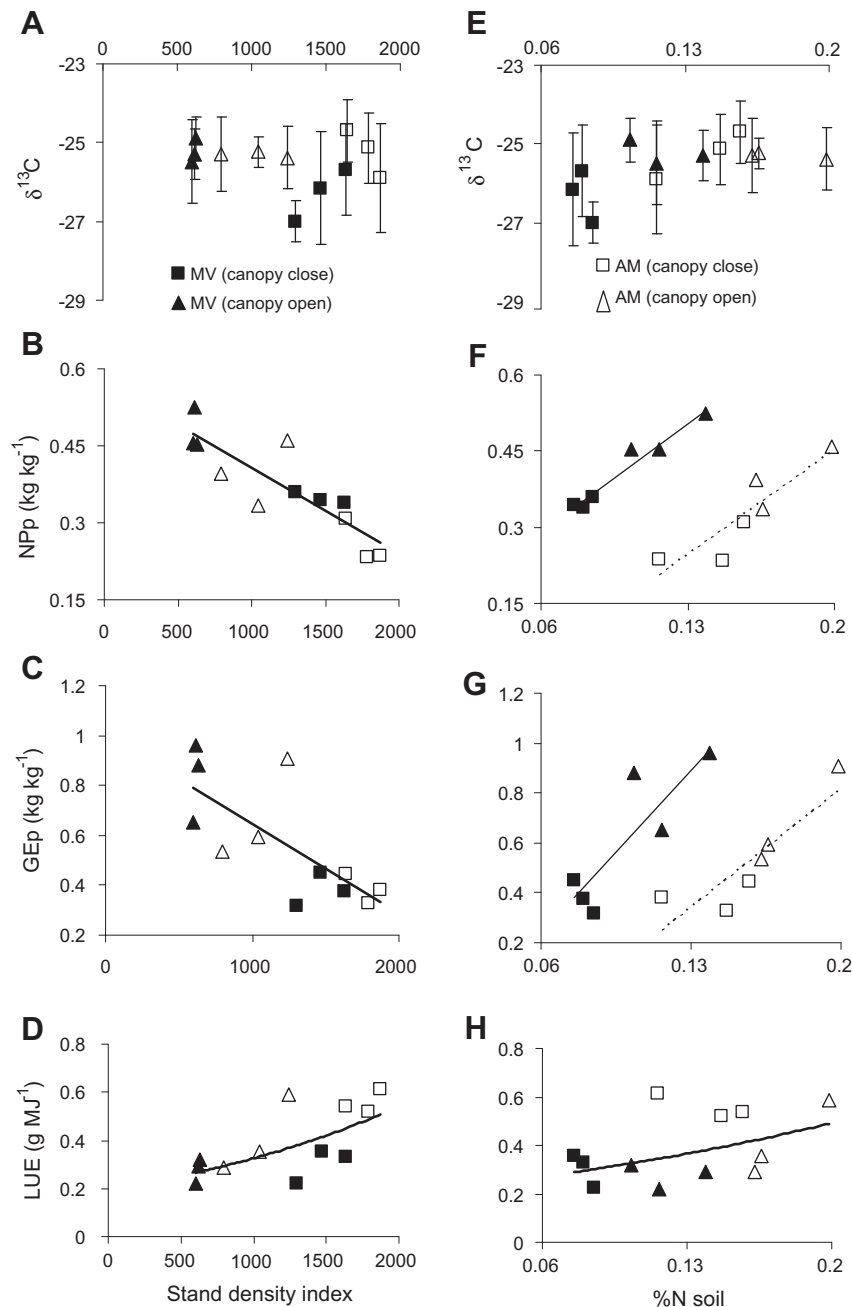


Fig. 4. Relationship between $\delta^{13}\text{C}$ in wood ring (average of the trees in each plot), nitrogen use efficiency (NPP), growth efficiency (GEp) or light use efficiency (LUE) at the plot level and stand density index, as a measure of competition level and canopy openness (left column, panels A, B, C and D) and soil nitrogen content (%N), as a measure of site fertility (right column, panels E, F, G and H) of *P. ponderosa* forests growing in Arroyo del Medio (AM) and Meliquina Valley (MV), NW Patagonia, Argentina. Filled and empty symbol represent data from MV and AM sites, respectively, meanwhile squares and triangles represent high (#1 to #3) and low (#4 to #6) density plots, respectively (see Table 2).

Some of our results are in agreement with other studies in *P. ponderosa*. The negative relationship between GEp and SDI was also observed in USA ponderosa pine forests (Zhang et al., 2013), as well as the lack of variation in $\delta^{13}\text{C}$ in relation to density management (Skov et al., 2004). However, other studies did actually find a decrease in iWUE as tree density increased in ponderosa pine native forests in Arizona (McDowell et al., 2006).

Hypothesis 2. RUE and resource availability-productivity.

When we planned the present study, we wanted to compare two sites differing in soil depth and water stress level based on previous results about water use and water status of the trees

growing in MV and AM sites (Gyenge, 2005; Gyenge et al., 2012). We considered that MV was a better site compared to AM in terms of forest productivity and resources availability on the basis of its general higher water availability for tree growth. However, we found in this study that fertility did also differ between sites, but in an opposite way, with AM site being more fertile (at least, considering soil N content) than MV. For this reason, we cannot strictly test the hypothesis about RUE and resource availability assuming that one site is better than the other, but we can only analyze patterns in relation to each particular resource availability ignoring which is the more limiting resource in each site.

Partially according to the hypothesis, within each site NP, LUE and GE showed a positive relationship with resource (N)

availability (Fig. 4). However, across sites, only LUE increases with N availability, thus being higher in AM than in MV, and GE and NP not differing between sites. The lower LUE in MV compared to AM, in spite of being the site with higher soil water availability, suggest that N is a more limiting resource for tree growth in MV than water. This agrees with studies carried out in *P. taeda* (Campoe et al., 2013) showing a very limited response to water addition but a huge increase in APAR and LUE when fertilization is applied. In contrast to the positive relationship between other RUE and soil N content, iWUE did not present any correlation with this environmental variable. However, results of WUE estimated from sapflow and stem productivity measured in the same sites but in different years than the present study, suggest that average WUE is higher in AM than in MV site (Fernández and Gyenge, 2009).

On the other hand, no clear relationship was observed between RUE or GE and water availability of the site, with all efficiencies being similar or even lower in MV – the site with higher water availability – than in AM. Thus, the trend of a positive relation of RUE and resource availability is rather weak as a generalization, but it depends on the resource which use efficiency is analyzed and the resource which its availability is considered.

On the other hand, our study can be used to test the part of the hypothesis about RUE and stand productivity or individual tree growth. Considering patterns at the stand level, only LUE presented the hypothesized pattern of a positive relationship with average plot annual aboveground productivity. No correlation was observed between GE_p and stand productivity, which contrasts with results of Zhang et al. (2013) showing a positive relationship between ponderosa pine GE_p and site index (higher GE_p in the most productive sites). NP and iWUE did not present a correlation with stand productivity.

At the individual tree level, since trees of each stand had the same age their size may be used as a proxy of their average growth. iWUE was higher in largest trees of a plot only under high competition level conditions (high density plots) (Fig. 2). This contrasts with previous findings of higher WUE in largest – more productive trees of a stand compared to the smallest – less productive trees irrespective of tree density in MV (Fernández and Gyenge, 2009). However, in the same study, no differences in WUE were observed in different size trees in AM (Fernández and Gyenge, 2009). Other studies did actually find a positive relationship between iWUE and tree growth (McDowell et al., 2006; Knapp and Soulé, 2011), and in other cases the relationship had being null in growing seasons with no marked water stress, and positive in a drought season (Gyenge et al., 2012). This highlights the complexity in interpreting iWUE patterns and also the need of distinguishing iWUE (from ¹³C or stomatal conductance and photosynthesis measures) from WUE (from transpiration and stem productivity) patterns. Allocation processes will mediate between both of them.

On the other hand, clear and positive relationships were observed between GE_t and NP_t with tree growth (estimated from their dbh), supporting the hypothesis of higher RUE in those trees which are growing faster within the stand, which in turn are those which are surely accessing to more resources (soil resources and radiation). A similar trend was observed in *P. taeda* considering their LUE, which was higher in the largest trees of the stand compared to the smallest ones, in correlation with their amount of captured resource (APAR) (Campoe et al., 2013). In addition, as was mentioned before, an increase in LUE and APAR of the trees was estimated in response to fertilization and irrigation (Campoe et al., 2013), that is, when more resources were available for the trees and their growth was also increased. These results reinforces the idea (proposed in Fernández and Gyenge, 2009) that RUE could be increased applying management practices leading to increase growth of selected trees, such as thinning, fertilization and irrigation (see below).

Hypothesis 3. Correlation between different resources use efficiency and GE.

The third hypothesis stated in this study was not supported with our results. The only significant correlation was that observed between NP and GE, with no correlation at all between iWUE and the other resources use or growth efficiency. This lack of relationship could be due to the hydraulic plasticity of *P. ponderosa* in response to water shortage. The capacity to produce short- and long-term adjustments in their water relations allows the species to maintain relatively constant values of iWUE even with high levels of intra-specific competition or climatic constraints (McDowell et al., 2006; Gyenge et al., 2012). Since carbon fixation cannot be maintained at the same level (Gyenge et al., 2012), then other resources use efficiency may decrease in parallel with growth uncoupling patterns with iWUE. However, it seems that maintenance of relatively constant iWUE is constrained when water and radiation are co-limiting carbon fixation as occurs in suppressed trees of plots with high degree of competition (SDI > 1300) (Gyenge et al., 2012).

4.1. Implications for forest management

Our results are in agreement with Zhang et al. (2013) and the widely observed principle that stands managed at lower densities grow trees of larger diameters. At the same time, tree size and the degree of intra-specific competition have a strong influence on resource capture and use efficiency (Gyenge et al., 2012; Zhang et al., 2013; Campoe et al., 2013). Thinning produces a decrease in resource competition (for example, for nutrients (Berthrong et al., 2009) and radiation (Binkley et al., 2013)) and also may increase the absolute amount of available resources such as water due to the decrease in precipitation interception (e.g. Licata et al., 2011). This higher resource availability may contribute to increase not only tree growth but also its RUE.

In this study soil N content was lower in the plots with high than in low SDI, maybe as a product of high biomass accumulation. A meta-analysis showed a decrease of soil N under forest plantations compared to other soil uses as a result of the capacity of trees to take up considerable amounts of nutrients from the soil (Berthrong et al., 2009). The amount of available nutrients may be crucial for forest RUE as it is suggested by some studies. The higher LUE in the more fertile (AM) compared to the less fertile site (MV) in the present study also feeds this idea, as well as the similar trends in WUE (based on stand transpiration and productivity) observed in a previous study (Fernández and Gyenge, 2009). Further research is needed in order to evaluate the relative importance of fertilization vs other silvicultural practices (thinning, irrigation) in interaction with species eco-physiological characteristics (Fernández et al., 2011) in determining RUE increases.

Acknowledgment

The authors wish to thank INTA (National Institute for Agricultural Technology of Argentina) and CONICET (National Council for Scientific and Technical Research of Argentina) for providing the financial support through PNFOR042131 and PNFOR042141 and PIP 1122008010239101, respectively.

References

- Aerts, R., Chapin III, F.S., 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30, 1–67.
- Allen, C.B., Will, R.E., Jacobson, M.A., 2005. Production efficiency and radiation use efficiency of four tree species receiving irrigation and fertilization. *For. Sci.* 51, 556–569.

- Araujo, P., 2006. Impactos de las plantaciones de pino sobre el ciclo de carbono a lo largo de un gradiente de precipitaciones en la Patagonia, Argentina. PhD Thesis, Facultad de Agronomía, Universidad de Buenos Aires, Argentina. p. 152.
- Binkley, D., 2004. A hypothesis about the interaction of tree dominance and stand production through stand development. *For. Ecol. Manage.* 190, 265–271.
- Binkley, D., Stape, J.L., Ryan, M.G., 2004. Thinking about efficiency of resource use in forests. *For. Ecol. Manage.* 193, 5–16.
- Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R., Fownes, J., 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. *Ecosystems* 5, 58–67.
- Binkley, D., Cargo Campoe, O., Gspalti, M., Forrester, D.I., 2013. Light absorption and use efficiency in forests: why patterns differ for trees to stands. *For. Ecol. Manage.* 288, 5–13.
- Berthrong, S.T., Jobbágy, E.G., Jackson, R.B., 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecol. Appl.* 19, 2228–2241.
- Campoe, O.C., Stape, J.L., Albaugh, T.J., Allen, H.L., Fox, T.R., Rubilar, R., Binkley, D., 2013. Fertilization and irrigation effects on tree level aboveground net primary production, light interception and light use efficiency in a loblolly pine plantation. *For. Ecol. Manage.* 288, 43–48.
- Cochran, P.H., 1992. Stocking levels and underlying assumptions for uneven-aged ponderosa pine stands. USDA. Forest. Service. Pacific Northwest Research Station. Portland, Oregon. Research Note PNW-RN-509. p. 10.
- Forrester, D.I., Collopy, J.J., Beadle, Ch.L., Warren, Ch.R., Baker, T.G., 2012a. A. Effect of thinning, pruning and nitrogen fertilizer application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation. *For. Ecol. Manage.* 266, 286–300.
- Forrester, D.I., Collopy, J.J., Beadle, Ch.R., Baker, T.G., 2012b. B. Interactive effects of simultaneously applied thinning, pruning and fertilizer application treatments on growth, biomass production and crown architecture in a young *Eucalyptus nitens* plantation. *For. Ecol. Manage.* 267, 104–116.
- Finzi, A.C., Norby, R.J., Calfapietra, C., Gallet-Budynek, A., Gielen, B., Holmes, W.E., Hoosbeek, M.R., Iversen, C.M., Jackson, R.B., Kubiske, M.E., Ledford, J., Liberloo, M., Oren, R., Polle, A., Pritchard, S., Zak, D.R., Schlesinger, W.H., Ceulemans, R., 2007. Increases in nitrogen uptake rather than nitrogen-use efficiency support higher rates of temperate forest productivity under elevated CO₂. *PNAS* 104, 14014–14019.
- Fernández, M.E., Fernández Tschieder, E., Letourneau, F., Gyenge, J.E., 2011. Why do *Pinus* species have different growth dominance patterns than *Eucalyptus* species? A hypothesis based on differential physiological plasticity. *For. Ecol. Manage.* 261, 1061–1068.
- Fernández, M.E., Gyenge, J.E., 2009. Testing Binkley's hypothesis about the interaction of individual tree water use efficiency and growth efficiency with dominance patterns in open and close canopy stands. *For. Ecol. Manage.* 257, 1859–1865.
- Fernández, M.E., Gyenge, J.E., Varela, S., de Urquiza, M., 2012. Improving adaptability to climate change in forestry species: drought effects on growth and wood anatomy of ponderosa pines growing at different competition levels. *For. Syst.* 21, 162–173.
- Fernández Tschieder, E., Fernández, M.E., Schlichter, T.M., Pinazo, M.A., Crechi, E.H., 2012. Influence of growth dominance and individual tree growth efficiency on *Pinus taeda* stand growth. A contribution to the debate about why stands productivity declines. *For. Ecol. Manage.* 277, 116–123.
- Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-color fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York, USA.
- Gyenge, J.E., 2005. Uso de agua y resistencia a la sequía de las principales especies forestales del noroeste patagónico, pino ponderosa y ciprés de la cordillera. PhD. Thesis. Universidad Nacional del Comahue, p. 364.
- Gyenge, J.E., Fernández, M.E., Schlichter, T.M., 2008. Testing a hypothesis of the relationship between productivity and water use efficiency in Patagonian forests with native and exotic species. *For. Ecol. Manage.* 255, 3281–3287.
- Gyenge, J.E., Fernández, M.E., Varela, S.A., 2012. Short- and long-term responses to seasonal drought in ponderosa pines growing at different plantation densities in Patagonia, South America. *Trees* 26, 1905–1917.
- Hoefs, J., Schidlowski, M., 1967. Carbon isotope composition of carbonaceous matter from the Precambrian of the Wirwatersrand system. *Science* 155, 1096–1098.
- Knapp, P.A., Soule, P.T., 2011. Increasing water-use efficiency and age-specific growth responses of old-growth ponderosa pine trees in the Northern Rockies. *Glob. Change Biol.* 17, 631–641.
- Laclau, P., 2003. Biomass and carbon sequestration of ponderosa pine plantations and native cypress forests in Northwest Patagonia. *For. Ecol. Manage.* 180, 317–333.
- Licata, J., Gyenge, J.E., Fernandez, M.E., Schlichter, T.M., Bond, B.J., 2008. Increased water use by Ponderosa pine plantations in northwestern Patagonia, Argentina compared with native vegetation. *For. Ecol. Manage.* 255, 753–764.
- Licata, J.A., Pypker, T.G., Weigandt, M., Unsworth, M.H., Gyenge, J.E., Fernández, M.E., Schlichter, T.M., Bond, B.J., 2011. Decreased rainfall interception balances increased transpiration in exotic ponderosa plantations compared with native cypress stands in Patagonia, Argentina. *Ecohydrology* 4, 83–93. <http://dx.doi.org/10.1002/eco.125>.
- McDowell, N.G., Adams, H.D., Bailey, J.D., Hess, M., Kolb, T.E., 2006. Homeostatic maintenance of ponderosa pine gas exchange in response to stand density changes. *Ecol. Appl.* 16, 1164–1182.
- Panarello, H.O., 1987. Relaciones entre isótopos de elementos livianos para estudiar procesos ambientales y paleotemperaturas. PhD thesis, Universidad de Buenos Aires, FCEN, Buenos Aires, Argentina, p. 105.
- Ryan, M.G., Waring, R.H., 1992. Maintenance respiration and stand development in a subalpine lodgepole pine forest. *Ecology* 73, 2100–2108.
- Skov, K.R., Kolb, T.E., Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. *For. Sci.* 50, 1–11.
- Stape, J.L., Binkley, D., Ryan, M.G., 2004. *Eucalyptus* production and the supply, use and efficiency of use of water, light and nitrogen across a geographic gradient in Brazil. *For. Ecol. Manage.* 193, 17–31.
- Waring, R.H., Thies, W.G., Muscato, D., 1980. Stem growth per unit of leaf area: a measure of tree vigor. *For. Sci.* 26, 112–117.
- Zhang, J., Ritchie, M.W., Maguire, D.A., Oliver, W.W., 2013. Thinning ponderosa pine (*Pinus ponderosa*) stands reduces mortality while maintaining stand productivity. *Can. J. For. Res.* 43, 311–320.