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Acclimation to irradiance of leaf photosynthesis and associated nitrogen reallocation in photosynthetic apparatus in the year following thinning of a young stand of *Chamaecyparis obtusa*

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Abstract

In order to quantify the effects of thinning on photosynthetic parameters and associated change in leaf nitrogen (N) contents**,** half of the trees in a 10-year-old *Chamaecyparis obtusa* (Sieb. *et* Zucc.) Endl. stand (36˚3'N, 140˚7'E) were removed, giving a final density of 1 500 trees ha^{-1}, in May 2004. Photosynthetic photon flux density (PPFD) and leaf N and carbon (C) contents in the lower (L), middle (M), and upper (U) crowns were monitored one, three, and five months after thinning in both the thinned stand and a non-thinned control stand. In addition, leaves' photosynthetic responses to CO_2 concentration were simultaneously measured *in situ* to estimate the maximum rates of carboxylation (V_{cmax}) and electron transport (J_{max}). Thinning increased PPFD in the L and M crowns but not in the U crown. V_{cmax} in both the L and M crowns of the thinned stand increased significantly in comparison with the same crown position of the control stand in the three and five months following thinning. In addition, the thinned stand exhibited an increase in N partitioned to ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) in the L and M crowns relative to the control stand three and five months after thinning, indicating that N had been redistributed within the photosynthetic machinery. Thinning did not affect N per unit area at any of the crown positions, but significantly increased the content of N as a fraction of the total leaf dry mass in the L and M crowns three and five months after thinning. This was a consequence of a decrease in leaf dry mass due to rapid shoot growth. Thus thinning did not cause a redistribution of N between leaves. Thinning improved irradiance in the L and M crowns of *C. obtusa*, leading to photosynthetic acclimation. Photosynthetic acclimation in the first year mainly occurred *via* redistribution of N within but not between leaves.

Additional key words: crown position; maximum rate of carboxylation; maximum rate of electron transport; nitrogen reallocation.

Introduction

Thinning is a management practice that is widely used to increase the stem diameter growth of the residual trees (Smith 1986). The growth response of residual trees is generally attributed to increases in crown volumes (and, thus, increases in photosynthetic surface area) (Lavigne 1988, Medhurst and Beadle 2001, Yu *et al.* 2003) together with increased availability of resources such as radiant energy, mineral nutrients, and water (Morikawa *et al.* 1986, Bréda *et al.* 1995, Kolb *et al.* 1998, Tang *et al.* 1999). Responses to thinning vary in magnitude even among stands of the same species (Ginn *et al.* 1991, Peterson *et al.* 1997, Tang *et al.* 1999, 2003). Several attempts have been made to model stand growth in relation to carbon (C) dynamics and resource availability (Landsberg and Waring 1997, Sabaté *et al.* 2002). The accurate estimation of C gain and stand productivity requires an understanding of the processes of C gain and photosynthate allocation as well as the variability in canopy physiology in response to environmental changes and forest management practices (Johnsen *et al.* 2000). To our knowledge, however, there have been few studies on physiological responses to silvicultural manipulations, and they have been limited to investigations of *Pinus taeda* L. (Ginn *et al.* 1991, Gravatt *et al.* 1997, Peterson *et al.* 1997, Tang *et al.* 1999, 2003), *P. ponderosa* var. *scopulorum* Engelm. (Kolb *et al.* 1998), *Betula papyrifera* Marsh. (Wang *et al.* 1995), and *Eucalyptus nitens* (Medhurst and Beadle 2005).

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Irradiance is a major determinant of leaf nitrogen (N) content, which in turn is an important factor in leaf photosynthesis because of the large proportion of N in the photosynthetic machinery (Evans 1989). Attenuation of the photosynthetic photon flux density (PPFD) within the canopy causes a decrease in leaf N content per unit area (N_a), which optimizes canopy photosynthesis (Brooks *et al*. 1996, Schoettle and Smith 1999, Wilson *et al*. 2000, Warren and Adams 2001, Meir *et al*. 2002, Han *et al*. 2003). Changes in leaf photosynthetic capacity within tree crowns are closely linked to changes in N allocation patterns between leaves. Changes in insolation can also trigger the reallocation of N within the photosynthetic machinery in mature leaves; this is another mechanism of acclimation to irradiance (Brooks *et al*. 1996). The redistribution of N between leaves appears to act over a longer time scale than reallocation within leaves. However, few studies have focused on the photosynthetic acclimation processes and associated changes in leaf N content that are likely to follow thinning in tree crowns (Medhurst and Beadle 2005).

Chamaecyparis obusta (Sieb. *et* Zucc.) Endl., a member of the Cupressaceae, is one of the most common evergreen coniferous afforestation species in Japan. Cupressaceae species are characterized by scaly leaves that can start or cease growth quickly depending on their current environment and have no distinct over-wintering bud in the shoot tip (Harry 1987). In this study, we thinned a 10-year-old stand of *C. obtusa* in May 2004 and monitored the ensuing changes in environmental factors, leaf morphology, and leaf physiology. The main objectives of this study were to (*1*) quantify the PPFD availability after thinning, (*2*) determine if leaf photosynthetic capacity acclimates to PPFD changes in the first year after thinning, and (*3*) examine if thinning causes any N reallocation between and/or within leaves.

Materials and methods

Study site: This study was carried out in a 10-year-old *C. obtusa* stand in a field of the Forestry and Forest Products Research Institute (36˚3'N, 140˚7'E). The soil was an andisol, developed from parent materials of volcanic ash. The total N and C concentrations in the top 20-cm layer were 0.29 and 3.68 %, respectively. Mean annual precipitation and temperature near the site were 1 228 mm and 13.4 °C, respectively (1961–2004; Japanese Bureau of Meteorology). The tree density was 3 000 trees per ha. The average tree height was 4.24 m and diameter at breast height was 6.50 cm in February 2004. The stand was completely closed before thinning and forest floor vegetation was sparse. In May 2004, a plot of 126 m^2 was thinned by removing every other diagonal row in order to maintain even spacing between residual stems, giving a final density of 1 500 trees per ha, and a plot of the same size separated by a 3.6-m buffer zone was left un-thinned. The resulting stands are referred to as the thinned and control stands in the following text.

Crown irradiance measurements: We monitored PPFD in two representative trees in both the thinned and control stands. Two first order branches at each of three canopy heights (approximately 1.0, 2.0, and 3.0 m above ground), and thus in total six first order branches from each tree, were chosen as sites for measuring PPFD; these heights are hereafter referred to as the lower (L), middle (M), and upper (U) crowns, respectively. Three to six GaAsP photodiodes (*G2711-01*, *Hamamatsu Photonics K. K.*, Hamamatsu, Japan) were attached directly to a leaf surface and positioned so as to cover the whole foliated portion of the corresponding first order branch insofar as possible. One sensor was positioned above the canopy to record the unobstructed PPFD. All photodiodes were calibrated against three PPFD sensors (*LI-190SA*, *Li-Cor*, Lincoln, NE, USA) under daylight conditions. The coefficients of determination of linear regression between both types of sensor were higher than 0.99 for all photodiodes. Since the photodiodes weighed only 0.16 g, they were mounted without adjusting the orientation of the attached leaves. The PPFD was measured every minute and recorded by data loggers (*NR-1000*, *KEYENCE*, Osaka, Japan).

Gas exchange was measured *in situ* in leaves adjacent to the photodiodes (*LI-6400*, *Li-Cor*) in June, August, and October 2004, *i.e.* one, three, and five months after thinning. One to three leaves of all age classes were chosen from the outer, middle, and inner crowns of the first order branches because it was difficult to distinguish the age classes of the scaly leaves, especially leaves older than one year (Harry 1987). Photosynthetic response curves to intercellular CO_2 concentration (P_N/C_i) were constructed by taking measurements at 10 CO_2 concentrations, ranging from 50 to 1 800 μmol mol^{-1} as described by Han *et al*. (2004). The leaf surfaces were exposed to the *6400-02B* LED light source at controlled PPFD (1 100 μmol m^{-2} s^{-1}). Leaf temperatures were kept at 28.4±1.9 °C in June, 30.4±1.8 °C in August, and 24.1±1.1 °C in October. The vapour pressure deficit in the chamber was less than 1.8 kPa during all measurements.

Leaf morphology, N and C contents: Leaves were harvested and placed in separate plastic bags after the gas exchange measurements and stored in a refrigerator prior to analysis. Projected leaf areas were measured using a scanner (*GT-9600*, *EPSON*, Tokyo, Japan) and image analysis software (*LIA32*, K. Yamamoto of Nagoya University, Nagoya, Japan). They were then dried at 70 °C for at least 48 h and weighed to calculate specific leaf areas (SLAs). Total N and C contents on a dry mass basis were determined with a gas chromatograph (*GC-8A*, *Shimadzu*, Kyoto, Japan) after combustion with circulating O_2 using an NC analyzer (*Sumigraph NC-900*, *SCAS*, Osaka, Japan) they were converted to a projected area basis using SLA.

Calculation of photosynthetic parameters: Nonlinear regression methods were used to estimate V_{cmax}, J_{max}, and dark respiration rate (R_D) from P_N/C_i curves using the model of Farquhar *et al.* (1980) following the procedures outlined by Medlyn *et al.* (2002). V_{cmax} and R_d were estimated from the P_N/C_i curve at $C_i < 200$ μmol mol^{-1}; it was assumed that below this level P_N was limited solely by the amount, activity, and kinetic properties of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) at low C_i (Wullschleger 1993). The value of J_{max} was estimated from the P_N/C_i curve when $C_i > 700$ μmol mol^{-1}, using a fixed value for the quantum yield of electron transport ($\alpha = 0.30$) and the value of R_D obtained in the V_{cmax} regression. Values for the Michaelis constants at 25 °C ($K_c = 404.9$ μmol mol^{-1} and $K_0 = 278.4$ mmol mol^{-1}), activation energies [$H_a(K_c) = 79.43$ kJ mol^{-1} and $H_a(K_0) = 36.38$ kJ mol^{-1}], and CO_2 compensation concentration [$\Gamma^* = 42.75$, $H_a(\Gamma^*) = 37.83$ kJ mol^{-1}] were obtained from Bernacchi *et al.* (2001). The temperature dependence of K_c, K_0, and Γ^* is described by:

$$f(T_k) = f(298)\exp[(T_k - 298)\,H_a/(298\,R\,T_k)]$$

where $f(T_k)$ is the value of a given parameter at leaf temperature T_k [K], $f(298)$ is the value of the parameter at 25 °C, and R is the gas constant (8.314 J mol^{-1} K^{-1}).

All V_{cmax} and J_{max} values were normalized to 25 °C using the temperature dependence of V_{cmax} and J_{max} described by the following equation (Medlyn *et al.* 2002):

$$f(T_k) = f(298)\exp\left[\frac{H_a(T_k - 298)}{298\,R\,T_k}\right]\frac{1 + \exp\left[\frac{298\,\Delta S - H_d}{298\,R}\right]}{1 + \exp\left[\frac{T_k\,\Delta S - H_d}{T_k\,R}\right]}$$

where H_d is the deactivation energy, c is a scaling constant, and ΔS is an entropy term, 0.65 kJ K^{-1} mol^{-1}. Temperature response parameters of H_a, H_d, and c were obtained by fitting the above equation to response curves of V_{cmax} and J_{max} to leaf temperature (data not shown) using *SigmaPlot* (*SPSS*, Chicago, IL, USA).

Based on *in vitro* RuBPCO kinetics, and the assumptions that all RuBPCO was fully activated and CO_2 transfer conductance was infinite, the model proposed by Niinemets and Tenhunen (1997) was used to estimate the proportion of leaf N in RuBPCO (P_R: g N in RuBPCO per g total leaf N) from the values of V_{cmax}:

$$V_{cmax} = 6.25\,V_{cr}\,N_a\,P_R$$

where 6.25 is the ratio of the mass of RuBPCO to the mass of N in RuBPCO, and V_{cr} is the specific activity of RuBPCO, which is assumed to be a function of temperature alone [20.48 mmol(CO_2) kg^{-1}(RuBPCO) s^{-1} at 25 °C].

Data analysis: The leaf irradiance environment (rPPFD) was defined by the ratio of the mean daily PPFD at the leaf over the two weeks preceding the gas exchange measurements on the leaf to the mean daily PPFD above the canopy during the same period.

We did not replicate treatments because it would lead to longer time cost for detailed gas exchange measurements within crowns. In consequence, it would be impractical to compare the effect of thinning on physiological changes of different crown positions because most physiological parameters tend to change seasonally. To test the effects of thinning without treatment replication, comparisons were carried out between the thinned and control stands in the same season and crown positions by *t*-tests using *StatView* (*SAS Institute*, Cary, NC). Two-way analysis of variance was used to test the influence of crown position (L, M, and U) and season (June, August, and October) on photosynthetic parameters, leaf N and C contents, and SLA within either the thinned or control stands.

Results

Effect of thinning on irradiance environment: In the control stand, leaves in the L crown of *C. obtusa* had rPPFD values as low as 0.01 (Fig. 1). Thinning significantly increased the rPPFD in both the L and M crowns. However, in the U crown, there was no significant difference in rPPFD between the thinned and control stands. There was a wide range of horizontal variation in leaf PPFD from the outer to the inner crown at the same vertical height, as observed in earlier studies on evergreen conifers (Brooks *et al.* 1996, Han *et al.* 2003).

Effects of thinning on V_{cmax} and J_{max}: The biochemical photosynthetic parameters V_{cmax} and J_{max} had different values at different crown positions and V_{cmax} exhibited seasonal changes in both the thinned and control stands (Table 1). Therefore we further compared the effects of thinning on these parameters at each crown position in the same month (Fig. 2). A month after thinning in June, there were no significant differences in V_{cmax} and J_{max} between the thinned and control stands at all crown positions. Three months after thinning in August, however, V_{cmax} in the L and M crowns of the thinned stand had increased by 60 and 35 %, respectively, relative to the control stand. These increases in V_{cmax} in the L and M crowns were also observed in October. A statistically significant increase in J_{max} due to thinning was observed only in the M crown, three and five months after thinning (Fig. 2*B*).

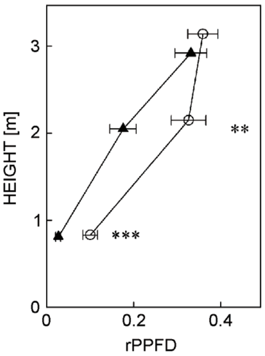

Fig. 1. Comparison of the relative photosynthetic photon flux (rPPFD) in the crowns of thinned (*circles*) and non-thinned control (*triangles*) stands of *Chamaecyparis obtusa*. Significant differences between the respective values of the two groups are: $^{**}p<0.01$; $^{***}p<0.001$. Means ± SE (n = 12–24 photodiodes).

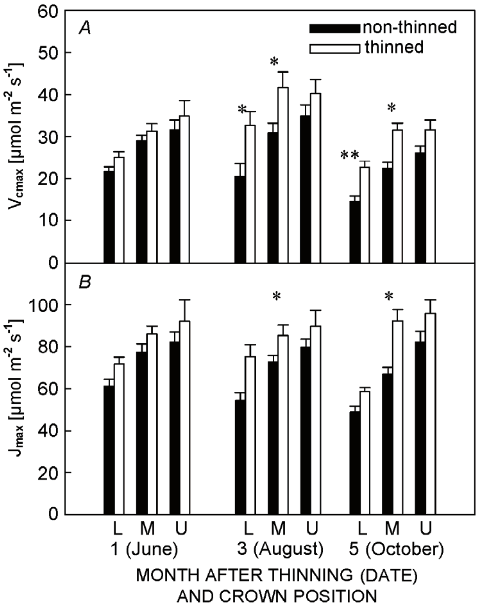

Fig. 2. Comparison of (*A*) the maximum rate of carboxylation (V_{cmax}) and (*B*) the maximum rate of electron transport (J_{max}) in the lower (L), middle (M), and upper (U) crown positions of *Chamaecyparis obtusa* between the thinned (*open bars*) and non-thinned control (*filled bars*) stands one, three, and five months after thinning. Significant differences between the respective values for the two groups are: $^{*}p<0.05$; $^{**}p<0.01$. Means ± SE (n = 12–24 leaves).

Effects of thinning on leaf morphology and leaf N and C contents: Significant differences in leaf N_a between the various crown positions were observed, but these did not change seasonally in either the thinned or control stands when all data were pooled (Table 1). When comparisons were made at each crown position in the same month, thinning was not found to have any significant effect on N_a other than in the M crown in August (Fig. 3*A*). Leaf N content per unit dry mass (N_m) was influenced by season and crown positions when all data were used in the analysis of variance (Table 1). The increase in N_m became significant in all crown positions in August, three months after thinning (Fig. 3*B*).

SLA differed significantly both between seasons and crown positions (Table 1). Thinning significantly influenced SLA in the U crown in August three months after thinning and in all crown positions five months after thinning (Fig. 3*C*). Excluding data on current-year leaves did not qualitatively change the conclusions reached (data not shown).

Leaf carbon content on aerea basis (C_a) was significantly influenced by season and crown position when all data were pooled in the analysis of variance (Table 1). Thinning affected C_a in the upper crown one month after thinning, and in all positions five months after thinning (Fig. 3*D*).

Table 1. Effects of crown position (C) and season (S) on photosynthetic parameters, leaf nitrogen and carbon contents, and morphology within either the thinned or non-thinned control stands of *Chamaecyparis obtusa* tested with a two-way analysis of variance. The interaction between crown position and season was not significant at $p>0.05$. V_{cmax} = maximum rate of carboxylation; J_{max} = maximum rate of electron transport; SLA = specific leaf area; N_m = total leaf nitrogen content on dry mass basis; N_a = total leaf nitrogen content on area basis; C_a = leaf carbon content on area basis; P_R = the proportion of leaf nitrogen in ribulose-1,5-bisphosphate carboxylase/oxygenase. Statistical significance: ns = $p>0.05$; $^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

	Source	V_{cmax}	J_{max}	N_a	N_m	SLA	C_a	P_R
Thinned	C	***3	***	***	*	***	***	ns
	S	***	ns	ns	***	***	***	***
Control	C	***	***	***	***	***	***	***
	S	***	*	ns	**	***	***	***

Effects of thinning on the proportion of leaf N in RuBPCO: Seasonal changes in this proportion (P_R) were observed in both the thinned and control stands when all data were pooled (Table 1). In the control stand, there was a distinct difference in P_R between different crown positions ($p<0.001$); this difference was not observed in the thinned stand (p=0.29). There was no significant increase in P_R in the thinned stand relative to the control stand one month after thinning (Fig. 4). However, in August, three months after thinning, the thinned stand exhibited an increase in P_R in the L and M crowns but not in the U crown. Similar results were also observed in October.

Discussion

Thinning increased PPFD in the L and M crowns of *C. obtusa* (Fig. 1). This increased photon availability enhanced photosynthetic capacity, and strongly significant differences in photosynthetic parameters such as V_{cmax} between the thinned and control stands were found three and five months after thinning (Fig. 2*A*). The increase in photon-saturated photosynthesis that follows thinning in lower crowns has also been investigated in *P. taeda* (Ginn *et al.* 1991, Gravatt *et al.* 1997, Tang *et al.* 1999, 2003) and *P. ponderosa* var. *scopulorum* Engelm. (Kolb *et al.* 1998). The results of the present and cited studies indicate that an increase in photon availability is the driving force for the detected increase in photosynthetic capacity. However, there were no reports on the effect of thinning on the spatial relationship between photosynthetic capacity and leaf N contents until very recently, when Medhurst and Beadle (2005) published the results of a study on *Eucalyptus nitens*. These authors concluded that enhanced photosynthesis observed in the second year after thinning was due to an increase in N_a. However, we found no increase in N_a in the first year after thinning in *C. obtusa* in this study (Fig. 3*A*). Kolb *et al.* (1998) also inferred that the increase in photon-saturated photosynthesis was not related to N_a in *P. ponderosa* var. *scopulorum*. This difference might be due to different measuring time after thinning because redistribution of N between leaves probably acts over a longer time scale than reallocation within leaves (Brooks *et al.* 1996). In our experiment, there was a distinct difference in P_R between different crown positions in the control stand, but not in the thinned stand (Table 1). In addition, P_R in the lower and middle crowns was significantly higher in the thinned than in the control stand three months after thinning (Fig. 4). This indicates increases of P_R in those crown positions in the thinned stand. However, no increase in N_a was measured (Fig. 3*A*). There is evidence showing N reallocation within photosynthetic apparatus such as photon harvesting and RuBPCO responding to irradiance change (Brooks *et al.* 1994, Evans and Poorter 2001). It is likely that before thinning, N was largely present in the light-harvesting complex due to the low irradiance, and that it might be redistributed to RuBPCO following the irradiance changes after thinning. Such a redistribution of N within leaves is a prime mechanism of photosynthetic acclimation to the current irradiance (Brooks *et al.* 1996).

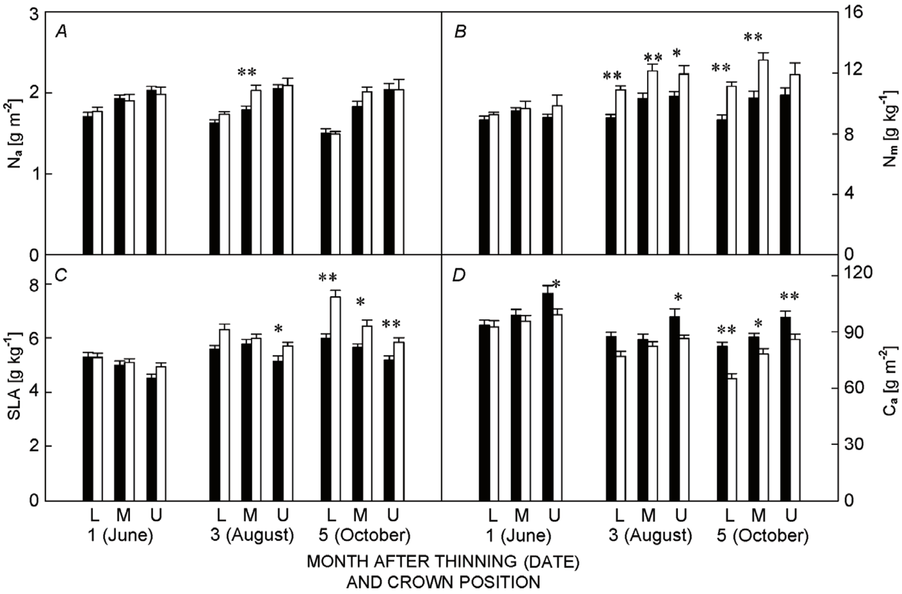

Fig. 3. Comparison of leaf nitrogen content per (*A*) unit area (N_a) and (*B*) unit dry mass (N_m), (*C*) specific leaf area (SLA), and (*D*) leaf carbon content per unit area (C_a) in the lower (L), middle (M), and upper (U) crown positions of *Chamaecyparis obtusa* between the thinned (*open bars*) and non-thinned control (*filled bars*) stands one, three, and five months after thinning. Significant differences between the respective values of the two groups: $^{*}p<0.05$; $^{**}p<0.01$. Means ± SE (n = 12–24 leaves).

Although thinning did not affect N_a (Fig. 3*A*), it influenced N_m in all crown positions in August three months after thinning (Fig. 3*B*). These differences in the responses between N_a and N_m are associated with changes in SLA. Although the SLA was greater in the L than the U crown, increases in irradiance increased SLA in all crown positions five months after thinning (Fig. 3*C*). These findings conflict with expectations in terms of irradiance acclimation, as it is generally accepted that leaf SLA decreases in response to increased irradiance (Meir *et al.* 2002, Han *et al.* 2003). SLA could increase either through increases in leaf area (although mature leaves are unlikely to expand) or through reductions in leaf dry mass. A comparison of SLA between the thinned and control stands based solely on mature leaves did not qualitatively change the conclusions reached (data not shown). Leaf C content per unit area was significantly lower in the thinned than in the control stand, and exhibited seasonal decreases (Fig. 3*D*). Branches are considered to be autonomous with regard to C during most of the growing season (Sprugel *et al*. 1991, Lacointe *et al*. 2004). This implies that most of the C required for shoots to grow is drawn from adjacent foliage, rather than from foliage on other branches. In the L crown of the thinned stand, an increase in photosynthetic capacity might result in the accumulation of more photosynthates in leaves. Cupressaceae species have scaly leaves that can start or cease growth quickly depending on their current environment (Harry 1987). The increased source activity of mature leaves that followed the thinning in the present study increased the translocation of photosynthates to the nearest metabolic sinks, promoting the elongation of emerging leaves and shoot growth (data not shown). These detected changes might lead to a reduction in mature leaf dry mass, which would in turn give rise to increase in SLA after thinning. The observed increases in N_m and constant N_a were probably due to reductions in leaf dry mass (Fig. 3*A*,*B*). These results suggest that there was no N reallocation between leaves within the tree crown in the first year of thinning, in accordance with earlier studies on *P. taeda* (Ginn *et al*. 1991).

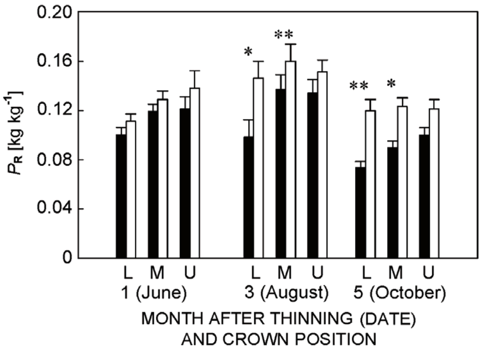

Fig. 4. Comparison of the proportions of leaf nitrogen in ribulose-1,5-bisphosphate carboxylase/oxygenase per total leaf nitrogen (P_R) at lower (L), middle (M), and upper (U) crown positions of *Chamaecyparis obtusa* between the thinned (*open bars*) and non-thinned control (*filled bars*) stands one, three, and five months after thinning. Significant differences between the respective values of the two groups: $^{*}p<0.05$; $^{**}p<0.01$. Means ± SE (n = 12–24 leaves).

In conclusion, the L crown foliage of *C. obtusa* was able to quickly utilize the increased irradiance resulting from thinning. Increases in photosynthetic capacity in the first year after thinning were mainly caused by the redistribution of N within the leaves' photosynthetic machinery; no redistribution of N between leaves was observed. Photosynthetic acclimation in *C. obtusa* in conjunction with the process of crown re-closure deserves further examination.

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