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Leaf Photosynthetic Responses to Thinning

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1. Introduction

Plants, as sessile organisms living in a changing light environment, exhibit a remarkable capacity to adjust their morphology and physiology to a particular set of light conditions by acclimation or, more broadly, phenotypic plasticity (Oguchi et al., 2005). Many studies have documented remarkable light-driven structural and functional modifications, with responses occurring from the level of the chloroplast to the whole plant. For instance, plants are able to adjust leaf area per unit biomass invested in leaves (i.e., specific leaf area) by altering leaf thickness (Niinemets, 1999). A linear relationship has been observed between growth irradiance and the reciprocal of specific leaf area between species, within species grown in different habitats and within individual tree crowns (Bond et al., 1999; Han et al., 2003). Photosynthetic capacity, measured in the form of either light saturated photosynthetic rate or the maximum rate of carboxylation, also varies according to growth irradiance.

Nitrogen, another key resource involved in the process of carbon fixation, plays an important role in the dynamics of the leaf canopy (Hikosaka, 2004; 2005). A linear relationship between photosynthetic capacity and leaf nitrogen concentration has been found in various species and canopies (Bond et al., 1999; Brooks et al., 1996; Han et al., 2004; Wilson et al., 2000); this is because of the large amount of nitrogen in the photosynthetic machinery (Evans & Seemann, 1989). In addition, fractional nitrogen within the leaf photosynthetic apparatus responds to changes in light and nitrogen availability. For example, the proportion of total leaf nitrogen partitioned into light harvesting proteins has been found to be higher in the lower crowns of deciduous broadleaf trees (Koike et al., 2001). Moreover, the proportion of total leaf nitrogen partitioned into ribulose-1,5-bisphosphate carboxylase/oxygenase (a key enzyme for carbon fixation) has been found to be higher at increased light levels in *Picea abies* (L.) Karst. (Grassi & Bagnaresi, 2001). These structural and functional responses enhance light capture, resource use and the photosynthetic efficiency of the whole tree crown, thus increasing plant performance and productivity.

Thinning, a common forest management practice used to reduce stand density, has been employed to enhance wood quality, for successive harvesting and to increase stand productivity (Cutini, 2001; Fujimori, 2001; Muñoz et al., 2008; Skovsgaard, 2009). Although the basic theory of the relationship between stand density and plant growth was developed in the early 1960s, the physiological mechanisms behind this traditional forest management practice are not well understood. At present, only 14 references with the words “thinning” and “photosynthesis” or “physiology” in the title can be found in the ISI Web of Science.

Species	Site location	DBH (cm)	Thinning treatments	Gas exchange measured after thinning	Source
<i>Chamaecyparis obtusa</i>	36°3'N, 140°7'E	6.5	From 3000 to 1500 trees ha ⁻¹ at 10 years old	1 st growing season	Han et al 2006
				2 nd to 4 th growing season	Han and Chiba 2009
<i>Pinus taeda</i>	31°11'N, 92°41'E	na	From 2990 to 731 trees ha ⁻¹ at 8 years old	5 th growing season	Gravatt et al 1997
				6 th growing season	Tang et al 1999
				8 th growing season	Tang et al 2003
	36°78'N, 80°08'W	14.2	From basal area 16.8 to 9.4 m ² ha ⁻¹ at 8 years old	1 st to 2 nd growing season	Ginn et al 1991
				3 rd to 7 th growing season	Peterson et al 1997
<i>Pinus ponderosa</i>	35°15'N, 111°42'W	na	Basal area thinned from 33.0, 38.0 to 18.0, 22.0 m ² ha ⁻¹ at 250 years old	1 st to 2 nd growing season	Skov et al 2004
	46°5'N, 114°15'W	na	From 420 to 280 trees ha ⁻¹ at 70 years old	8 th to 9 th growing season	Sala et al 2005
	44°25'-30'N, 121°37'-40'W	58.4 - 79.2	Basal area thinned from 31.4-60.0 to 8.4-12.2 m ² ha ⁻¹ at 250 years old	7 th to 15 th growing season	McDowell et al 2003
	35°16'N, 111°44'W	40.9, 30.5, 26.7, 10.7	Basal area maintained to 6.9, 18.4, 27.6, 78.2 m ² ha ⁻¹ by thinning for 32 years commencing at 43 years old	32 nd growing season	Kolb et al 1998
<i>Eucalyptus nitens</i>	43°21'S, 146°54'E	na	From 1430 to 250 trees ha ⁻¹ at 8 years old	2 nd to 3 rd growing season	Medhurst and Beadle 2005
<i>Betula papyrifera</i>	na	na	From 11000-31000 to 400, 1000 and 3000 stems ha ⁻¹ at 9-13 years old	2 nd to 3 rd growing season	Wang et al 1995
<i>Juglans nigra</i>	40°19'N, 86°42'W	23.1	From 612 to 74 trees ha ⁻¹ at 19 years old	1 st to 2 nd growing season	Gauthier and Jacobs 2009

Table 1. List of studies on the effect of thinning on photosynthesis

However, global warming has heightened awareness of the importance of estimating the amount of carbon that is fixed by forests and, in addition, separating the effects on carbon fixation caused by silvicultural manipulation from those due to climate change. The accurate estimation of carbon gain requires an understanding of the processes and the allocation of photosynthates, as well as the variation in canopy physiology in response to

environmental changes and forest management practices (Chiba, 1998; Johnsen et al., 2000; Simioni et al., 2008). In this chapter, changes in resource availability and leaf photosynthetic response after thinning are summarized, based on information from the limited number of reports available (Table 1). The focus is on the effects of thinning on (1) the availability of light, nitrogen and water, and (2) photosynthetic acclimation to changes in resource availability.

2. Changes in resource availability

Stand productivity is closely related to resource availability, especially when the latter is limited. Total leaf area and its distribution within a tree crown, the unit of photosynthesis at the individual level, are important determinants of canopy photosynthesis (Monsi & Saeki, 1953). The optimum leaf area index (LAI, total leaf area per ground area), when canopy photosynthesis is maximized, is closely related to light attenuation within the canopy and nitrogen distribution between leaves. When the stomata open to allow carbon dioxide (CO₂) to diffuse into the leaf, water is lost through transpiration. Water supply and demand interactions regulate conductance of CO₂ via the stomata and thus affect photosynthesis. Therefore, soil water availability is as important a resource as light and nutrients in relation to stand productivity. Thinning improves the availability of resources such as light, mineral nutrients and water available to the retained trees.

2.1 Light

Thinning obviously increases light intensity. The magnitude of light increase varies between canopy positions and depends on the stand density before thinning, thinning intensity, tree size/age and species. For example, in an eight-year-old *Pinus taeda* L. stand (see Table 1 for detailed site information), photosynthetic photon flux density (PPFD) increased by 28-52% as a result of thinning (Tang et al., 1999). In most studies, PPFDs are measured at various points down through the canopy or individual tree crown. As trees grow taller, a wide range of horizontal variation in leaf PPFD develops from the outer to the inner crown at the same vertical height (Brooks et al., 1996; Han et al., 2003). Therefore, light improvement after thinning also varies with respect to horizontal crown position, especially in shade tolerant species with a large proportion of leaves along first-order branches. For example, relative PPFD in the lower crown in a completely closed 10-year-old *Chamaecyparis obtusa* (Sieb. Et Zucc.) Endl. stand (Table 1, Figure 1), varied from 0.05-0.24 with average of 0.11 in the thinned stand, while the proportion was 0.03 in the unthinned control stand (Han et al., 2006). As shown in Figure 1, the improved rPPFD in all crown positions decreased progressively with height growth and the process of crown re-closure in the thinned stand, although values were still higher than those at the same heights in the control stand three years after the thinning operation.

2.2 Nutrients

In most regions, nutrients limit forest productivity. Thinning influences the nutrient cycle and thus has a direct impact on soil fertility. Therefore, thinning is an important management practice for both the production of high-quality timber and the conservation of soil fertility. For example, Blanco et al (2008) found that thinning seems to affect nutrient returns mainly by reducing aboveground biomass and litterfall in *Pinus sylvestris* L. forests

in northern Spain. Inagaki et al (2008) reported that net nitrogen mineralization in the surface soil and fresh-leaf nitrogen concentration in thinned plots was significantly greater than in control plots in two *Chamaecyparis obtusa* plantations in southern Japan. The increase in nitrogen mineralization rate after thinning is considered to be related to soil microbial activity, caused by changes in soil temperature and soil water content (see next section), and increases in the pool of soil inorganic nitrogen and other nutrients due to reduced plant uptake. In addition, Inagaki et al considered increases in the input of fresh leaves after thinning because of the high frequency of severe typhoons in the study region. Moreover, both studies were conducted one to two years after thinning. Such short-term effects are usually temporary, and the ammonium or nitrate pool size, net mineralization, microbial activity and potentially mineralizable nitrogen usually return to pretreatment values within only a few years of thinning (Sala et al., 2005).

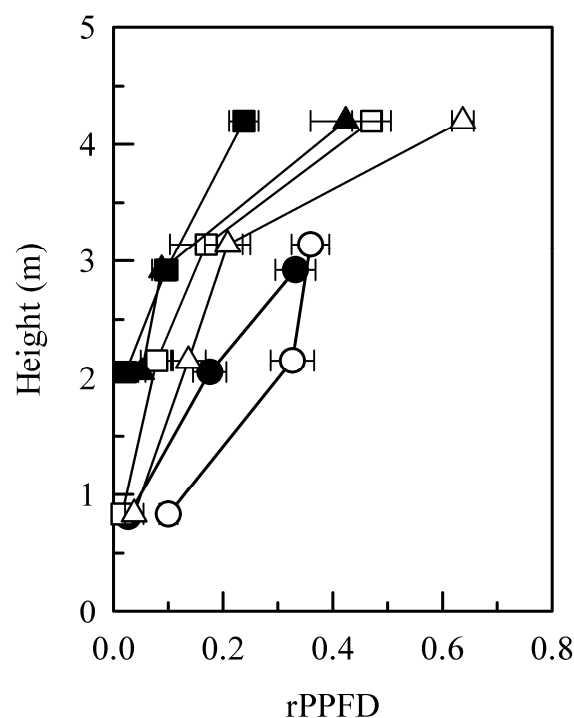


Fig. 1. Comparison of the relative photosynthetic photon flux density (rPPFD, monthly averaged value in October) in the crowns of thinned (open symbols) and non-thinned control (filled symbols) stands of *Chamaecyparis obtusa* in 2004 (circles), 2005 (triangles), and 2006 (squares). Values are means \pm SE ($n = 12$ to 24 photodiodes). With kind permission from Springer Science+Business Media: <Journal of Forest Research, Leaf photosynthetic responses and related nitrogen changes associated with crown reclosure after thinning in a young *Chamaecyparis obtusa* stand, 14, 2009, 349-357, Q. Han & Y. Chiba, Fig.1 >.

Thinning also improves the nutrient supply indirectly due to reduced competition between the retained trees. However, thinning may result in an increase in understory biomass, which also competes for nutrients. Consequently, nutrient resources for retained trees may be more limited than expected. For example, in a study of *Pinus ponderosa* var. *scopulorum* Engelm. stands (Table 1), basal area was maintained at 6.9, 18.4, 27.6 and 78.2 m² ha⁻¹ by frequent thinnings for 32 years (Kolb et al., 1998). Leaf nitrogen concentration was greatest in trees in the intermediate basal area plots, probably because the total competition for

nitrogen between a tree and its neighbors, herbaceous plants and shrubs was less than the total competition for nitrogen at either higher or lower basal areas.

2.3 Water

Thinning leads to an increase in transpiration by the retained trees because a larger portion of the crown is exposed to the sun, leading to increased air temperature and a greater vapor pressure deficit (Jiménez et al., 2008; Lagergren et al., 2008; Morikawa et al., 1986). In contrast, stand transpiration decreases because of the reduction in number of trees per ground area (Jiménez et al., 2008; Morikawa et al., 1986). Less water consumption at the stand level results in increased soil water availability (Bréda et al., 1995; Inagaki et al., 2008; Jiménez et al., 2008; Lagergren et al., 2008). The improvement in tree water status is more significant at dry sites, in dry climates, and for species that are sensitive to soil water availability (Moreno & Cubera, 2008).

Soil water availability is affected by thinning not only through changes in transpiration, but also through canopy interception, soil evaporation and stem throughfall. A reduction in leaf area reduces the capacity of the canopy to store intercepted water and, therefore, the evaporation of intercepted water is reduced (Bréda et al., 1995; Stogsdili et al., 1992). The effect on throughfall could have a greater impact, since an increase in throughfall will increase the amount of water that infiltrates into the soil. For example, soil water content increased by 2.9-4.1% in a 50-year-old *Pinus sylverstris* forest in central Sweden after thinning, despite an increase in transpiration; this was interpreted as being the result of reduced interception and increased throughfall (Lagergren et al., 2008).

It is worth noting that soil water behaves differently at different depths and the distribution of the rooting zone is species-specific. Ignoring the link between these two issues would lead to different conclusions when exploring the effect of thinning on transpiration and soil water availability. For example, Sala et al (2005) reported increased predawn leaf water potential in thinned *Pinus ponderosa* Dougl. Ex. Laws stands, but no significant difference in soil water content was found at a depth of 15 or 45 cm, indicating that soil water measurements may not accurately reflect soil water potentials in rooting zones.

3. Photosynthesis acclimation

Photosynthetic responses and acclimation to changes in resource availability after thinning occur at the single leaf as well as the whole crown level. The occurrence, duration and magnitude of photosynthetic acclimation are apparently related to stand density and thinning intensity, site quality, and tree species, age, and vigor. In this section, the photosynthetic response to thinning is summarized with respect to three types of tree: coniferous species, evergreen broadleaf species, and deciduous broadleaf species. The site location, species and thinning information for the research examined are summarized in Table 1.

3.1 Coniferous species

Photosynthetic rates and stomatal conductance were found to increase in the lower crown in 8-year-old *Pinus taeda* trees from the first to the third growing season after thinning (Ginn et al., 1991; Peterson et al., 1997). However, this thinning effect on needle physiological parameters was not observed from the fourth growing season onwards (Peterson et al.,

1997). Thinning was not found to change leaf nitrogen concentration. The enhanced photosynthetic rates were attributed to increased light in the lower crown because the improved light availability disappeared in the fourth growing season. In contrast, at another site with the same species and with trees of the same age, this enhancement in photosynthesis persisted into the sixth and eighth growing seasons (Tang et al., 1999; Tang et al., 2003). The different durations of thinning effect between the two studies were due to different thinning intensities: the former site was thinned by 50% whereas the latter was subjected to 75% thinning. Thus, thinning intensity appears to be a key factor in determining the length of time that the impact of thinning on crown physiology persists. Like *Pinus taeda*, experimental maintenance of basal area by frequent thinnings in 43-year-old *Pinus ponderosa* stands over 32 years demonstrated that photosynthetic rate and predawn leaf water potential increased as basal area decreased from 78.2 to 6.9 m² ha⁻¹ (Kolb et al., 1998). Similar results were observed 8 years after thinning in a 70-year old *Pinus ponderosa* forest (Sala et al., 2005), and 7-15 years after thinning in stands containing 250-year-old trees of the same species (Mcdowell et al., 2003). At these two sites, photosynthetic increase was accompanied by higher predawn leaf water potential and stomatal conductance but more limited changes in leaf nitrogen concentration, indicating that changes in water availability were the dominant control over gas exchange in these old-growth forests. Furthermore, predawn leaf water potential, canopy gas exchange, and subsequent growth remained higher as long as leaf area index at stand level remained lower than the pretreatment value, indicating that forest managers can manipulate old-growth stands effectively on an infrequent basis. Moreover, ontogeny alters a plethora of plant physiological and structural traits in coping with limited light, including allometry and crown architecture. Foliage photosynthetic capacities and specific leaf areas invariably decrease with increasing tree size and age (Bond, 2000). Tree height-related enhancement in water use efficiency occurs at the expense of nitrogen due to greater leaf hydraulic limitation (Han, 2011). These ontogenic adjustments suggest that tree size and age modify the effect of thinning on photosynthetic response (Skov et al., 2004).

Although photosynthetic rate was enhanced after thinning in all the species mentioned above, none of them were found to exhibit a significant increase in leaf nitrogen concentration or a decrease in specific leaf area. The enhancements in photosynthetic rate after thinning were mainly the result of changes in light and water availabilities. It is not clear where photosynthetic capacity changes after thinning. Only recently, in a 10-year-old *Chamaecyparis obtusa* stand (Table 1), the effect of thinning on photosynthetic capacity was intensively studied over a period of four years in combination with variations in nitrogen concentration at different locations within the crown (Han et al., 2006; Han & Chiba, 2009).

The maximum rate of carboxylation exhibited significant increases in the middle and lower crown three months after thinning (Figure 2a). Although thinning did not affect leaf nitrogen concentration per unit area at any of the crown positions (Figure 2b), the thinned stand exhibited an increase in nitrogen partitioned to ribulose-1,5-bisphosphate carboxylase/oxygenase in the lower and middle crowns relative to the control stands three and five months after thinning (Figure 2c). These results indicate that nitrogen reallocation occurs within the leaves' photosynthetic apparatus: from light harvesting to carboxylation in response to improved light availability. Specific leaf area increased significantly in all crown positions five months after thinning (Figure 2d). This was a consequence of a decrease in leaf dry mass due to rapid shoot growth, which may relate to the species' unique scaly

leaves that can quickly switch between quiescence and growth depending on the sink-source relationship. These results indicate that the increase in photosynthesis in the first year after thinning mainly occurred as a result of redistribution of nitrogen within but not between leaves.

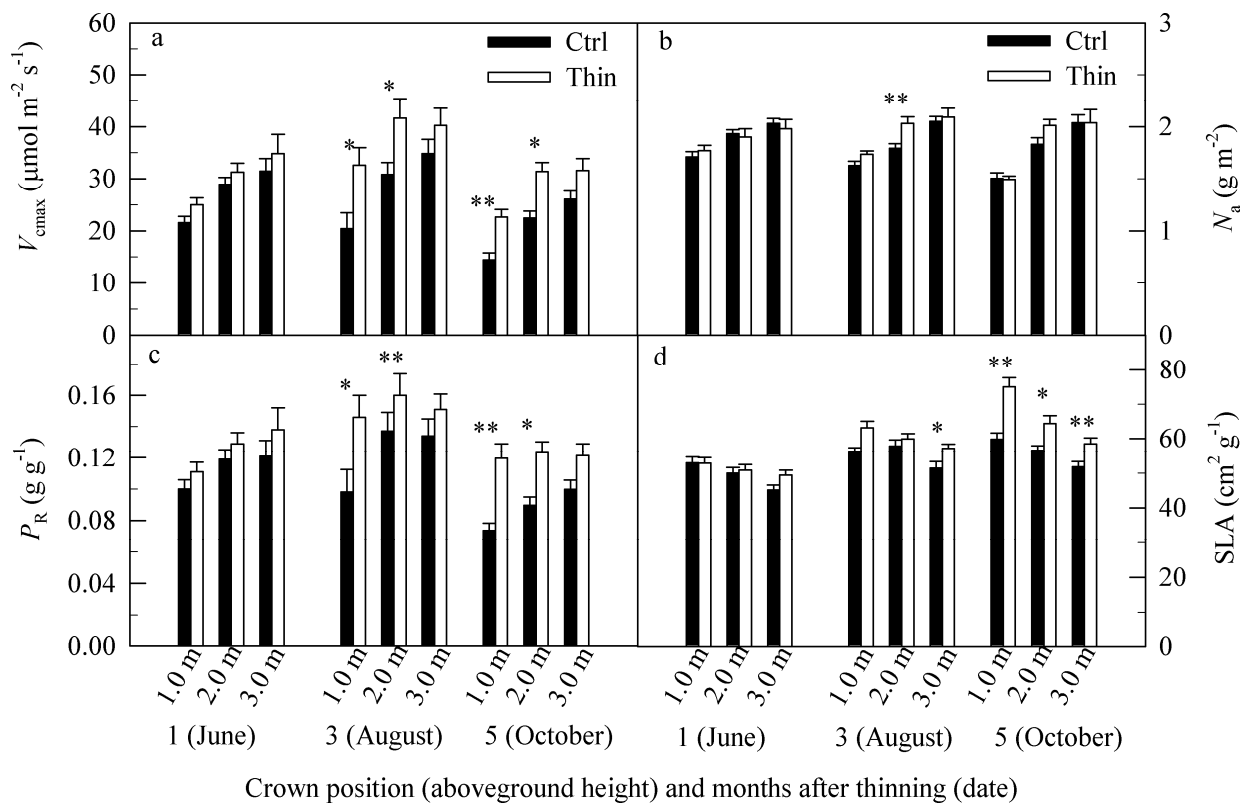


Fig. 2. Comparison of (a) the maximum rate of carboxylation (V_{cmax}), (b) leaf nitrogen concentration (N_a), (c) the proportion of leaf nitrogen in ribulose-1,5-bisphosphate carboxylase/oxygenase per total leaf nitrogen (P_R) and (d) specific leaf area (SLA) in the lower (aboveground height, AGH: 1.0m), middle (AGH: 2.0 m) and upper (AGH: 3.0 m) crown of *Chamaecyparis obtusa* between the thinned (open bars) and unthinned control (filled bars) stands one, three and five months after thinning. Significant differences between the respective values of the two groups: * $p < 0.05$; ** $p < 0.01$. Each value is the mean \pm SE ($n = 12\text{--}24$ leaves). With kind permission from Springer Science+Business Media: <Photosynthetica, 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*, 44, 2006, 523-529, Q. Han, M. Araki & Y. Chiba, Figs.2-4 >.

In the second year after thinning, nitrogen concentration in newly developed leaves was found to be generally higher in a thinned stand than in an un-thinned control (Han & Chiba, 2009). Thus, the redistribution of nitrogen between leaves enhanced photosynthetic capacity even in the upper crown in the thinned stand of *Chamaecyparis obtusa*. Furthermore, thinning affected the slope of the linear relationship between nitrogen concentration and photosynthetic capacity (Figure 3, Table 2). In the first year, the slope of the linear regression line representing the relationship between photosynthetic capacity and nitrogen concentration in the thinned stand was shallower than in the control stand, reflecting enhanced photosynthetic capacity in the lower crowns (Figs. 2a and 3a, Table 2). In the

second year, however, the slope in the thinned stand was higher than in the control stand, reflecting the enhanced photosynthetic capacity in the upper crown (Fig. 3b, Table 2). As is the case with the response to light conditions, redistribution of nitrogen between leaves appears to act over a longer time scale than reallocation within leaves (Brooks et al. 1996; Han et al. 2006). These results suggest that photosynthetic acclimation after thinning involves different leaf nitrogen reallocation/redistribution mechanisms driven by light changes during the process of crown re-closure. These results indicate the importance of considering the time since thinning when evaluating acclimation of photosynthesis and associated nitrogen relations with respect to silvicultural manipulation.

In the third year, the effect of thinning on the slope of the linear regression line representing the relationship between photosynthetic capacity and leaf nitrogen concentration became negligible again (Fig. 3c and Table 2), although both leaf nitrogen concentration and photosynthetic capacity were still higher in the thinned stand than in the control stand. The higher nitrogen concentration was due to improved nitrogen availability for the retained trees. Based on the leaf nitrogen difference and total leaf biomass difference in the two stands, the authors concluded that nitrogen redistribution driven by light changes, along with the nitrogen supply and demand balance in conjunction with the process of crown re-closure, resulted in the relations between leaf nitrogen and photosynthetic capacity in the thinned stand converging with those in the control stand, three years after thinning.

3.2 Evergreen broadleaf species

Eucalyptus species, in fast-growing commercial plantations, play an important role worldwide in satisfying both an increasing demand for wood and the provision of environmental services. Practices to manage growth have been intensively studied, but little research has examined the associated physiological responses. The only study to date was conducted in the Creekton plantation in southern Tasmania (43° 21'S, 146° 54'E), which was thinned when it was eight years old from a density of 1254 to 250 trees ha⁻¹ (Medhurst & Beadle, 2005). Thinning enhanced light-saturated photosynthetic rates throughout the crown and the greatest increases were recorded in the lower and middle crowns. Thinning increased leaf nitrogen and phosphorus concentrations because of a significant decrease in specific leaf area after thinning. Photosynthetic rate was positively related to leaf nitrogen and phosphorus concentrations per unit area. All these changes were mainly driven by increased light levels after thinning, as found for the coniferous species described above.

3.3 Deciduous broadleaf species

Enhanced photosynthesis has been detected in the second growing season after thinning in two deciduous species (Table 1) (Gauthier & Jacobs, 2009; Wang et al., 1995). Like *Eucalyptus*, photosynthetic acclimation in deciduous species has also been attributed to increases in light availability and nitrogen concentration as well as a decrease in specific leaf area. In comparison with the second growing season after thinning, decreases in photosynthetic rates in *Betula papyrifera* were found in the third growing season, indicating a gradual reduction of thinning effect due to expansion of the trees' crowns. In contrast to *Chamaecyparis obtusa*, no photosynthetic response was found immediately after thinning in *Juglans nigra* in which thinning was carried out approximately 80 days after bud burst. There are two types of leaf development in deciduous species: indeterminant and determinant (Koike, 1990). *Juglans nigra* exhibits the later type. In mature leaves, photosynthetic

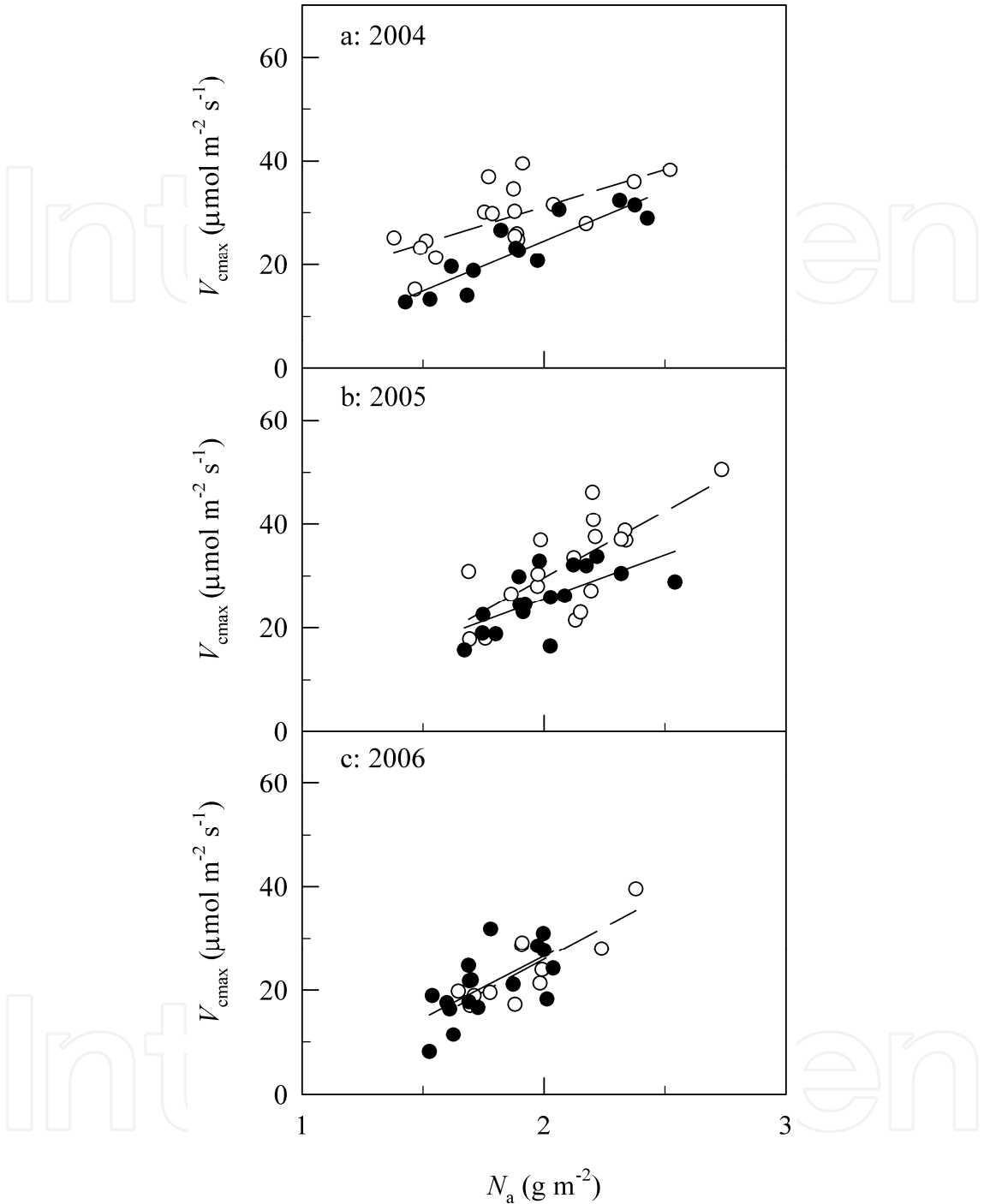


Fig. 3. The relationship between leaf nitrogen concentration (N_a) and the maximum rate of carboxylation (V_{cmax}) within a *Chamaecyparis obtusa* crown in thinned (open circles and dashed line) and unthinned control (closed circles and solid line) stands after thinning in May 2004. Regression results are presented in Table 2. Each value is the mean \pm SE ($n = 3-6$ leaves) measured in October. With kind permission from Springer Science+Business Media: <Journal of Forest Research, Leaf photosynthetic responses and related nitrogen changes associated with crown reclosure after thinning in a young *Chamaecyparis obtusa* stand, 14, 2009, 349-357, Q. Han & Y. Chiba, Fig.7 >.

acclimation to sudden increases in light intensity differs between species because of differences in leaf anatomy (Oguchi et al., 2005). In species that have empty spaces along the mesophyll cell surface that are not occupied by chloroplasts or other organelles (i.e. *Betula ermanii* Cham.), the photosynthetic capacity of mature leaves developed in low light acclimates rapidly to high light levels. On the other hand, in species where little of the mesophyll cell surface is unoccupied by chloroplasts (i.e. *Fagus crenata*), the photosynthetic capacity of mature leaves is unable to respond to light increases. These species-specific physiological traits are important when selecting appropriate times to conduct thinning in commercial forestry operations.

Year	Thinned stand			Control stand		
	slope	intercept	r^2	slope	intercept	r^2
2004	14.11 ^a	2.92	0.45	19.34 ^b	-14.06	0.80
2005	25.74 ^a	-21.91	0.53	17.02 ^b	-8.50	0.43
2006	24.91 ^a	-23.91	0.68	23.78 ^a	-21.02	0.43

Table 2. Linear regression results for the data shown in Figure 3 describing inter-annual variations in the slope of the leaf nitrogen (N_a ; g m⁻²) to the maximum rate of carboxylation (V_{cmax} ; μmol m⁻² s⁻¹) in both the thinned and control stands after thinning in 2004. All slopes were significant ($P < 0.01$), but none of the non-zero intercepts were significant ($P > 0.05$). Different letters adjacent to each slope indicate a significant difference between the two stands in the respective year ($P < 0.05$, ANCOVA test).

4. Conclusion

Thinning of closed-canopy stands dramatically alters the light regime experienced by the retained trees. Enhanced leaf photosynthesis after thinning can be attributed to an increase in light availability or improved water and/or nutrient supply. The magnitude of the increase in leaf photosynthesis is species-specific and site-specific, and is also dependent on the thinning method employed. Species-specific physiological traits are important when selecting appropriate timings and intensities of thinning. Enhancements in canopy gas exchange and subsequent growth continue as long as the leaf area index at the stand level remains lower than the pretreatment value. Enhanced photosynthesis as a result of thinning virtually disappears after the canopy re-closes, providing further evidence that light is crucial for driving thinning responses. All these factors should be taken into account by land owners and managers when considering stand management and thinning regimes.

5. Acknowledgements

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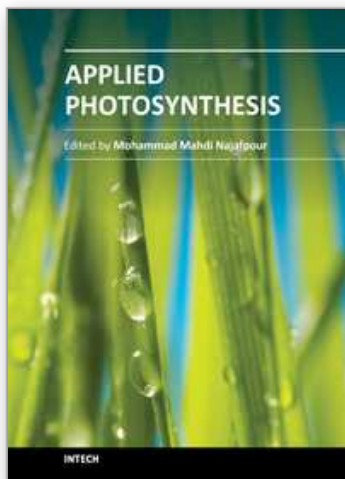
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Photosynthesis is one of the most important reactions on Earth, and it is a scientific field that is intrinsically interdisciplinary, with many research groups examining it. This book is aimed at providing applied aspects of photosynthesis. Different research groups have collected their valuable results from the study of this interesting process. In this book, there are two sections: Fundamental and Applied aspects. All sections have been written by experts in their fields. The book chapters present different and new subjects, from photosynthetic inhibitors, to interaction between flowering initiation and photosynthesis.

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