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Space-related resource investments and gains of adult beech (*Fagus sylvatica*) and spruce (*Picea abies*) as a quantification of aboveground competitiveness

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For my beloved family

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• Summary

In a field study, cost-benefit relationships of aboveground resource allocation were analysed in branches of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.). The study identified response patterns in allocation of resources under different light conditions in both species. It was postulated that resource investment and gains based on crown volume have the potential to quantitatively describe the plant's competitive ability (i.e. competitiveness). Three cost-benefit ratios (efficiencies) were defined to compare trees of contrasting growth form and leaf type, thereby considering metabolic processes involved in C allocation (Grams et al. 2002): (1) Efficiency of space sequestration (occupied aboveground or belowground space per unit of resource investment), (2) efficiency of space exploitation (resource gain per unit of aboveground or belowground space) and (3) efficiency of "running costs" (in terms of occupied aboveground or belowground space per unit of respiration or transpiration).

This study was conducted within the framework of a collaborate research program with the title "Sonderforschungsbereich 607: Growth and Parasite Defense - Competition for Resources in Economic Plants from Agronomy and Forestry" funded by the 'Deutsche Forschungsgemeinschaft', project SFB 607-B4. Ten spruce and ten beech trees within a mixed forest stand "Kranzberger Forst" north of Munich/ Germany were investigated for two years (1999-2000). In each tree a study branch from the upper sun and from the lower shade crown were chosen to cover the range of morphological and physiological variability within individual trees. The crown volume occupied by a branch was approximated based on a frustrum model enveloping the foliage of the branch. Assessment of crown volume was readily performed, low-cost and uncomplicated to calculate. Biomass of foliage and axes of each study branch was monitored non-destructively by means of allometric relationships, derived and validated on comparable harvested trees. CO_2 and H_2O leaf gas exchange was analysed with a portable infrared gas exchange system throughout the annual course by measuring light & CO_2 dependencies and respiration. Gas exchange data was used to parameterise a leaf gas exchange model. The annual gas exchange was calculated in ten-minute intervals based on microclimate (light from four sensors per branch, temperature, humidity, and CO_2 concentration), and was scaled biometrically to the branch level. A custom made system was developed to continuously measure respiration of axes. Respiration was scaled dependent on temperature to the surface area of the whole branch. Ozone was applied in the second year of investigation as an experimental tool to chronically disturb the homeostasis of resource allocation within branches. Whole crowns of five spruce and five beech study trees were fumigated with twice ambient ozone. Leaf area and mass distribution

was derived from optical measurements of leaf area index in the vertical profile within the stand.

Growth form and foliage type are contrasting in the coniferous and evergreen spruce and the deciduous and broadleaved beech. Still, it could be shown that the annual gross carbon gain was very similar in adult trees of spruce and beech when related to units of foliated space. Running costs of transpiration and respiration were also rather similar in this aspect. Apparently, differences in leaf level characteristics can vanish when relating physiological performance to space. The annual gross carbon gain scaled from branch to the stand level of spruce and beech showed good agreement to studies of gross primary production in forest stands.

The annual carbon balance was negative in all investigated shade branches of beech and in part of the shade branches of spruce. Some of these branches were sustained by the trees over years. This contradicts the ‘theory of branch autonomy’ and is not a common finding, as it probably occurs in branches within the lower shade crown of shade-tolerant species only. The light compensation point of the carbon balance was at lower light availability in beech than in spruce branches, which is of advantage for growth and persistence of shade branches and subordinate individuals of beech. On the stand level, the annual carbon balance was deteriorated in spruce due to negative carbon balances. In beech, the fraction of shade branches with a negative carbon balance was small and therefore the carbon balance was affected to a minor extent compared to spruce at the stand level.

Predominantly, spruce and beech were different in their efficiencies of space sequestration. Sun branches of spruce compared to beech sequestered crown volume with lower carbon investments of foliage and axes. This seems more advantageous to spruce during undisturbed growth of a stand as by sequestration of the same amount of space and inherently a similar carbon gain, a higher proportion of carbon than in beech sun branches remains that can be allocated to stem and roots. This was in line with published findings, where spruce was reported to dominate over beech through faster growth in southern Germany including the study site ‘Kranzberger Forst’. However, the relative annual increment of crown volume was larger in sun branches of beech than in spruce. This can be of advantage to beech e.g. in disturbed environments with new gap formation in the canopy. However, losses of invested carbon through the direct interaction of swaying tree crowns were considerably higher in beech compared to spruce trees. The lost carbon mass was equivalent to a loss of a similar amount of space in both species. It appears that larger gap size with decreasing potential of crown abrasion is important for beech to benefit through a rapid volume increment. The disturbance of spruce and beech through elevated ozone concentrations had not taken effect on the efficiency of space sequestration within *one* season of fumigation, which confirms the findings of other studies. Different strategies of space sequestration determined competitiveness in this study. This was also concluded in a study of hedgerow-species differing in successional status and in a phytotron study with competition among young trees.

In general, space-related efficiencies have the power to address competitiveness quantitatively, which allows comparison of contrasting species. It is encouraged to include space-related resource gains and investments in competition studies as space appears to be a resource itself and object of competitive interactions. The transfer and the expansion of space-related analysis to studies of e.g. responses in different environments, interactions in herbaceous and woody plants, belowground interactions or invading neophytes, is very promising, as new insights and understanding of the processes can be expected that determine competitiveness of species and individual plants.

Zusammenfassung

In einem Mischbestand wurden Kosten-Nutzen-Bilanzen der oberirdischen Ressourcen-Allokation analysiert. An Zweigen von Fichte (*Picea abies* [L.] KARST.) und Rotbuche (*Fagus sylvatica* L.) wurden Muster in der Veränderung der Ressourcen-Allokation unter verschiedenen Lichtbedingungen ermittelt. Der Versuchsansatz basierte darauf, dass Ressourcen-Investitionen und -gewinne im Bezug auf einen besetzten Kronenraum, das Konkurrenzverhalten von Pflanzen quantitativ wiedergeben. Dazu wurden drei Qutotienten (Effizienzen) gebildet in welche die metabolischen Prozesse eingehen, die an der Kohlenstoff-Allokation beteiligt sind, um Bäume von unterschiedlichem Wuchs- und Laub-Typus vergleichen zu können (Grams et al. 2002): (1) Effizienz der Raumbesetzung (besetzte Raumeinheit pro investierter Ressource), (2) Effizienz der Raumausnutzung (Ressourcengewinn pro Raumeinheit) und (3) Effizienz der ‚laufenden Kosten' (Raum pro Einheit veratmeten Kohlenstoffs oder transpirierten Wassers).

Diese Studie war Bestandteil des Sonderforschungsbereichs 607 mit dem Titel „Wachstum und Parasitenabwehr – Wettbewerb um Ressourcen in Nutzpflanzen aus Land- und Forstwirtschaft“, finanziert von der Deutschen Forschungsgemeinschaft. Je zehn Buchen und Fichten wurden für zwei Jahre (1999-2000) im Mischbestand „Kranzberger Forst“ nördlich von München untersucht. Je Baum wurde ein Zweig aus der oberen Sonnenkrone und ein Zweig aus der unteren Schattenkrone ausgewählt, um die Spannweite morphologischer und physiologischer Variabilität zu erfassen. Der Kronenraum, der von einem Zweig eingenommen wurde, wurde durch einen das Laub umhüllenden Körper aus Kegelstümpfen beschrieben. Die Volumenvermessung war kostengünstig, leicht durchzuführen und das Volumen unkompliziert zu berechnen. Die Biomasse jedes Messzweiges wurde am Anfang und Ende des Jahres non-destruktiv mittels allometrischer Beziehungen erhoben, welche an vergleichbaren geernteten Bäumen abgeleitet und validiert worden waren. Der CO_2- und H_2O-Gaswechsel von Blättern und Trieben wurde im Jahresverlauf mit einem tragbaren Infrarot-Gaswechselmessgerät durch Messungen von Atmung, Licht- und CO_2- Abhängigkeiten analysiert. Mit den Gaswechseldaten wurde ein Blattgaswechselmodell parametrisiert und der Jahresverlauf des Gaswechsels in 10-minütigen Schritten anhand des Mikroklimas (Licht von vier Sensoren pro Zweig, Temperatur, relative Feuchte und CO_2-Konzentration) berechnet und über biometrische Beziehungen auf Zweigebene hochgerechnet. Zur kontinuierlichen Messung der Achsenatmung wurde eine Gaswechselmessanlage entwickelt. Die Atmungsrate der Achsen wurde aus Verläufen der Messung mittels der Temperatur und der Oberfläche der Achsen auf den ganzen Zweig hochgerechnet. Im zweiten Jahr der Untersuchung wurde Ozon als experimentelles Werkzeug zur chronischen Belastung und damit zur Störung der

Ressourcen-Allokation eingesetzt. Dazu wurde herrschende Ozonkonzentrationen in der gesamte Krone von jeweils fünf Fichten und fünf Buchen (Messbäume) über ein neuartiges Freiland-Begasungssystem verdoppelten. Anhand von optischen Blattflächenindex-Messungen im vertikalen Profile des Bestandes wurden die Blattflächen- und Blattmassenverteilungen in Buchen- und Fichtenkronen bestimmt.

Trotz des unterschiedlichen Wuchs- und Laub-Typus des immergrünen Nadelbaums Fichte und des wechselgrünen Laubbaums Buche war die Jahres-Brutto-Kohlenstofffixierung in ausgewachsenen Bäumen sehr ähnlich, wenn die Fixierung auf das besetzte Astvolumen bezogen wurde. Das gilt weitgehend auch für die „laufenden Kosten“ der Transpiration und Atmung. Offensichtlich können bestehende Unterschiede in der Physiologie bei Bezug auf die Biomasse oder Oberfläche durch Bezug auf den Raum aufgehoben werden. Die Hochrechnung der Jahres-Brutto-Kohlenstoffixierung des Bestandes zeigte gute Übereinstimmung mit Werten die für die Brutto-Kohlenstoffaufnahme von Wäldern der gemässigten Zone angegeben werden.

Die Jahres-Kohlenstoffbilanz war in allen Schattenzweigen der Buche und in einem Teil der Schattenzweige der Fichte negativ. Einige dieser Zweige wurden über Jahre hinweg von den Bäumen beibehalten. Über solche Befunde, die im Widerspruch zur ‚Theorie der Ast-Autonomie’ stehen, wurde bisher selten berichtet, da negative Jahres-Bilanzen wahrscheinlich nur in dem unteren Kronenbereich von schattentoleranten Arten vorkommen. Der Lichtkompensationspunkt der Jahres-Kohlenstoffbilanz der Zweige lag in Buche verglichen mit Fichte bei einem niedrigeren Lichtangebot. Das ist sowohl für Schattenzweige als auch für unterständige und unterdrückte Individuen der Buche ein Vorteil. Auf Bestandesebene wurde die Jahres-Kohlenstoffbilanz der Fichten durch die negativen Bilanzen der Schattenzweige stärker herabgesetzt als bei Buche. Bei Buche war der Anteil an Ästen mit negativen Bilanzen so gering, dass sich nur eine geringe Auswirkung auf die Jahres-Kohlenstoffbilanz zeigte.

Der hauptsächliche Unterschied zwischen Buche und Fichte trat in der Raumbesetzung auf. Sonnenzweige der Fichte besetzten im Vergleich mit Buche den Kronenraum mit niedrigeren jährlichen Kohlenstoff-Investitionen für Laub und Achsen. Das erscheint vorteilhaft für Fichte bei störungsfreien Bestandeswachstum, da bei gleichem besetztem Volumen und damit gleichen Kohlenstoffgewinn wie bei Buche mehr Kohlenstoff zur Allokation in den Stamm und die Wurzeln bleibt. Diese Annahmen stimmen mit veröffentlichten Ergebnissen überein, wonach in Süddeutschland die Fichte wegen besserem Wachstum über Buche dominiert.

Der jährliche Zuwachs an besetzen Kronenraum war in Sonnenzweigen der Buche grösser als bei Fichte, was für die Buche beispielsweise bei Lückenbildung durch Störungen im Bestand von Vorteil sein kann. Jedoch waren die Kohlenstoff-Verluste durch Astabbrüche in den Kontaktzonen zu den Nachbarbäumen bei Buche wesentlich höher als bei Fichte. Der durch Astbrüche eingebüsste Kronenraum war bei beiden Baumarten wiederum ähnlich. Es scheint, dass grössere Bestandeslücken mit geringerer Häufigkeit von direkten Kroneninteraktionen für die Buche mit ihrem raschen Raumzuwachs von Vorteil sind.

Die Störung der Allokation in Buche und Fichte durch Erhöhung der Ozonkonzentration hat sich nach *einem* Jahr der Begasung nicht erkennbar auf die Raumbesetzung ausgewirkt.

Unterschiede in der Strategie der Raumbesetzung bestimmten in dieser Studie die Konkurrenzkraft. Das war auch die Folgerung einer Heckenstudie mit Holzpflanzen unterschiedlicher sukzessionaler Stellung und in einem Konkurrenzexperiment mit jungen Pflanzen in Phytotronen.

Zusammenfassend kann man sagen, dass die raumbezogenen Kosten-Nutzen-Bilanzen das Konkurrenzverhalten quantitativ beschreiben, wodurch man sehr unterschiedliche Arten vergleichen kann. Es wird empfohlen raumbezogene Gewinne und Investitionen in Konkurrenzstudien künftig mit einzubeziehen, da Raum an sich als eine Ressource aufgefasst werden kann und zum Gegenstand der Konkurrenzinteraktionen wird. Die Übertragung und Erweiterung von raumbezogenen Analysen, beispielsweise auf Studien über Reaktion auf veränderten Umweltbedingungen, über Interaktionen von krautigen und holzigen Pflanzen, über unterirdische Wechselwirkungen oder über Interaktionen mit Neophyten, scheint vielversprechend, da neue Erkenntnisse über Prozesse, die das Konkurrenzverhalten von Arten und Einzelpflanzen steuern, und ihr besseres Verständnis erwartet werden können.

• Abbreviations

Abbreviation	***Description***	***Unit***
C	carbon	
CB	annual carbon balance	[mol m^{-2} ground yr^{-1}] [mol m^{-3} crown yr^{-1}]
LAD	leaf area density	[m^{2} foliage m^{-3} crown volume]
LAI	leaf area index	[m^{2} foliage m^{-2} ground]
PPFD	photosynthetic photon flux densities	[µmol m^{-2} s-^{1}]
PPFD$_{season}$	sum of photosynthetic photon flux densities during the period of the growing seasons (1st June until 30th October)	[kmol m^{-2} season^{-1}]
rheight	relative height, the vertical distance normalized between the base of the crown (=0) and the tree top (=1)	[-]
SLA	specific leaf area of projected leaf area	[m^{2} kg^{-1} drymass]
SNL	specific needle length	[m g^{-1}]

1 Background and Concept

1.1 General introduction

Plants function as a balanced system of uptake of abiotic resources (energy: light, temperature, and matter: carbon, nutrients, water) and resource use (Heilmeier et al. 1997). Therefore plants continuously interact with their environment, which is changed through this interaction (Bazzaz and Pickett 1980). Besides gradients of abiotic resources within the plant itself (Larcher 2001), the specific environment of a plant is substantially influenced by the presence and the vicinity of neighbouring plants. Neighbouring plants, provided they have the same requirements, also share the same resources. Once a resource becomes limiting among neighbours, competition amongst these plants exacerbates for that resource per unit of time and space. As a result, at least one of the competitors is constrained in resource uptake (Figure 1, Goldberg 1990). By uptake of a resource (effect, Figure 1A), the resource is available in less quantity. Plant organs individually react to such a change in resource (response, Figure 1A) in physiology, structural architecture and abundance. Besides indirect plant-plant interactions via a resource, plants can also interact directly through mechanical interplay of plant parts, which can raise (effect) the abundance of the resource (Figure 1B).

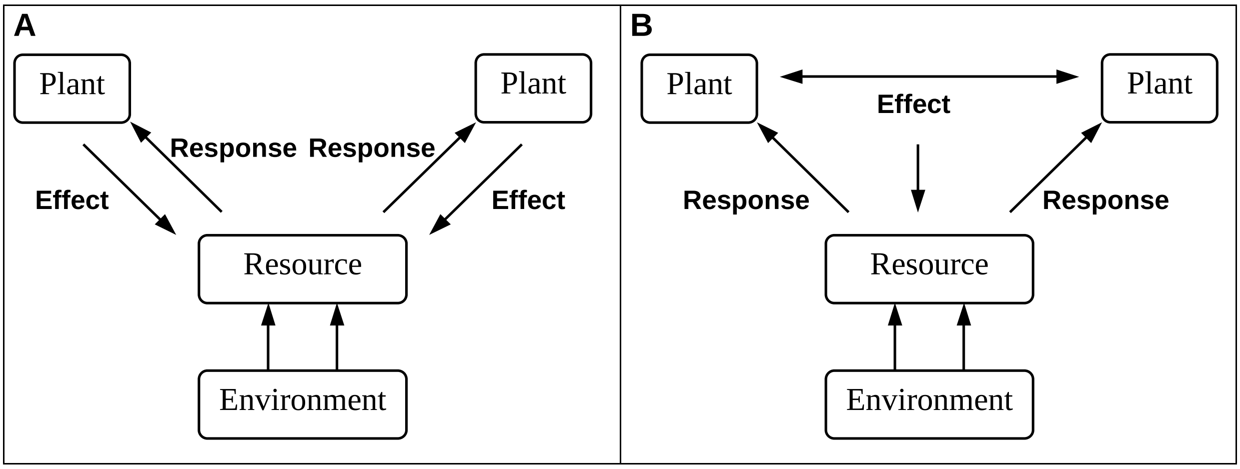


Figure 1: Interactions of neighbouring plants. Environmental conditions provide an abundance of a resource. (A) Indirect interaction. A change in the resource (e.g. depletion of light) through one or more plants can invoke a response in the plants to the changed abundance of the resource (B) Direct interaction e.g. crown abrasion of the plants effects the abundance of the resource, which again leads to a response in the plant to the change in abundance of the resource (adapted from Goldberg 1990).

The approach by Goldberg (1990) integrates an ongoing discussion initiated by Grime (1977) and Tilman (1982) on the importance of effects and responses by competitors to a resource. There is little doubt that density, structural architecture, and physiological activities of neighbours modify the allocation inside the individual plant (Heilmeier et al. 1997). Allocation is the flux of carbon to plant organs and to physiological or biochemical processes in the plant. Still the questions, how plants respond to lowered availability of resources, and how such a response can be quantified, in particular in terms of the extent and changes of the plant’s competitive ability (i.e. competitiveness) are under discussion and are main topics in the research field of ecophysiology (Mooney et al. 1991, Monteith et al. 1994, Schulze 1994, Smith and Hinckley 1995a, Smith and Hinckley 1995b, Bazzaz and Grace 1997)

Plants employ a wide range of strategies in resource acquisition, reaching from active foraging to sit-and-wait strategies (Hutchings and de Kroon, de Kroon and Hutchings). The quantitative response to resource availability is not only species-specific (Pedersen and Howard 2004, but see Müller et al. 2000), but also specific for plant individuals, e.g. reproduction depends on social status (Heilmeier et al. 1997). Species have also been shown to allocate differently with age (Wirth et al. 2004), nutrition (Poorter et al. 1995) and soil type (Egli et al. 1998). Aboveground competition for resources (i.e. predominantly light) within plant stands is evident and has been investigated in many aspects (e.g. Cannell and Grace 1993, Küppers 1994, Newton and Jolliffe 1998). However, belowground competition for resources is also important (Cable 1969, Fowler 1986, Casper and Jackson 1997, Carlen et al. 1999, Leuschner et al. 2001, Maina et al. 2002).

Plants are postulated to respond to changes in resource availability in different environments by altered allocation to primary (growth) and secondary (defence) metabolism (Figure 2A, Herms and Mattson 1992, Matyssek et al. 2002b), which is regarded as an plant internal conflict or trade-off (Figure 2B). The categorization into primary and secondary metabolism is not always applicable, as a number of metabolites can serve growth and defence, e.g. lignin, starch, pigments. Allocation of resources (i.e. metabolites, nutrients and water) to plant organs result in distinct biomass partitioning. However, changes in resource availability and altered allocation to primary metabolism do not necessarily imply changes in the ratio of resources allocated to plant compartments i.e. C partitioning, growth pattern (Poorter 2002).

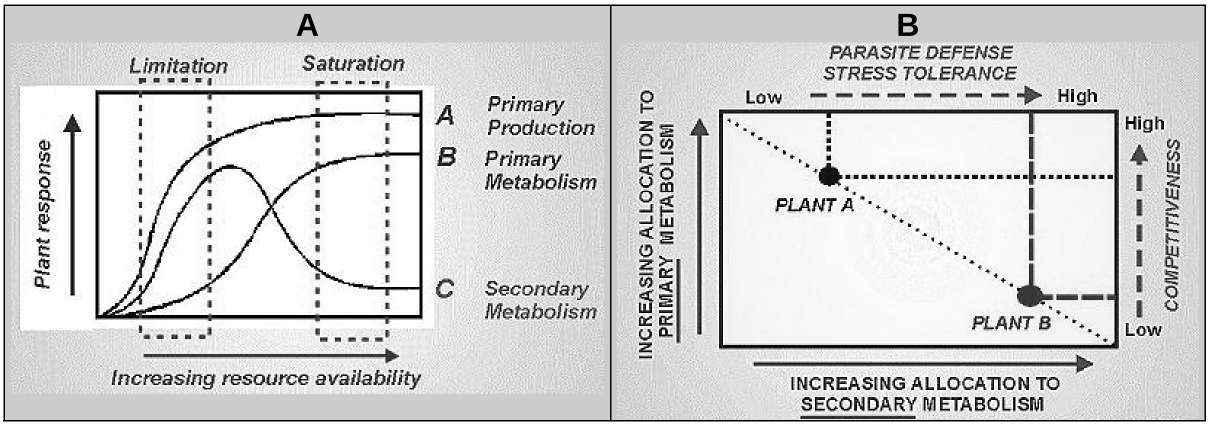


Figure 2: Conceptual model of resource allocation. (A) Impact of resource availability on primary production as well as primary and secondary metabolism. (B) Trade-off between competitiveness and parasite defence (www.sfb607.de, adapted from Herms and Mattson 1992).

1.2 How can responses to resources abundance be quantified ?

Many models and experiments conceive plant allocation to function in economic ways according to cost/benefit relationships (see Bryant et al. 1983, Matyssek 1984, Lorio 1986, Sprugel 1987, Küppers 1989, Field 1991, Witowski 1997, Eamus and Prichard 1998, Agrawal and Karban 1999, Bosc 2000, Henriksson 2001, Sprugel 2002, Falster and Westoby 2003, Gayler et al. 2004).

We defined an economic context based on cost/benefit relationships which is suitable for wild and economic plants, as well as woody and herbaceous species (Grams et al. 2002). The approach is expressed as efficiencies of investments and gains related to a spatial extension, which was crown volume in aboveground and root length in belowground investigations (cf. partner project B5, Kozovits 2003). However, the focus was on aboveground plant organs in this study and the efficiencies were defined and extended as (i) space sequestration at the branch and crown level as related to investment into foliage mass, (ii) space exploitation in terms of the annual carbon gain per unit of the sequestered volume and (iii) 'running costs' in terms of sequestered volume to be sustained per unit of respiratory carbon release and transpiratory water loss. These ratios are efficiencies, as they represent a gain *versus* a concurrent resource use (Lide 2003). Other studies have also postulated and demanded *efficiencies*, in varying terms, which are associated with plant *morphology and physiology within spatial relationships* (cf. Yodzis 1978):

Sprugel et al. 1991 state that (i) the volume occupied by a tree crown has areas of variable resource availability and that (ii) trees that forage "efficiently" (i.e. put most of their new leaves in areas with high light level) will have a clear advantage over trees that need more investments to access the same resources. This is consistent with the findings by Schulze (1986) that carbon relations must be analysed together with the growth pattern in order to understand the "efficiency" by which a plant exploits its habitat, or with findings by Tremmel and Bazzaz (1995) who showed that competitive ability expressed as resource acquisition ability depends on the spatial plant organs' placements in relation to the available resources.

1.3 Aim of the study

The aim of the study was to analyse the efficiencies by which space is being sequestered, exploited and sustained under contrasting environmental conditions in the sun and shade crown, and how experimental disturbance, introduced with twice ambient ozone fumigation, might modify allocation and allometric relationships in plants.

Two tree species, deciduous broadleaved *Fagus sylvatica* and evergreen coniferous *Picea abies*, were chosen, which represent contrasting extremes in growth habit and leaf physiology among the trees of Central Europe (Pisek and Tranquillini 1954, Schulze 1981). Both species are strong competitors across a broad range of edaphic and climatic conditions in managed forest ecosystems (Ellenberg 1996, Pretzsch 2003) and are of major economic interest in Central-European forestry.

1.4 Experimental design and project structure

Space-related resource turnover was quantified in individual trees. To cover the whole range within a tree, branches from the upper sun and the lower shade crown were chosen. For these branches the carbon investment into space, the carbon return from that space and the ‘running’ respiratory and transpiratory costs for that space were evaluated.

An experiment to disturb carbon partitioning within branches was conducted, by means of a free-air ozone fumigation of whole crowns. The aim of the ozone fumigation was to reduce the available resources in branches of the fumigated trees. Ozone was not viewed as an air-pollutant, but as an ecophysiological tool to enable analysis of induced changes in carbon allocation. Prevailing ozone concentrations (ambient) were doubled, but restricted to a maximum of 150 ppb (2xO_3), thereby exposing ten tree crowns to chronic ozone stress. Fumigation started in the second year of investigation, after the branch characteristics without disturbance through ozone had been investigated in the first year (Figure 3).

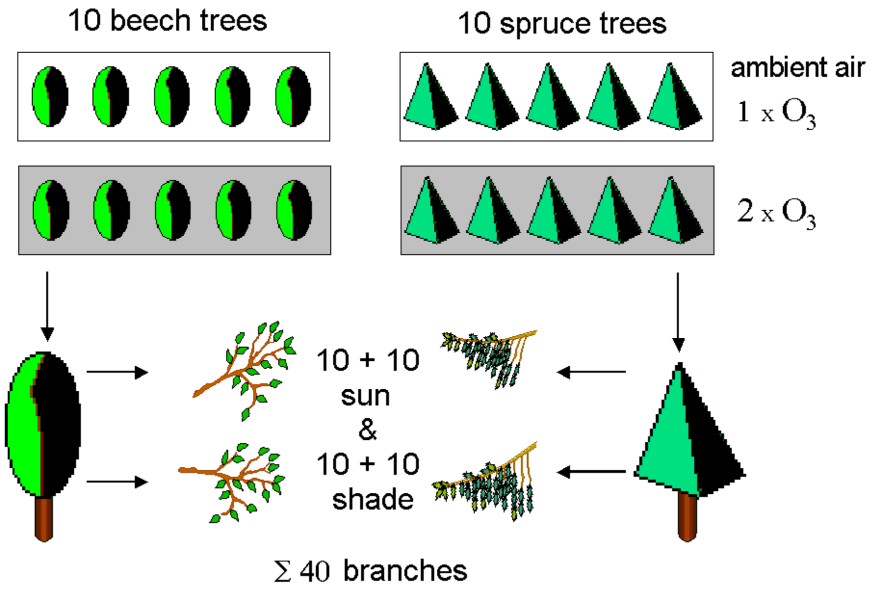


Figure 3: Experimental design. Ozone fumigation with twice ambient ozone (2xO_3) started in the second year of investigations in 2000.

This study was performed during the first phase of project B4 within the framework of an interdisciplinary research program (Sonderforschungsbereich 607: “Growth and Parasite Defence – Competition for Resources in Economic Plants from Agronomy and Forestry”, www.sfb607.de) funded by the ‘Deutsche Forschungsgemeinschaft’. The program deals with the allocation of resources and the adjustment to altered resource availability in competitive interactions of plant-plant, plant-mycorrhizosphere and plant-parasite (or pathogen) relations (see ellipses in Figure 4). The experimental concept is being pursued on economic plants from forestry and agronomy. The aim of the program is to identify the mechanisms underlying the control of resource allocation at different organisation levels from the cell to the plant, in a broad range of life forms, ontogenetic stages of plants and growth conditions.

It is to unravel to what extent general principles in the regulation of resource allocation exist in plants. The central hypothesis of the program is that “*Regardless of the kind of stress, plants regulate their resource allocation in a way that increase in stress tolerance and resistance (in particular against pathogens and phytophages) inherently leads to constraints on growth and competitiveness*” (Matyssek et al. 2002b).

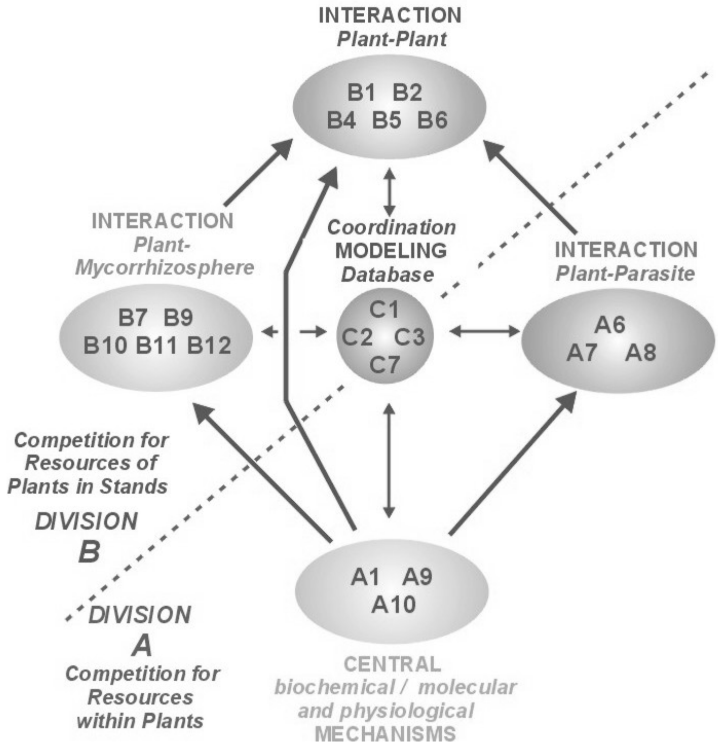


Figure 4: Project structure within the collaborate research program, Sonderforschungsbereich 607. This study was based on project B4.

1.5 Structure of thesis

The introduction of the concept is followed by a space-related analysis of the branch. At first the modules of the branch are investigated separately - the foliage as the plant’s productive capital and the axes as the supportive structures of the foliage- and then the synthesis of space-related traits of foliage and axes. Thereafter influence of disturbance of space-related investments and gains in terms of direct interference with neighbouring crowns and ozone are presented. The crown volume as defined and measured in this study is discussed in relation to size effects of the branch volume and of the investigated trees, is then compared to other studies that also implied a space-related approach, further a method is presented to integrate measured and modelled volume. In a last step it was asked, to what extent findings on the space related cost/benefit relationships have the potential of explaining qualitative observation of the competitive behaviour of these trees in quantitative terms. In the annex and predominantly scaling of leaf area and leaf morphology as applied for this study is described.

1.6 Site description

The study was conducted in a mixed forest of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* [L.] KARST) at ‘Kranzberger Forst’ (48°25’08’’N 11°39’41’’E, 490 m a.s.l., near Freising/Germany; plot size 5312 m^2, inclination 1.8° towards N, Pretzsch et al. 1998, Figure 5). The soil is a luvisol (ger.: ‘Parabraunerde’), derived from loess, with good water and nutrient supply (Schuhbäck 2004), and with a mean rooting depth of 1 m. Mean air temperature during the two-year study (1999 and 2000) was 9.2°C with 847 mm of precipitation, and 14.4°C with 568 mm of precipitation during the growing seasons from May to October (Table 1). Scaffoldings and a canopy crane allowed access to individual tree crowns (see Nunn et al. 2002, Häberle et al. 2003). Spruce was planted in 1951, seven years after beech which had been established as groups, according to common silvicultural practices (Rebel 1922, Hehn 1997, Figure 6). The beech group within the experimental plot consisted of 60 individuals (Figure 7).

Table 1: Annual and monthly mean of air temperature and precipitation from year 1999 to 2003 of the study site (24 m height, tower 1; C.-Heerdt, H. Werner, Bioclimatology, Technische Universität München) and of the 1 km distant meteorological station inside the forest (Waldklimastation, Sachgebiet II, Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising).

	mean air temperature [°C]					***precipitation [mm]***				
year/ month	***1999***	***2000***	***2001***	***2002***	***2003***	***1999***	***2000***	***2001***	***2002***	***2003***
April	8.6	10.2	6.0	7.7	8.6	66.9	61.9	63.4	19.5	24.9
May	14.4	14.8	14.7	13.2	15.0	106.5	101.6	72.5	100.2	101.9
June	15.3	17.6	13.9	17.8	20.9	93.4	73.7	113.3	67.8	43.6
July	20.8	15.4	17.2	17.1	19.0	74.5	128.4	44.9	127.0	76.0
August	18.2	19.0	18.1	17.3	22.4	54.5	77.9	118.1	164.8	30.2
September	15.7	13.6	10.2	11.3	14.1	57.9	101.8	125.0	78.9	27.5
October	8.1	9.7	11.3	8.0	5.9	31.6	104.4	55.8	87.7	80.4
annual mean or sum	9.0	9.4	7.9	8.8	9.1	796	897	1091	1015	558
April-October	14.5	14.3	13.1	13.2	15.1	485	650	593	646	385

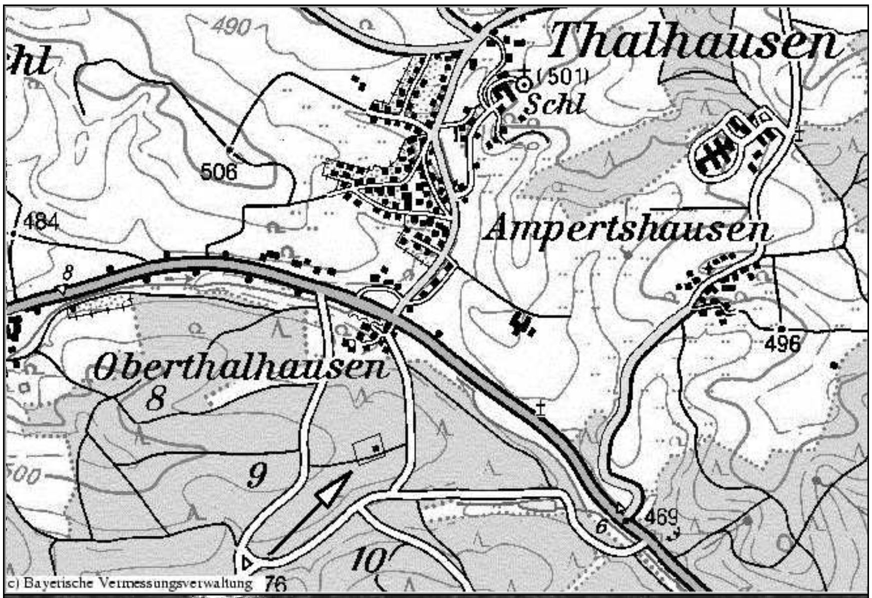


Figure 5: Topographic map of the ‘Kranzberger Forst’ south of Oberthalhausen. The location of the study site is pointed at with an arrow in the lower half of the map (Bayrisches Landesvermessungsamt 2004).

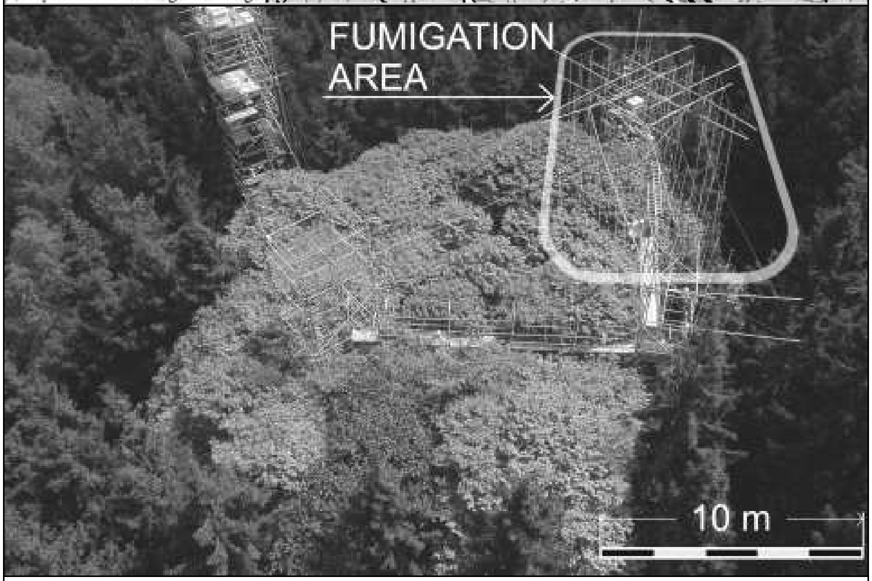


Figure 6: Arial view, taken from the research crane, on the experimental site of the ‘Kranzberger Forst’. Frame outlines the canopy with “free-air” ozone fumigation. Canopy depicted in light-grey denotes beech trees, dark-grey colours spruce trees. (From Nunn et al. 2002).

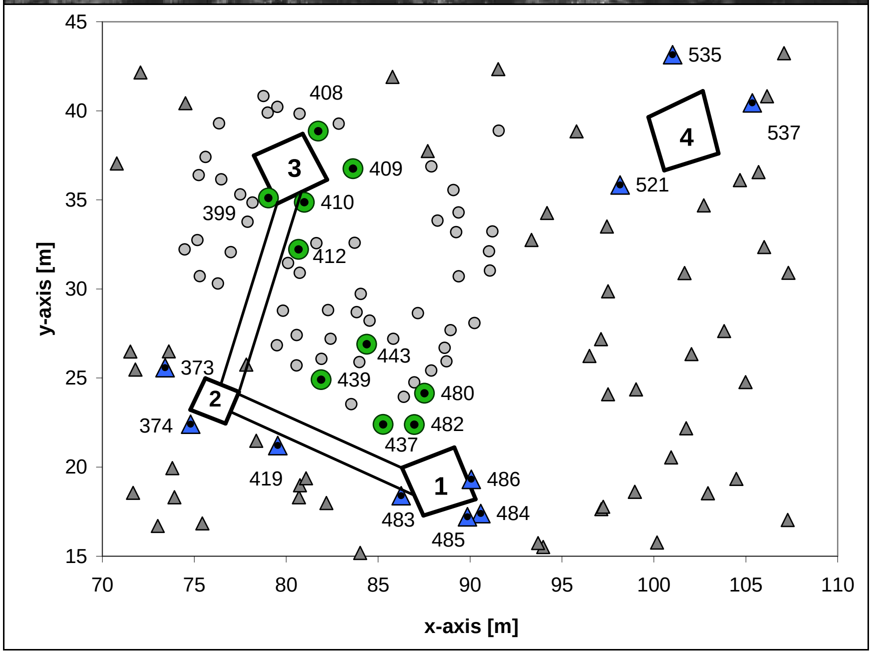


Figure 7: The experimental plot of the ‘Kranzberger Forst’ (cf. Figure 6). Round symbols represent beech, triangles spruce. Larger dotted symbols correspond with the study trees (cf. experimental design, Figure 3; Table 2), the adjacent values are the identification numbers of the tree individuals. Frames represent towers and scaffoldings. Towers are numbered 1 to 4. Three towers (1,2,3) are connected with gangways.

1.7 Study trees and study branches

Ten study trees each of beech and spruce were selected (Figure 7, Table 2) from the tree vigour classes 1 to 4 according to “Kraft” (Kraft 1884). The diameter at breast height of the study trees were evenly distributed within the range of diameters and represented more than 80 % of the individuals present of each species at ‘Kranzberger Forst’ (Figure 8, Pretzsch et al. 1998). Regardless of the “Kraft” class, tree crowns, although forming a closed canopy, did not intermingle with neighbours as a characteristic of the stand structure. In each study tree, one branch in the sun and one in the shade crown was chosen to cover the extremes of the structural and ecophysiological variability within the crowns. In both species, the investigated shade and sun branches were located at 14.5 to 20.3 m (lower edge of shade crowns) and 20.5 to 26.6 m aboveground (foliage predominantly exposed to open sky), respectively, and covered the entire range of compass directions and associated light regimes.

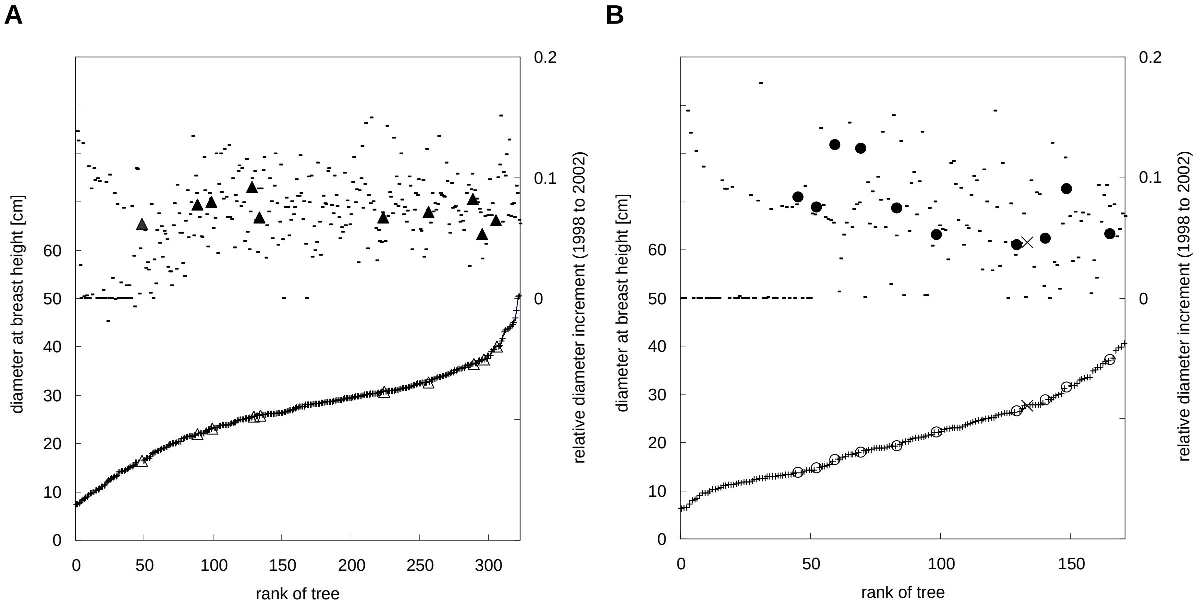


Figure 8: Ranking of (A) spruce and (B) beech trees of the study site according to their diameter at breast height in September 1998 (+), with spruce study trees marked as open triangles and beech study trees marked as circles. Based on these diameters, the relative diameter increment from September 1998 to September 2002 is shown (-), with spruce study trees marked as black triangles and beech study trees marked as black circles (data from partner project C3, Pretzsch et al. 1998).

Table 2: Ozone fumigation regime, crown and stem characteristics of the study trees

tree species & number	***ozone fumigation since***	***tree height [m]***			***height of crown base [m]***	***diameter at breast height September [cm]*** [1]			***projected crown area [m^2]*** [1]
	2000	***1998***	***1999***	***2000***	***1999***	***1998***	***1999***	***2000***	***1999***
spruce									
373	No	22.3	22.4	22.6	11.0	16.4	17.4	17.4	1.2
374	No	25.8	26.3	26.8	13.8	30.7	32.1	32.4	11.7
419	Yes	24.4	24.9	25.3	13.1	25.5	26.9	27.1	9.0
483	Yes	27.5	28.0	29.5	10.2	40.0	41.5	41.9	4.7
484	Yes	29.9	29.9	30.4	11.3	32.7	34.1	34.5	6.0
485	Yes	24.3	24.8	25.3	10.0	21.9	23.0	23.2	4.7
486	Yes	22.8	23.2	23.6	9.0	23.1	24.3	24.6	4.3
521	No	23.8	24.0	24.4	13.9	25.9	27.0	27.2	15.8
535	No	25.9	26.2	26.9	11.6	36.4	37.8	38.4	20.0
537	No	27.2	27.6	28.0	12.4	37.3	37.8	38.3	20.2
beech									
399	No	23.7	24.2	24.7	12.7	17.9	19.2	19.5	6.9
408	No	22.5	23.0	23.4	12.5	26.5	27.4	27.5	13.1
409	No	22.5	23.0	23.4	16.1	28.8	29.9	30.0	27.0
410	No	22.4	22.8	23.1	12.2	13.7	14.7	14.7	4.0
412	No	22.8	23.1	23.2	13.0	16.4	17.6	17.9	9.0
437	Yes	---	23.2	23.5	11.3	19.3	20.4	20.5	0.7
439	Yes	22.0	22.4	22.8	10.8	14.7	15.6	15.6	2.2
443	Yes	24.7	25.1	25.5	11.6	22.1	23.2	23.2	7.3
480	Yes	22.7	23.1	23.6	12.7	31.5	32.5	33.4	34.1
482	Yes	24.2	24.6	25.1	12.1	37.1	37.2	38.6	33.3
417	No	---	24.5 [1]	---	12.0	27.6	28.6	28.7	15.1

[1] data from the partner project C3, Chair of Forest Yield Science, Technische Universität München.

All spruce branches were first order axes (S1-axes/ Schütt et al. 1992), except the sun branch in tree 485 and the shade branch in tree 535, which were second order axes (S2-axes/ Schütt et al. 1992). Beech branches were of zero (stem) to forth order axes (Table 3). Light sensors were positioned equidistantly on the foliated part of the main axis. Sap flow gauges and dendrometers were, if installed, positioned on the unfoliated main axis of the study branch, respiration cuvettes too wherever possible (see Figure 9). Measurements of sapflow and dendrometers readings were evaluated elsewhere (Hägele 2001). Temperature and humidity sensors were installed in the vicinity of the study branches. Separate temperature and humidity sensors were installed in sun and shade crown.

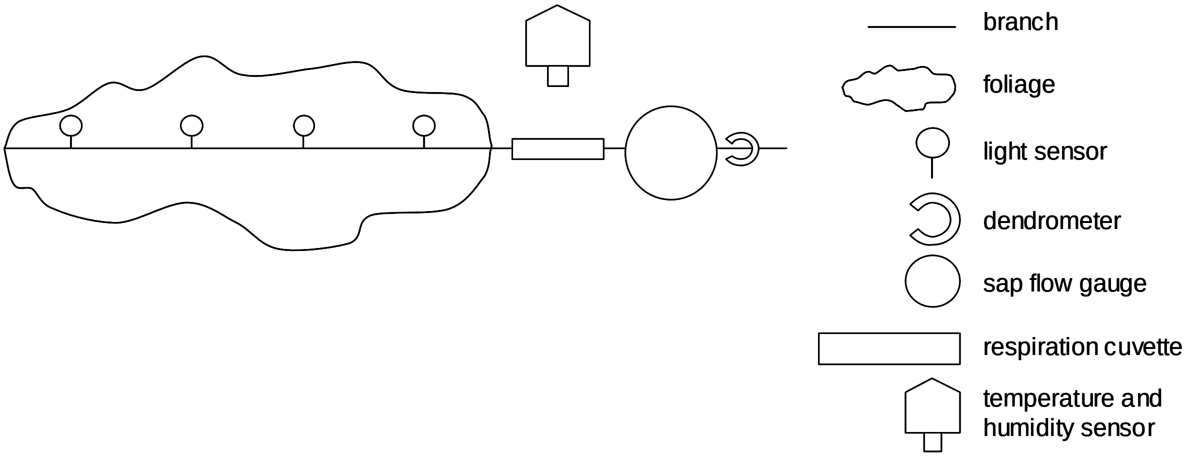


Figure 9: Scheme of study branch and its equipment with sensors.

Table 3: Characteristics of the study branches, inclination and height was measured

tree number	***branch order***		***branch inclination***		***proximal height***	***distal height***	***proximal height***	***distal height***
branch type	***shade***	***sun***	***shade [°]***	***sun [°]***	***shade [m]***	***shade [m]***	***sun [m]***	***sun [m]***
spruce								
373	1	1	21	33	16.8	18.1	21.3	21.1
374	1	1	6	26	19.9	19.3	23.2	23.3
419	1	1	15	19	18.1	17.7	21.7	22.2
483	1	1	14	19	18.0	17.0	23.5	24.0
484	1	1	44	26	18.2	17.3	25.7	26.6
485	1	2	12	5	16.7	16.8	22.5	22.3
486	1	1	11	5	17.6	17.8	21.5	21.7
521	1	1	20	3	15.9	15.8	20.4	17.0
535	1	1	34	28	17.3	18.4	21.5	22.9
537	2	1	18	15	16.6	17.0	20.4	21.0
beech								
399	1	2	0	71	19.5	19.5	19.5	19.5
408	2	2	10	49	18.2	18.6	22.6	24.2
409	2	2	0	48	19.5	19.5	21.0	22.7
410	1	1	0	47	19.5	19.5	21.5	22.7
412	2	1	0	90	18.0	18.0	21.3	22.6
437	2	1	33	81	18.0	19.5	22.2	24.0
439	2	0	43	50	19.2	20.3	20.2	21.6
443	3	3	0	44	17.7	17.7	21.5	23.0
480	3	3	24	81	14.5	14.9	21.4	22.8
482	2	4	19	55	14.5	19.5	24.1	21.7

1.8 Description of species

Picea abies and *Fagus sylvatica* share mutual and geographic climatic ranges (Table 4) and distribution across Europe (Figure 10). They are strong competitors for a broad range of site conditions (Ellenberg 1996). However, *Picea abies* and *Fagus sylvatica* follow opposite productivity gradients in a north-south transect within Germany, with spruce being more competitive in the south and beech in the north (Pretzsch 2003).

1.8.1 Picea abies [L.] KARST.

General habit: *Picea abies* (Scott 2003) is an evergreen tree and usually 30 m to 40 m high, with a diameter in breast height of 40 cm to 90 cm. Large trees may be 50 m high and have a diameter at breast height of up to 200 cm. Maximum age is about 300 years. The crown is pyramidal and almost always tapering to a conical pointed top. The stem is typically straight, cylindrical and slender, with little taper. Growth is monopodial. The number of branches depends strongly on stand density and the shape of the crown can be very variable and adaptable. *Picea abies* exhibits a high number of morphological variations, e.g., dwarf growth, pillar growth. Wide crowns are usual in trees growing at lower altitudes, whilst more tapered and slender crowns are usual in northern Europe and in subalpine and montane regions.

Branch characteristics: Branches are short and stout, the upper ones level or ascending, the lower branches drooping. *Picea abies* varies in branching habit. Three different types of crown are usually distinguished: (1) the normal 'brush' form with a plume of spreading shoots giving a crown of even density; (2) a 'comb' form with level branches ascending at the tips, hung with dense short 'curtains' of shoots, but far enough apart for daylight to show between branches (Scott 2003, c.f. Figure 55). This growth form is said to be more sustainable in terms of its ability to cope with snow loads and wind and is therefore well adapted to subalpine and montane regions (Ellenberg 1996); (3) a 'plate' form with layered branches. Old trees become very thin in the crown, usually with long straggling pendulous shoots.

Foliage characteristics: The needle cross-section is rhomboidal (cf. Annex, section B.5), with stomatal bands on all 4 sides. The needles are 1-2 cm long, rarely to 2.5 cm, about 1 mm in diameter. Needles grown in sun conditions are rigid and pointed with a brush-like bend at the top. Needles grown in shade conditions are projected rather horizontally. Needles are shed every 5 to 10 years. Leaf flushing normally begins in May.

Climatic conditions: *Picea abies* is a tree of cool temperate climate (Table 4) in its natural habitat. However, plantations have been established outside the natural range, as *Picea abies* can adapt to different climatic conditions (see Figure 10). An exception are coastal areas, as *Picea abies* is not very tolerant of winds and salt winds. *Picea abies* is frost resistant and cold hardy in Central Europe, but is susceptible to late spring frosts. As long as the relatively high soil water demand of *Picea abies* is available, it will exhibit satisfactory increment rates in Central, northern and eastern Europe from sea level to alpine mountain regions. The main limiting factor is summer drought in combination with a low soil water supply.

Table 4: Characteristics for species *Picea abies* and *Fagus sylvatica* (from Scott 2003)

	unit	***Picea abies***	***Fagus sylvatica***
Altitude	**[m]**	0 - 2300	0 - 2700m
Rainfall	**[mm]**	180 - 1200	450 - 2000
Temperature			
Mean annual	**[°C]**	-10 to 10	4 to 15
Mean coolest month	**[°C]**		-9 to - 6
Mean hottest month	**[°C]**	3 to18	19 to 31
Absolute minimum:	**[°C]**	-35	-45
Maximum age	**[years]**	300	600-930[1]

[1] Nooden 1988

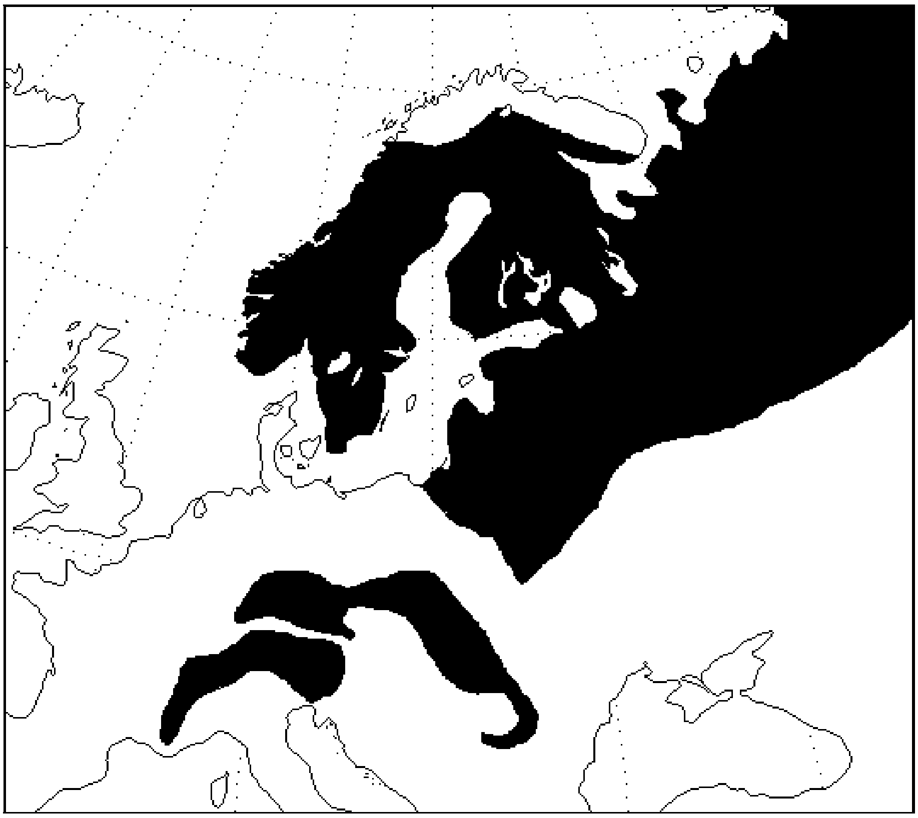
1.8.2 *Fagus sylvatica* L.

General habit: *Fagus sylvatica* (Scott 2003) is a deciduous, monoecious, mono- and polycormic tree. Isolated open-grown trees develop an extremely wide, spreading crown with branches springing from low down the stem. Trees grown in a forest stand can develop up to 25 m. On good sites, mature beech will attain an average height of 35 m and mean diameter at breast height of 45 cm. Largest tree dimensions recorded are 50 m height and 290 cm diameter at breast height. Stem form of beech depends strongly on environmental conditions and competition. Straight, branchless stems with little taper will form when beech is grown with competing trees in a stand. In other conditions, beech will tend to develop forked, crooked or twisted stems. With decreasing crown symmetry, stems also tend to develop increasing eccentricity. *Fagus sylvatica* assumes a shrub-form when growing at the timberline.

Shoot and foliage characteristics: Twigs are green after flushing and become reddish-brown during lignification. Two types of shoots may be distinguished: (i) long shoots with alternate buds which branch out regularly; and (ii) short shoots which only develop a terminal bud, do not branch out, and are frequently located at the twig base. Leaf length ranges from 3 to 14 cm, leaf width between 2 and 8 cm. Petiole up to 12 mm long. Cuticular ornamentation and obvious wax crystalloids are absent. Two types of leaves can be distinguished: (i) sun leaves with multi-layered palisade parenchyma; and (ii) shade leaves with a single-layered palisade parenchyma, half leaf-thickness, fewer veins and fewer stomata.

Climatic conditions: *Fagus sylvatica* occurs in temperate and warm temperate climatic zones (Figure 10). It prefers a moist or maritime climate with some rainfall throughout the summer period, and annual rainfall exceeding 750 mm. Beech can endure dry periods of up to 3 months, depending on topography and soil conditions, and can tolerate high temperatures when not combined with long dry periods (Table 4). In Central Europe, beech growth increases with higher temperatures as long as precipitation is not limiting (>450 mm annual precipitation). High growth rates appear with climatic parameters of 7 to 8℃ mean annual temperature and 600 to 700 mm annual precipitation.

Picea abies



Fagus sylvatica

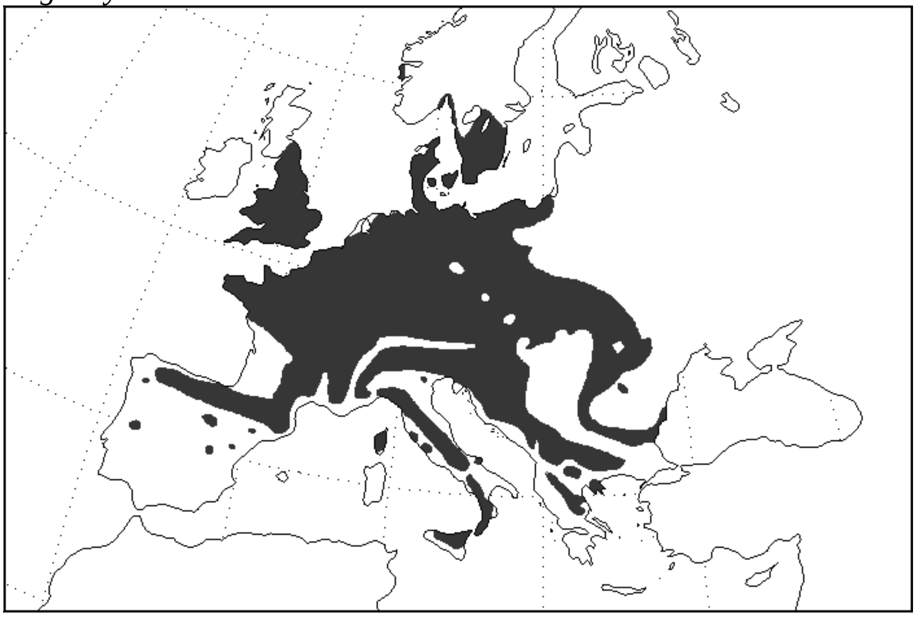


Figure 10: Distribution (black area) of *Picea abies and Fagus sylvatica* in Europe (from Schneider 2004).

2 Space related resource gain and investments

2.1 Foliage

2.1.1 Introduction

Assimilate formation requires plants to access energy (light, temperature) and matter (carbon, water, nutrients). Once these resources become limiting, competition amongst plants exacerbates per unit of time and space. As a result, at least one of the competitors is constrained in resource uptake (Goldberg 1990). Plant species differ in the structural and functional differentiation of roots and shoots and in their responsiveness to internal and external factors (biotic and abiotic site conditions, ontogeny, Egli et al. 1998, Bond 2000), which altogether determines the way space is sequestered and exploited for above and belowground resources. The quality (i.e. attractiveness) of space in providing energy and matter provokes plants to adjust their physiology and structural architecture (Küppers 1984, Küppers 1985, Grabherr 1997).

Focusing on aboveground competition, resource investment into space sequestration through formation of shoot axes and foliage is a prerequisite of resource exploitation (i.e. light) and hence carbon fixation. The investment demands for ‘running costs’ (e.g. transpiration, respiration) to sustain the functionality of the structures involved in resource gain. Plant performance can be quantified in terms of functional efficiencies that relate resource investments to resource gains. Such efficiencies have been postulated (Küppers 1984, Schulze et al. 1986, Sprugel et al. 1991) and defined in a preceding study (Grams et al. 2002).

In forests, foliated volumes of organs, individuals and stands have been modelled at various scales and by different degrees of complexity. However, only few studies exist that explicitly measured enveloping volumes, e.g. in stands (Cermak et al. 1997), crowns (Küppers 1985, Hagemeier 2002), branches (Fleck 2001) or shoots (Küppers 1985). The crown architecture of adjacent trees is not only species-specific but also neighbour-dependent (Hagemeier 2002, Frech et al. 2003). Hence, shapes as changing with tree age (Bond 2000) and size (Frelich and Reich 1999, Connolly et al. 2001) result from the ability of branches to sequester space (Küppers 2001b) and from disturbance, e.g. abrasion through mechanical interference with branches of neighbours (Milne 1991, Rudnicki et al. 2001).

Investments and costs might be low in relation to gains (Matyssek 1986), but gains not necessarily need to be high in relation to occupied space (Küppers 1984). Grams et al. (2002) reported the efficiency in space sequestration rather than exploitation for carbon to determine competitiveness in juvenile beech (*Fagus sylvatica)* and spruce (*Picea abies)* – two species which represent as deciduous broadleaved and evergreen coniferous trees, respectively, contrasting extremes in growth habit in Central Europe (Ellenberg 1996). In this present study, the concept introduced for juvenile trees was examined, throughout two growing seasons, for the foliage of sun and shade branches in adult beech and spruce trees within a mixed forest stand.

We hypothesized for the foliage of beech and spruce branches that

hypothesis 1 sun branch volume is characterized by higher investments into foliage mass compared to shade branches,

hypothesis 2 the space-related carbon gain is higher in sun than in shade branches, and

hypothesis 3 annual carbon and water costs for sustaining the foliated space are low, wherever space-related C gain is low.

Hence, investment into the foliated space around branches, the C gain retrieved from that space, and the “running costs” of keeping the space occupied will be quantified. It will then be asked to which extent findings may characterize competitiveness.

2.1.2 Material and Methods

2.1.2.1 Efficiencies of resource investment and gain

Efficiencies were defined (Grams et al. 2002**)** as:

(i) space sequestration at the branch and crown level as based on C investment into foliage mass, Eq. 1

(ii) space exploitation in terms of the sum of annual carbon gain of each branch sector per unit of sequestered volume, Eq. 2,

(iii) 'running costs' in terms of sequestered crown volume to be sustained per unit of respiratory carbon release and transpiratory water loss, Eq. 3.

According to definitions in physics (Lide 2003), efficiency is conceived as a ratio of gain *versus* concurrent resource use (cf. photosynthetic gain by water or light use as water and light-use efficiency, Larcher 2001). Regarding the efficiency of space sequestration, C investment represents, therefore, the denominator; in the case of the efficiency of space exploitation, it is the amount of space occupied as the denominator that yields gain in light as the attractive energy resource and, hence, carbon; and given the efficiency of "running costs", it is the consumption of water and C resources as the denominator which confine the space that can be occupied.

$$ESS = \frac{sequestered\ volume}{invested\ \ biomass} \tag*{Eq. 1}$$

$$ESE = \frac{sequestered\ carbon}{sequestered\ volume} = \frac{\sum_{sector=1}^{4} sequestered\ carbon_{\ sector}}{sequestered\ volume} \tag*{Eq. 2}$$

$$ESR = \frac{sequestered\ volume}{running\ \ costs} \tag*{Eq. 3}$$

$$i.e.\ \frac{sequestered\ volume}{\sum_{sector=1}^{4} transpired\ \ water_{sector}}, \frac{sequestered\ volume}{\sum_{sector=1}^{4} respired\ \ carbon_{sector}}, \frac{sequestered\ volume}{lost\ biomass}$$

2.1.2.2 Assessment of foliated crown volume

The foliated volume of branches that had been sequestered in the tree crowns (V, Eq. 4) was approximated in spruce and beech branches through measurements of the maximum horizontal (d_{hi}) and vertical (d_{vi}) extension of the foliage at n positions along the foliated part of the main axis (l). The vertical and horizontal extensions at position i, with $0<i\leq n$, provide the diameters of ellipses as cross-sections of foliated volumes. V is the sum of frustra as based on such ellipses and the distance (l_{i+1} - l_i) between them (Grams et al. 2002).

$$V = \sum_{i=0}^{n-1} \frac{\pi \cdot (l_{i+1} - l_i)}{12} \cdot \left(d_{vi} \cdot d_{hi} + \sqrt{d_{vi} \cdot d_{hi} \cdot d_{vi+1} \cdot d_{hi+1}} + d_{vi+1} \cdot d_{hi+1}\right) \qquad \text{Eq. 4}$$

2.1.2.3 Foliage biomass and surface area:

The biomass and surface area of the foliage was assessed within branch volumes, and specific leaf area (SLA) provided the basis for scaling within branches and the canopy (cf. Grote and Reiter 2004). In 1999 and 2000, leaves or needles at stem-distal positions were harvested from branches representative and in the proximity of the study branches. In beech, one sample consisted of five leaves, and in spruce, of 50-100 needles from two to three shoots. Foliage was scanned at 300 dpi, and projected foliage area and needle length were determined with DT-Scan (Delta-T Devices Ltd., Burwell, Cambridge, UK). We used the projected one-sided foliage area and dry mass (60°C, 2 d) in beech and spruce to calculate SLA. Specific needle length (SNL, Eq. 5, n=99, R^2=0.84, p<0.001) and SLA (Eq. 6, n=99, R^2=0.87, p<0.001) depended on needle age (age, current year = 1) and position in the crown, with $rheight$ being the relative crown height normalized in proportion between apex = 1 and base of foliated crown = 0, $rlength$ was the normalized proportion of foliated length along the main branch axis (distal = 0, proximal = 1). See Annex A for details of SLA and SNL approximation.

$$SNL = \max[2.8\,, -2.049 \cdot \ln(age) - 4.756 \cdot rheight + 1.914 \cdot rlength + 8.63] \qquad \text{Eq. 5}$$

$$SLA = \max[2.8\,, -1.836 \cdot \ln(age) - 4.261 \cdot rheight + 1.482 \cdot rlength + 7.83] \qquad \text{Eq. 6}$$

Beech: The mass of foliage on a branch, shortly after full leaf expansion, was $Mfol_{branch}$ (Eq. 7), and $Afol_{branch}$ was the one-sided (projected) leaf area of a branch (Eq. 8). The number of beech leaves were counted at the beginning of the season n_{beg}, and at the end of the season, the branches were wrapped into nets to collect the shed leaves. The leaves of each beech branch were counted (n_{end}) and weighed ($Mfol_{end}$, 60°C, 2 d). Herbivory was estimated on an area basis (A_{herb}) for each leaf, and the lost biomass calculated through average SLA_{mean}. SLA which did not display seasonal shifts between the end of June (after completion of leaf growth) and late September (prior to autumnal leaf discolouration in beech) was assessed twice, in mid-July (SLA_{mean}, peak period of herbivory, estimation of related biomass loss) and at the beginning of October (SLA_{pro} & SLA_{dis}). The latter sampling date was advantageous in estimating, on an SLA basis, the durable C investment in beech leaves before shedding, as resource retranslocation out of the leaves proceeded at still unchanged leaf area (Chapin and Kedrowski 1983, Regina and Tarazona 2001). SLA and cumulative leaf mass linearly increased from *dis*tal to *pro*ximal branch positions within the study branches (Eq. 9), as adopted from assessments outside the study plot (R^2>0.94).

$$Mfol_{branch} = \frac{Mfol_{end} \cdot n_{beg}}{n_{end}} + \frac{A_{herb}}{SLA_{mean}} \qquad \text{Eq. 7}$$

$$Afol_{branch} = \int_{l=0}^{lfolbr} Mfol_{branch}^{beech} \cdot SLA(l) \qquad \text{Eq. 8}$$

$$SLA(l) = \frac{(l - l_{dis}) \cdot (SLA_{pro} - SLA_{dis})}{l_{pro} - l_{dis}} + SLA_{dis} \qquad \text{Eq. 9}$$

<u>*Spruce:*</u> The foliated lengths ($lfoltw_{age}$) of the current-year, one-year and two-year-old shoots as well as the total foliated length of age classes older than two years were determined on each spruce study branch. The average shoot lengths of age classes older than two years were approximated with the average shoot length of the youngest three age classes. The sum of needle length on a branch was based on measured age-dependent needle densities (d_{age}; 23.2, 22.9, 22.7, 21.6, 19.8, 13.2, 8.7, 9 [n cm^{-1}] for age classes of 1=current to 8 years, respectively) and a mean needle length (l_{mean}) of 14.84 mm (sd = 1.071 mm, n = 109 shoots). The functions of SNL and SLA (Eq. 5 & Eq. 6) were applied to calculate the total foliage mass ($Mfol_{branch}$, Eq. 10), the projected leaf area ($Apfol_{branch}$, Eq. 11) and the total leaf area ($Atfol_{branch}$, Eq. 12) on branches. For gas exchange assessments, the conversion factor of projected *versus* total surface area of needles (ko_{OREN} =2.6, cf. Eq. 12) was adopted from Oren et al. (1986). We validated the calculated with measured foliage mass of sampled branches (R^2>0.87). On the basis of this relationship foliage biomass was calculated for all spruce study branches.

$$Mfol_{branch} = \sum_{age,\ position,\ height} \frac{lfoltw_{age} \cdot d_{age} \cdot l_{mean}}{SNL_{age,position,height}} \qquad \text{Eq. 10}$$

$$Apfol_{branch} = \sum_{age,\ position,\ height} \frac{lfoltw_{age} \cdot d_{age} \cdot SLA_{age,position,height} \cdot l_{mean}}{SNL_{age,position,height}} \qquad \text{Eq. 11}$$

$$Atfol_{branch} = \sum_{age,\ position,\ height} \frac{lfoltw_{age} \cdot d_{age} \cdot SLA_{age,position,height} \cdot l_{mean} \cdot ko_{OREN}}{SNL_{age,position,height}} \qquad \text{Eq. 12}$$

2.1.2.4 Fraction of sequestered crown space in the canopy

We estimated the fraction of sequestered crown volume in a canopy layer by division of the averaged leaf area density [m^2 m^{-3}] of a canopy layer by the averaged leaf area densities of the foliated branch volumes in that layer. The leaf area distribution of the stand was measured optically (LAI-2000, Li-Cor Inc., Lincoln, Nebraska, USA) along three vertical profiles of spruce and seven of beech by intervals of 0.5 m. The raw projected leaf area of spruce was computed (C2000, Li-Cor Inc., Lincoln, Nebraska, USA) and corrected as described in the Annex, section C. The hemi-surface area, as proposed by Chen and Black (1992), of spruce needles was required to calculate vertical profiles of foliage areas from LAI-2000 assessments, which was achieved by substituting the conversion factor ko_{OREN} (Eq. 12) with a SLA-dependent function fko (Eq. 13; n=50, R^2=0.63, p<0.001, this study and Matyssek 1985, Perterer and Körner 1990, Götz 1996, Sellin 2000, see Annex, section B, for details). The mean conversion factor of the individual branches (ko_{branch}, Eq. 14) was scaled with the relative height ($rheight$) in the spruce crowns (fko_{height}, Eq. 15; n=19, R^2=0.85, p<0.001):

$$fko = -1.232 \cdot \ln(SLA) + 4.672 \qquad \text{Eq. 13}$$

$$ko_{branch} = Atfol \cdot Apfol^{-1} \qquad \text{Eq. 14}$$

$$fko_{height} = 0.854 \cdot rheight + 2.342 \qquad \text{Eq. 15}$$

2.1.2.5 Gas exchange

C gain, respiration and transpiration were modelled at the leaf level through PSN6 (Falge et al. 1996), as based on Farquhar et al. (1980) and von Caemmerer and Farquhar (1981); model parameterisation according to Harley and Tenhunen (1991). Calculation of stomatal conductance was based on Ball et al. (1987) and Baldocchi (1994). The model inputs were microclimate by ten-minute intervals, as well as species and branch-specific variables of foliage parameters. Climatic data consisted of photosynthetic photon flux density ($PPFD$) from four sensors per branch at distal to proximal positions, leaf temperature, water vapour pressure deficit, atmospheric pressure and CO_2 concentration. The species-specific parameters were adopted (Falge et al. 1997, EUROFLUX datasets/ Valentini 2003, Patzner 2004) or measured (see Table 5): In the proximity of each study branch, analytical gas exchange measurements (Li-6400, LI-COR Inc., Nebraska, USA) were performed at 25°C six times on each branch throughout 1999 and 2000 in beech, and 2000 and 2001 in spruce after development and construction of a spruce gas exchange cuvette for the LI-6400 (see Figure 18D, page 48). Apparent quantum yield (α) was calculated as the slope of the regression between net CO_2 uptake rate and low $PPFD$ (< 80 µmol m^{-2} s^{-1}) which preceded measurements at high $PPFD$ (full induction of photosynthesis, 10 minutes at $PPFD$ of 1500 µmol m^{-2} s^{-1}, before assessment of photosynthetic CO_2 dependence). Thereafter, dark respiration (during daytime) was measured. Vc_{max} and J_{max} (Farquhar et al. 1980) were iteratively derived from the CO_2 dependence of photosynthesis (least sum of squared residuals, Excel, Microsoft Corporation, Redmond, WA, USA). Minor temperature deviations from 25°C were corrected (Harley et al. 1992, Bernacchi et al. 2001). Vc_{max} and J_{max} were highly correlated to each other (Leuning 1997, Medlyn et al. 2002). Missing data of Vc_{max}/J_{max} pairs were calculated (Eq. 16) from the slope $ppsl$ of their regression forced through the origin. Vc_{max} and J_{max} were standardized by means of a common specific leaf area SLA_{St}, through a linear shift along the slope of their regression with the specific leaf area (Eq. 17, n_{beech}=104, n_{spruce}=42, R^2>0.55,). In beech, Vc_{max} and J_{max} (represented as P in Eq. 18) were related to phenological observations (Brügger 1998, Roberntz 1999) during leaf development and changes in gas exchange throughout the growing season. Leaf development was approximated sigmoidally beginning at bud break (SGS-$dSGS$, in day of the year doy) until 30 days after mid-flush (SGS, leaves fully visible, but still folded; Boltzman function, Origin 6.0 Microcalc Inc., Northampton, MA, USA), where P_A was the logarithmically fitted value of the seasonal maximum Vc_{max} and J_{max} 30 days after mid-flush, and $pcurve$ was the deflection factor determining the slope of the decline of $P(doy)$ until the end of the growing season (EGS, Nunn et al. 2002). No such seasonal change was found in spruce (cf. Falge et al. 1996), however, an age-dependent decline was considered: The mass-based photosynthetic capacity declined exponentially with increasing needle age, based on study trees and Lange et al. (1986), Weikert et al. (1989), Götz (1991), Wedler et al. (1995). The capacity of previous-year shoots were set to 100 % ($ffolweigh_{age=2}$ =1, Eq. 19). To account for the differences in photosynthetic capacity, we weighted the total mass of each age class ($Mfol_{age}$) relative to age class 2 ($ffolweigh$) and obtained $Mfolweigh_{branch}$ (Eq. 20). The annual gas exchange by the whole branch was then $Mfolweigh_{branch}$ multiplied by the annual mass-based rate of gas exchange of previous-year shoots. Finally Vc_{max} and J_{max} were specifically scaled to each branch sector (Eq. 17).

Apparent quantum yield α (Eq. 21) and mitochondrial respiration (R_{mito}, Eq. 22) under daylight (Villar et al. 1994) and darkness (Noguchi et al. 2001) were linearly coupled to J_{max} (Table 5) and thereby followed the seasonal course in beech and the inter-annual changes in spruce. All study branches were subdivided into four sectors along the foliated main axis. Each sector was backed by its specific $PPFD$ assessment (Reitmayer et al. 2002) and individually parameterised in terms of its specific biometry.

$$J_{\max} = ppslp \cdot Vc_{\max} \qquad \text{Eq. 16}$$

$$\begin{aligned} Vc_{\max\cdot St} &= SLA \cdot pvcsla - SLA_{St} \cdot pvcsla + Vc_{\max}\ ; \\ J_{\max\cdot St} &= SLA \cdot pjsla - SLA_{St} \cdot pjsla + J_{\max} \end{aligned} \qquad \text{Eq. 17}$$

$$P(doy) = \left\{ \begin{array}{ll} P_A \cdot \dfrac{\dfrac{6}{\left(1+e^{\frac{doy-SGS}{dSGS}}\right)}+6}{\dfrac{6}{\left(1+e^{\frac{(SGS+30)-SGS}{dSGS}}\right)}+6} & ;\ SGS - dSGS \geq doy > SGS + 30 \\ P_A \cdot \dfrac{\log(EGS + pcurve - doy) - \log(pcurve)}{\log(EGS + pcurve - SGS) - \log(pcurve)} & ;\ SGS + 30 \geq doy > EGS \end{array} \right\} \qquad \text{Eq. 18}$$

$$ffolweigh_{age} = 1.2143 \cdot e^{-0.1237 \cdot age} + 0.0518 \qquad \text{Eq. 19}$$

$$Mfolweigh_{branch} = \sum_{age=1}^{8} Mfol_{age} \cdot ffolweigh_{age} \qquad \text{Eq. 20}$$

$$\alpha = J_{\max} \cdot palpha^{-1} \qquad \text{Eq. 21}$$

$$R_{mito} = \left\{ \begin{array}{ll} prmito \cdot J_{\max} \cdot 0.6 & ;PPFD > 25 \\ prmito \cdot J_{\max} \cdot (1 - (0.016 \cdot ppfd)) & ;25 \geq PPFD > 0 \\ prmito \cdot J_{\max} \cdot 0.7 & ;PPFD = 0 \end{array} \right\} \qquad \text{Eq. 22}$$

2.1.2.6 Microclimate

Atmospheric pressure and CO_2 concentration in the canopy were measured at the site. Air temperature and humidity were measured at 16 positions in the sun and shade crowns of spruce and beech as half-hour means. Photosynthetic photon flux density ($PPFD$) was recorded by 160 novel sensors with circumradial view (2 π), based on light transmittance through polyethylene cables while intercepting the sum of direct and diffuse radiation (Reitmayer et al. 2002). Linear regression between $PPFD$ and global radiation measured above the stand enabled the elaboration of a continuous $PPFD$ dataset throughout 1999 and 2000 and the consideration of natural light fluctuations.

Table 5: Model parameters of beech and one-year-old spruce foliage. Values in brackets were adopted in calculations, in the absence of assessments at the study site.

Parameter	***Unit***	***Value spruce***	***Value beech***
Carboxylase kinetics			
$f(K_C)$	-	(299.469)	(404)
$Ea(K_C)$	J mol^{-1}	(65000)	(59500)
$f(K_O)$	-	(159.597)	(248)
$Ea(K_O)$	J mol^{-1}	(36000)	(35000)
f(tau)	-	(2339.53)	(2339.53)
Ea(tau)	J mol^{-1}	(-28990)	(-28990)
O_2	o/oo	(210)	(210)
Carboxylase capacity			
V_{cmax} , *Eq. 17*	µmol m^{-2} s^{-1}	18.2 – 26.4[a]	28.3 – 101[a]
$\Delta Ha(V_{cmax})$	J mol^{-1}	(75750)	(69000)
$\Delta Hd(V_{cmax})$	J mol^{-1}	(200000)	(198000)
$\Delta S(V_{cmax})$	J K^{-1} mol^{-1}	(656)	(660)
Electron transport capacity			
Jmax , *Eq. 17*	µmol m^{-2} s^{-1}	33.2 – 55.2[a]	48.8 – 178[a]
$\Delta Ha(Pml)$	J mol^{-1}	(47170)	(40000)
$\Delta Hd(Pml)$	J mol^{-1}	(200000)	(200000)
$\Delta S(Pml)$	J K^{-1} mol^{-1}	(643)	(655)
Scaling of V_{cmax} *&* J_{max}			
ppslp, Eq. 16	-	2.00	1.75 / 1.74[b]
SLA_{St}, *Eq. 17*	m^2 kg^{-1}	5.6 / 3.3[b]	36.6 / 11.0[b]
pvcsla, Eq. 17	µmol kg m^{-4} s^{-1}	3.28	-1.28 / -1.28[b]
pjsla, Eq. 17	µmol kg m$^{-4\ s-1}$	5.48	-2.26 / -2.39[b]
SGS, Eq. 18	day of year		115 – 129[a]
dSGS, Eq. 18	days		30
EGS, Eq. 18	day of year		250 – 314[a]
$Vc_{max\ St/Ac}$, *Eq. 17 & Eq. 18*	µmol m^{-2} s^{-1}	13.2 – 28.6	13.0 – 92.1[a]
$J_{max\ St/Ac}$, *Eq. 17 & Eq. 18*	µmol m^{-2} s^{-1}	25.4 – 54.6	20.4 – 182[a]
pcurve, Eq. 18	-		0.001 – 102[a]
Light use efficiency			
palpha, Eq. 21	µmol m^{-2} s^{-1}	4680	1960 / 2070[b]
Dark respiration			
prmito, Eq. 22	J mol^{-1}	87.9	87.5 / 87.9[b]
Stomatal conductance			
g_{fac}	-	(9.8)	9.57 – 10.6[a]
g_{min}	-	(1)	26.8 – 88.1[a]
width of leaf	cm	(0.1)	3.53 – 5.30[a]

[a] range: shade – sun foliage
[b] year 1999 and 2000 respectively
[c] subscript 'St' refers to spruce, 'A' to beech
.

2.1.2.7 Data processing

Statistical evaluation was performed with SPSS (version 11.0, SPSS Inc., Chicago, IL, USA, summary in Table 6) and Origin (version 6.0, Microcalc Inc.). Data management was based on Excel (version 9.0, Microsoft Corporation) and Diadem (version 8.1, National Instruments Corporation, Austin, TX, USA). The PSN6 model was compiled in Fortran (Fortran Visual Workbench, version 1.00, Microsoft Corporation). For the conversion of biomass published in literature to C mass, we used a dry mass-related C concentration of 46 % (Ebermayer 1882). For recalculations of the efficiency of space sequestration (Table 7) of *Pinus radiata*, specific leaf area of 3.5, 4.5 and 5.5 m^2 kg^{-1} was assigned for sun, intermediate and shade crown, respectively (Raison et al. 1992). From the data and the cross-section given in Lilienfein et al. (1991), foliated volumes were calculated as based on a cylinder with two adjacent hemispheres (see Annex D).

2.1.3 Results

2.1.3.1 Foliar space sequestration

Beech tended to occupy more crown volume than spruce per unit of C investment into the standing foliage mass of branches, which was consistent along the normalized trunk lengths throughout the sun and shade crowns (Figure 11). This space-related investment, i.e. the efficiency of space sequestration, decreased towards the apex in both species.

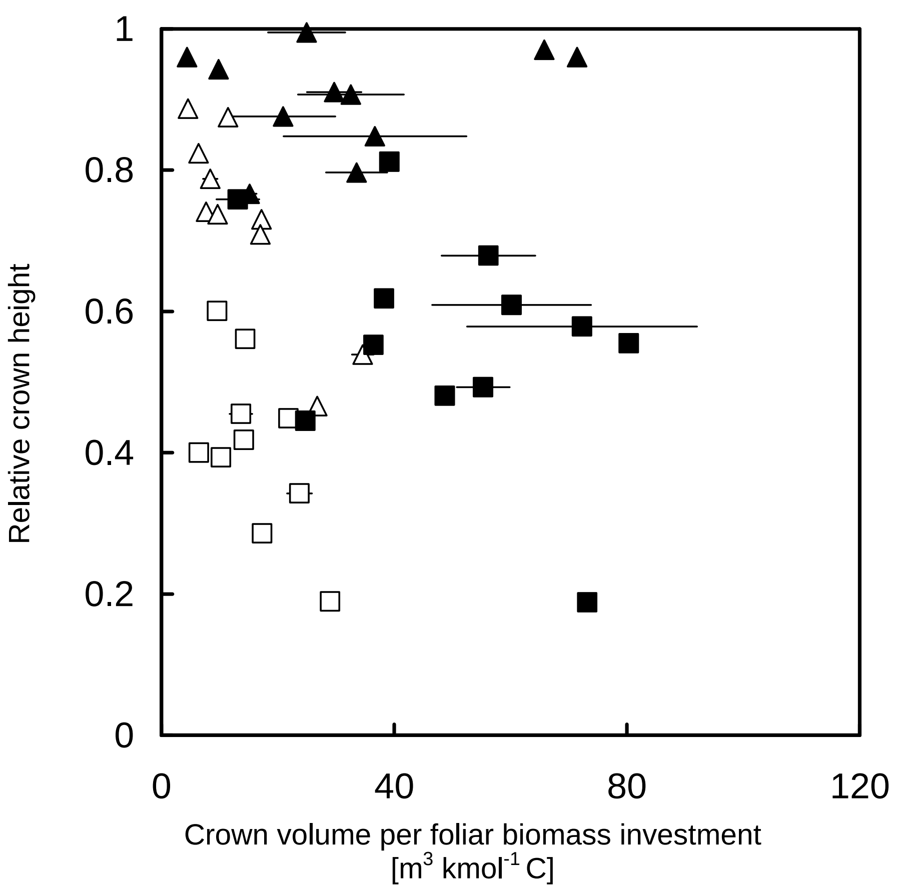


Figure 11: Sequestered crown volume per unit of C investment in the standing foliage mass along the vertical profile of the foliated crown. Relative crown height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1). Depicted are means of the years 1999 and 2000, bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No bars are present if branch died or broke off.

Although beech had been planted seven years prior to spruce, the 60-year-old beech trees had been overtopped by spruce in absolute terms by up to 4 metres in height. The vertical extension of the foliated crown of spruce had become 3 times longer than in beech (Figure 12A). The canopy dominated by beech was homogeneously closed and densely foliated (Figure 12A). In contrast, spruce branches sequestered a lower fraction of the available canopy volume (Figure 12A) which was reflected by gaps between the branches and the absence of canopy closure (cf. picture/ Nunn et al. 2002). In beech, the foliage was concentrated, on average, at 22.5 m stem height within a compact layer of the uppermost 4 m beneath the apex. Within this zone, also spruce displayed its maximum in leaf area density, although the foliage was spread between 16 and 28 m of stem height (Figure 12A).

Hence, the maxima of canopy foliation, expressed as the fraction of sequestered space and reflecting intense competition for space and light, occurred in both species at the time of the study at similar stem height.

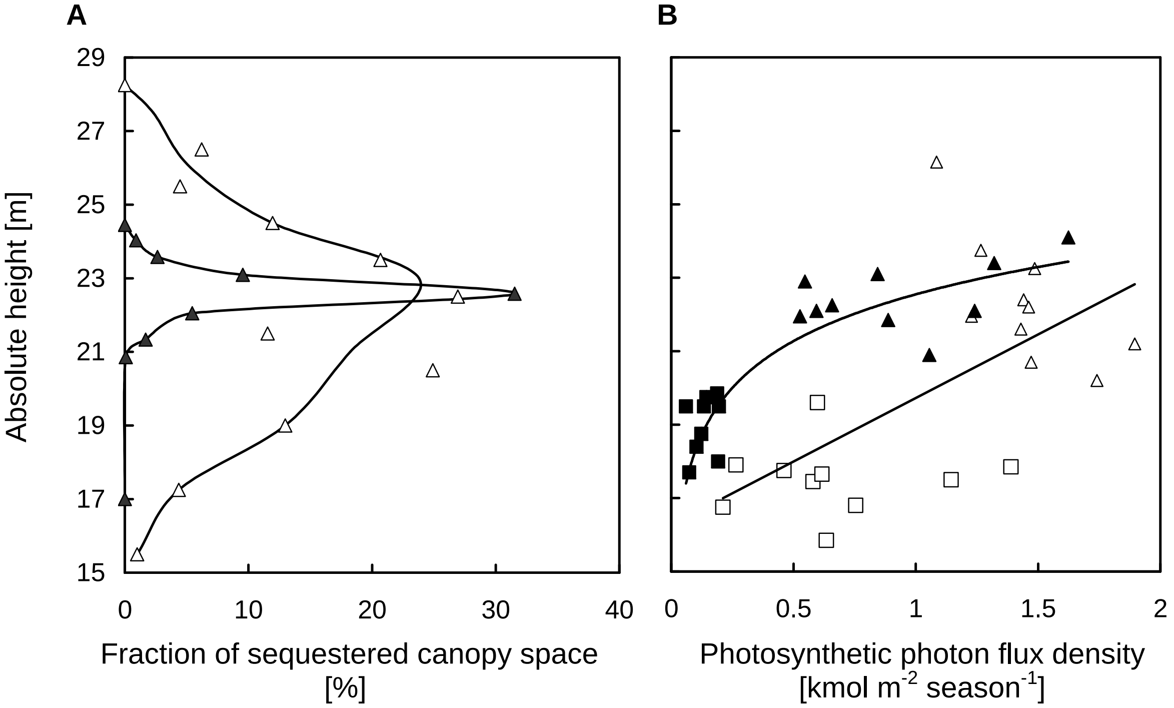
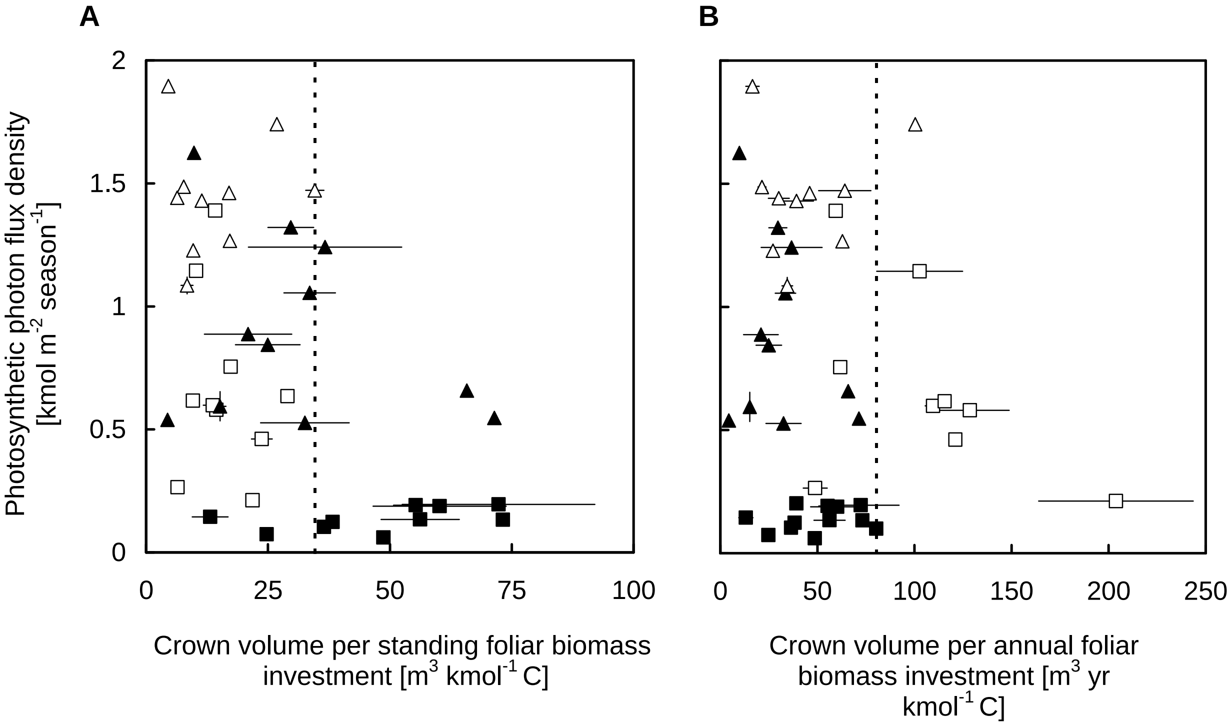


Figure 12: Vertical profile of the canopy in spruce (open symbols) and beech (closed symbols) of (A) the mean fraction of space sequestered by the foliage in the canopy, 100 % = closed canopy, and of (B) the sum of photosynthetic photon flux densities (PPFD) of sun (triangles) and shade (squares) branches of spruce and beech during the concurrent period of their growing seasons (1st June until 30th October), approximated by a logarithmic fit for beech ($r^2=0.68$) and a linear fit for spruce ($r^2=0.45$).

The sum of photosynthetic photon flux density (*PPFD*) intercepted by the foliage differed substantially between the species due to both the shorter growing season in deciduous beech than evergreen spruce and the contrasting patterns of space sequestration at the stand level (Figure 12A). The mean incident radiation on branches was, therefore, standardized as the sum of *PPFD* between 1st June and 30th September to compensate for the different lengths of growing seasons and to prevent bias in relation to space sequestration. Light was rather linearly reduced in spruce from the apex downwards to the base of the crown, as compared to the exponential reduction in beech (Figure 12B). In spruce, light availability was substantial also below the zone of maximum leaf area density**:** mean sums of *PPFD* were high in spruce, because the foliage was less self-shaded than in beech. Lowest light sums, being too low for sustaining spruce branches, were found in the shade branches of beech. When related to the sum of *PPFD*, the differences in space sequestration (i.e. crown volume per standing C mass) between the species became less distinct (Figure 13A): Beech and spruce did not differ in the sun branches.



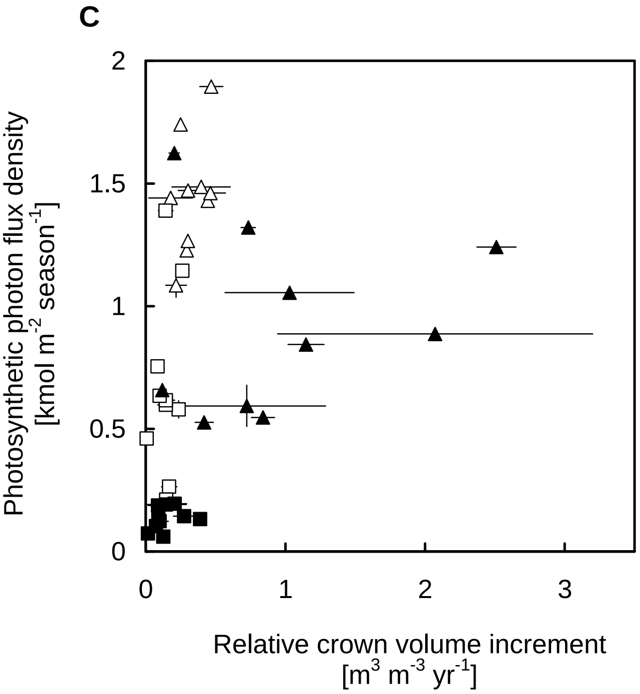


Figure 13: Space sequestration:
(A) Sequestered crown volume per unit of *standing* C investment of the foliage and (B) sequestered crown volume per unit of *annual* C investment of the foliage as related to *PPFD* (see legend Figure 12). Depicted are means of sun (triangles) and shade branches (squares) in beech (closed symbols) and spruce (open symbols) of the years 1999 and 2000, bars represent the range between the years. The dotted line denotes the maximum crown volume per unit of invested biomass in (A) spruce and (B) beech. (C) Annual increment of foliated volume of branches during year 1999, relative to the volume occupied during the previous year, as related to *PPFD* (cf. Figure 12B), symbols as in A&B (statistics cf. Table 6/ lines 1-3).

However, the shade branches of beech showed a wide range in mass-related space sequestration at low light availability. The lower the mass-related space sequestration at similar seasonal *PPFD* (Figure 13A), the higher was the position of a branch along stem height (cf. Figure 11). This tendency is a consequence of the age of the branch, as architectural changes in branching due to increased shading proceed more slowly than do the year-by-year decrease in light availability and changes in leaf morphology (e.g. specific leaf area, Grote and Reiter 2004). Beech differed from spruce at low light levels by having a distinctly larger crown volume per unit of standing C foliage mass (Figure 13A, dotted line denoting maximum efficiency of spruce). These findings contrast with the C investment-related foliar space on an annual basis (i.e. new flush of foliage plus, in spruce, C incorporation into older needles) which was distinctly higher in spruce than in beech (Figure 13B). Sequestration of new space relative to the space occupied during the previous year (Figure 13C) was higher in sun than in shade branches of both species, although beech sun branches, being initially similar in size, sequestered 3 times the volume of respective spruce branches. As a consequence beech was more rapid on an annual basis in relative crown volume increment. Overall, space sequestered at the branch level did not only differ between the species in terms of investments and their incremental rate, but also through the way of acquisition: Compared to beech, spruce had higher standing investments at similar light availability (Figure 13A), but invested less on an annual basis in sequestering new space and sustaining the previously occupied space (Figure 13B), which as a consequence resulted in a restricted expansion of the branch volume (Figure 13C).

2.1.3.2 Foliar space exploitation

How do C investments associated with space sequestration relate to C gains (i.e. space exploitation – being regarded, here, as gross C uptake prior to respiratory C release) ? Both species displayed a similar relationship of C gain per unit of sequestered crown volume within the 10 to 75 % range of intercepted *PPFD* sums, indicating a rather conservative space-related C gain across the species (Figure 14). Beech sun branches, however, tended to reach higher space-related C gains, whereas shade branches tolerated lower *PPFD* respective to spruce branches (cf. Figure 12B), but also achieved less C gain.

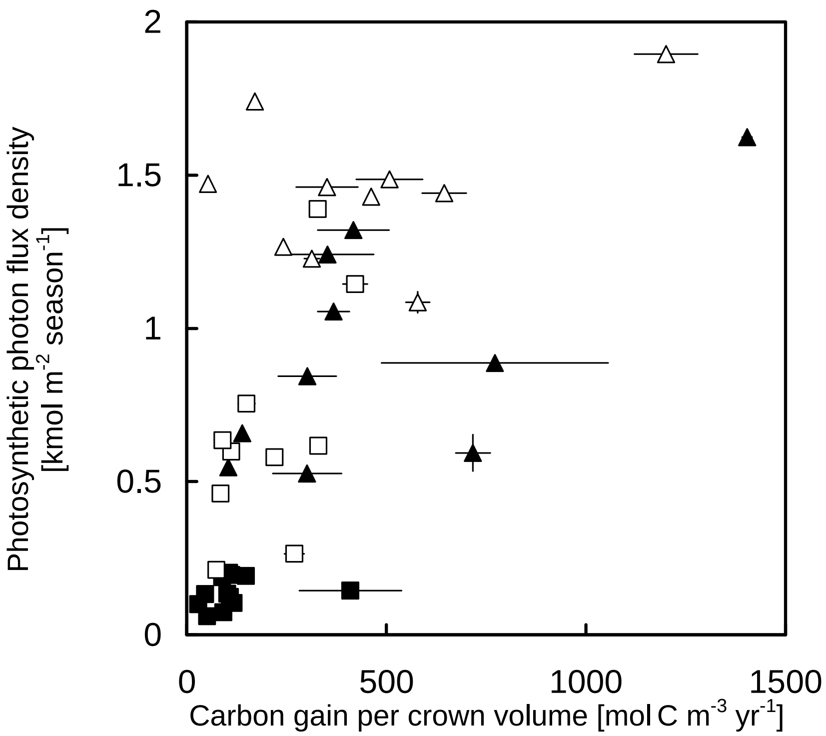


Figure 14: Gross C gain of spruce and beech branches as related to *PPFD* (cf. Figure 12B), symbols as in Figure 13A (statistics cf. Table 6/ line 4).

2.1.3.3 Foliar 'running cost' for space

Foliar respiration (Figure 15A) and transpiration (Figure 15B), being conceived as "running costs", which are the prerequisite for sustaining space sequestration and exploitation, were similar in both species on an annual basis and when related to the space occupied by the foliage, except that shade branches of spruce compared to beech tended to be more efficient in terms of transpiratory running costs (dotted line in Figure 15B). Nevertheless, the space sustained per unit of 'running cost' did not change with decreasing light availability, unlike the space exploitation (cf. Figure 14).

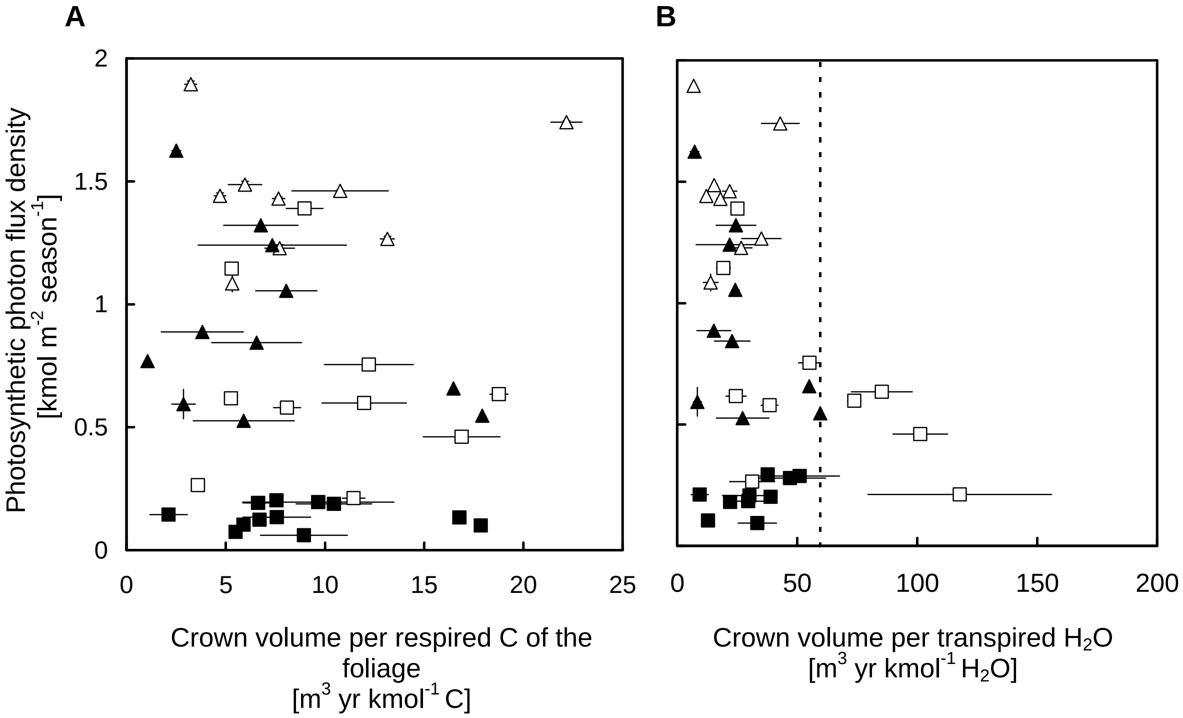


Figure 15: (A) Occupied crown volume per unit of respired carbon and (B) occupied crown volume per unit of transpired water of spruce and beech branches as related to *PPFD* (cf. Figure 12B), symbols as in Figure 13A (statistics cf. Table 6/ line 5&6). The dotted line denotes maximum efficiency of beech branches.

2.1.3.4 Foliar carbon balance

The annual net C balance (Figure 16 white or black sections of bars) of the foliage was mainly determined by the C gain and respiration (cross-hatched section). C investments into foliage (vertically and horizontally hatched sections) represented a minor and nearly constant proportion in both species within the C gain across the whole range of light availability. This proportion tended to be lower in spruce than in beech. The proportion of respiration increased with decreasing light availability similarly in both species, although the highest proportion was found in beech shade branches. In both species, light availability of 11 % and less of the above-canopy irradiance intercepted by shade branches resulted in a negative C balance (black sections). This effect was more expressed in shade branches of beech than of spruce, and most of such branches survived for more than one year (Figure 16).

Table 6: Statistical analysis between (A) species and (B) light environments , “>” denotes higher than , “<“ lower than , and “~” no difference between species or foliage types (Tukey HSD, p<0.05). ESS = efficiency of space sequestration , ESE = efficiency of space exploitation, ESR = efficiency of “running” respiratory and transpiratory costs for keeping space occupied.

	Foliage parameters	*Figure*	**A** *Sun*		*Shade*		**B** *Beech*		*Spruce*	
			Spruce	*Beech*	*Spruce*	*Beech*	*Shade*	*Sun*	*Shade*	*Sun*
1	ESS (volume vs. standing C investment)	Figure 13A	**<**		**<**		~ (**>**)[1]		~	
2	ESS (volume vs. annual C investment)	Figure 13B	~		**>**		~ (**>**)[1]		>	
3	Relative rate of annual volume increment	Figure 13C	~		**>**		<		~ (**<**)[1]	
4	ESE (C gain vs. volume)	Figure 14	~		~		**<**		**<**	
5	ESR (volume vs. respiration)	Figure 15A	~		~		~		~	
6	ESR (volume vs. transpiration)	Figure 15B	~		~		~		~	
7	Carbon balance vs. volume	Figure 16	~		~		**<**		~ (**<**)[1]	

[1] no differences , but significant linear trend with covariate light

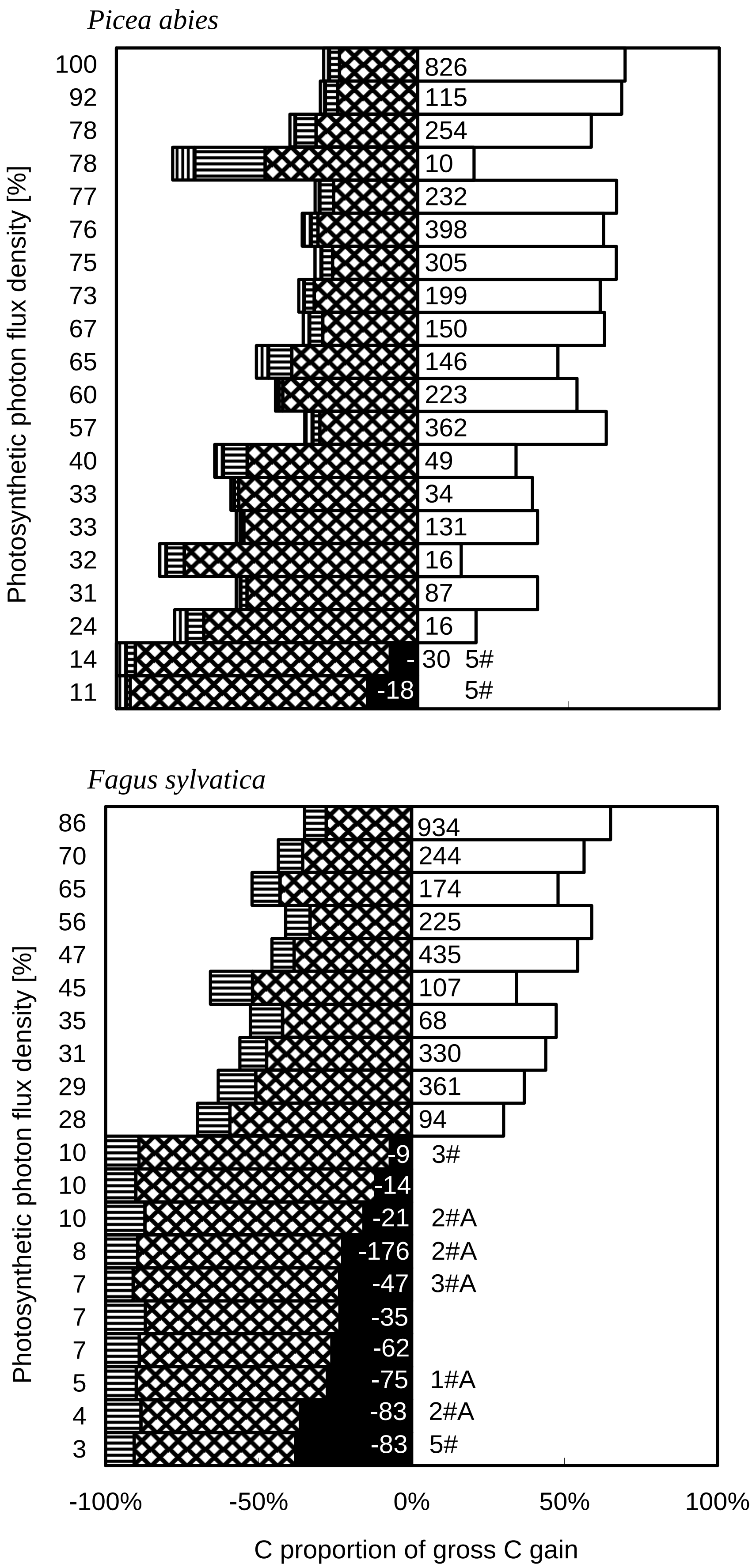


Figure 16: Mean annual carbon balance of the foliage of spruce (*Picea abies*) and beech (*Fagus sylvatica*) branches ranked by the order of *PPFD* (cf. Figure 12B, statistics cf. Table 6/ line 7). White sections denote the excess of the gross C uptake (positive balance) after deduction of respiration (crossed sections), investments for current-year foliage (horizontally hatched sections) and carbon investments of spruce for older needle age classes (vertically hatched sections). Black sections denote negative C balances. Numbers inside black and white bars are absolute values of the C balance (mol m^{-3} yr^{-1}). Branches with a negative balance are marked with the number of years (#) of survival. Branches are marked with an ‘A’, if their dying coincided with an outbreak of a fungal infection of *Apiognomonia errabunda* (Hartmann et al. 1995).

2.1.4 Discussion

Ratios were used in this present study similar to those of Schwinning (1996: “resource uptake”) or Cermak (1989: “solar equivalent leaf area”) that quantitatively relate physiological plant performance, to the sequestered space harbouring the attractive resource. Such approaches provide a basis for comparing plants of different growth habit (cf. Zimmermann et al. 1971; Table 7).

2.1.4.1 Foliar space sequestration

Although space sequestration has found its way into textbooks (Küppers 2001a, Küppers 2001b), studies hardly addressed the volume occupied and exploited by branches, but focussed on whole crowns or fractions of the whole canopy. The volume sequestered by the foliage of branches is different from the volume of whole crowns in that crowns have large non-foliated portions, which is reflected in the space-related C investment. If crowns are broken down, however, into layers or voxels, the space-related C investment of sun crowns converges with that of branches (see Table 7: *Fagus sylvatica, Picea abies, Pinus sylvestris*). Beech branches displayed a distinct gradient in the space-related C investment. The investment declined with decreasing light availability (Table 6/B1, Figure 13A, acceptance of hypothesis 1 for beech). This gradient is consistent with other findings at the branch level of *Fagus sylvatica* and *Quercus petraea*, as well as at the crown layer level of *Fagus sylvatica*, *Picea abies* and *Corylus avellana* (Table 7), but was not confirmed at the branch level of spruce in the present study (Table 6/B1, rejection of hypothesis 1 for spruce). This latter outcome appears to result from the rigid, “one-directional” growth pattern of spruce branches (Brunig 1976), which are constrained, therefore, in adjusting to gradually limiting light conditions and in “precisely” sequestering (*sensu* de Kroon and Hutchings 1995) favourable light patches (Figure 12). Spruce generally had a higher standing C investment of foliage than beech per unit of space. However, deciduous beech had to completely reinvest its foliage each year into the previously sequestered space, whereas evergreen spruce had lower annual investment costs, particularly in shade branches (Table 6/B2; acceptance of hypothesis 3 for annual biomass investments; in analogy to the comparison between the deciduous conifer larch and evergreen spruce: Matyssek 1986).

Table 7: Efficiencies of space sequestration based on standing C investment of the foliage ($\mathrm{m}^3\ \mathrm{kmol}^{-1}$).

Species	***Scale***	***Sun crown***	***Intermediate or mean***	***Shade crown***	***Source***
Corylus avellana	crown	54	100	180	Lilienfein et al. (1991)
Fagus sylvatica	branch	34	-	48	this study
	branch	24	45	80	tree Bu38, Fleck (2001)
	branch	57	110	210	tree Gr12, Fleck (2001)
	branch[1]	-	20	-	Grams et al. (2002)
	branch[1]	14	-	-	Küppers (1985)
	crown voxel, 1 dm^3	15	-	84	Hendrich (2000)
	crown voxel, 16 dm^3	34	-	350	Hendrich (2000)
	crown voxel, 128 dm^3	60	-	870	Hendrich (2000)
	crown layer	550	1300	2600	Hagemeier (2002)
	crown		690		Terborg 1998
Picea abies	branch	14	-	16	this study
	crown[1]	-	7.8	-	Grams et al. (2002)
	crown voxel, 1 dm^3	3.3	-	10	Hendrich (2000)
	crown voxel, 16 dm^3	5.8	-	21	Hendrich (2000)
	crown voxel, 128 dm^3	8.6	-	37	Hendrich (2000)
	foliated crown segment	13	35	63	Falge et al. (1997)
	foliated crown layer	8.9	27,77,670[2]	1800	Schulze et al. (1977)
	foliated crown	-	93.5	-	Matyssek (1985)
Larix decidua	foliated crown	-	261	-	Matyssek (1985)
leptolepis	foliated crown	-	318	-	Matyssek (1985)
dec x lep	foliated crown	-	251	-	Matyssek (1985)
Pinus sylvestris	branch	-	20	-	Cermak et al. (1997)
	crown	-	40, 120[3]	-	Cermak et al. (1997)
Pinus radiata	crown voxel, 1 dm^3	3.2	4.6	5.2	Whitehead et al. (1990)
Quercus petraea	branch	20	32	110	Fleck (2001)

[1] foliage *and* wood are included in C mass, [2] layers from upper to lower crown,
[3] based on ellipsoid and cylindrical model, respectively

2.1.4.2 Foliar space exploitation

In both species, the efficiency in space exploitation increased from the shade to the sun branches (Table 6/B4, acceptance of hypothesis 2). Although the standing foliage C mass was lower in beech than in spruce per sequestered volume at the branch and crown level, the space exploitation (i.e. space-related C gain resulting from light interception) was similar in both species. This is consistent with findings on spruce and beech by Kozovits (2003) comparing crowns of young trees. In a hedgerow study, early-successional *Prunus spinosa* and *Crataegus* x *macrocarpa* displayed C gains twice as high on a crown volume basis as those of mid-successional *Acer campestre* (Küppers 1985, Schulze et al. 1986). The net C gains on a crown volume basis of *Prunus spinosa* and *Crateagus* x *macrocarpa* were similar to the gross C gain of shade branches in beech, although they included mitochondrial respiration.

2.1.4.3 Foliar 'Running costs' for space

"*Running" respiratory and transpiratory costs* for sustaining occupied space did not significantly differ between beech and spruce, or sun and shade branches (Table 6/A5-6, rejection of hypothesis 3 for respiratory and transpiratory costs). Transpiratory costs in relation to foliated branch volume have only been published for the above mentioned hedgerow species (Küppers 1985), where *Acer campestre* consumed about 15 times less water than did the shrub species. However, *Prunus spinosa* and *Crateagus* x *macrocarpa* resembled, in this respect, the sun branches of spruce and beech. In consistency with our findings on carbon and water relations, we postulated the space-related nutrient investment in the foliage mass to be similar in beech and spruce as well, given the positive correlation between photosynthetic capacity and demands for water and nitrogen across foliage types, although the turnover of nitrogen may differ on a long-term scale (Matyssek 1986, Stitt and Schulze 1994).

2.1.4.4 Foliar carbon balance

Regarding the annual C balance (CB), branch C autonomy is a conception that regards trees as an aggregation of C-autonomous modules (i.e. branches; Franco 1986), which differ by their source strength in C export (Grossman and DeJong 1994, cf. Mooney et al. 1991, Schulze 1994). Sprugel (1991) argued that evergreen and deciduous tree species with determinate shoot growth (like spruce and beech) possess C-autonomous branches (after completion of shoot growth), which die when their CB approaches zero. Our results conflict in showing the annual CB of the foliage of shade branches at the crown base to be negative in beech and spruce (rejection of hypothesis 3 for CB, cf. Figure 16 and Table 6/B7). In spruce and beech, branches with negative CB did survive for up to five years (until the end of observation). If dieback occurred, it was predominantly associated with an outbreak of fungal infection (Hartmann et al. 1995, cf. Figure 16) so that the low CB appeared to limit not only growth, but also defence against pathogens (Matyssek et al. 2002b).

Sustaining unproductive branches may reflect a sit-and-wait foraging (de Kroon and Hutchings 1995) or gambling strategy (Falster and Westoby 2003) with respect to the incidental occurrence of canopy gaps, e.g. through foliage loss or break-down of neighbouring branches or trees. Through gap formation, the space occupied by these unproductive branches can be exposed to increased irradiance that could not have been intercepted, if this portion of crown space had been given up too early by such branches. Gaps are common in temperate and tropical forests (Connell et al. 1997) and essential in ecosystem development, as was proposed by the mosaic-cycle concept (Remmert 1991). Mature trees close to gaps have been shown to profit from the increased resources but taxonomic groups differed in their quantitative response (Pedersen and Howard 2004). Leaves of crop plants having negative *CBs* were interpreted as e.g. storage organs (Lemon and Wright 1969, Thomas and Sadras 2001) and as decoy for predators and pathogens (Farnsworth and Niklas 1995). Also in spruce, storage rather than photosynthetic productivity may be one major function of ageing (shaded) needle cohorts (Bauer et al. 1997, Niinemets 1997). Regarding woody species, few studies reported negative foliar *CBs* in the field (on a daily basis: *Prunus spinosa* and *Ribes uva-crispa*, Küppers 1987; *Carica papaya* and *Cecropia obtusifolia*, Ackerly 1999; on an annual basis for young understorey trees in the tropical rain forest: 6 of 11 *Psychotria* species, Pearcy et al. 2004). Foliar *CBs* of crown layers in spruce (recalculated from Schulze et al. 1977) were positive, even in the lowest layer, although the maximum net C gain in the uppermost crown layer of 280 mol m^{-3} yr^{-1} confirms the findings of the spruce and beech sun branches in our study. Also, foliage of Scots pine at the crown base yielded positive *CBs* (Witowski 1997). The annual *CB* of shade branches in larch approached zero without becoming negative before they were given up by the trees (Matyssek and Schulze 1988). One has to be aware, however, that contrasting with shade-tolerant beech and spruce, pine and larch represent light-demanding trees (Ellenberg 1996) that rely on productive shade branches and, hence, only tolerate moderate light limitation within the crowns. The ecological significance of negative *CBs* deserves further attention, in particular, to understand C allocation in trees and in modelling of whole-tree C budgets (e.g. Bartelink 1998, Genard 1998, Kurth 1998), with respect to contrasting soil quality and its effects on leaf differentiation and phenology (Host and Isebrands 1994, Egli et al. 1998, Gond 1999) and the entire ontogeny of trees and stands (cf. Ritchie and Keeley 1994, Schoettle 1994, Kull and Tulva 2000). By which means the above findings on the level of the foliage are related to competitiveness, is presented in the ‘General discussion’, section 5.1.

2.2 Axes

2.2.1 Introduction

Woody species' architecture, below and aboveground, is determined by the growth pattern of individual modules of stem, roots and branches (Franco 1986, applied by e.g. List and Küppers 1998). Besides being links to resource transport to the stem, roots and other branches, branches are a positioning system for assimilation organs, and are place holders in space. Branches have demonstrated numerous ways of how to adapt to changing environmental conditions through changes in morphology, anatomy, growth direction, timing of growth and physiology:

The abiotic environment, e.g. light quality, has proven to direct growth in herbaceous and woody plants (Gautier et al. 1997, Gilbert et al. 2001). Shading increased resource partitioning to branches and stems in seedlings of *Fagus sylvatica* and *Quercus robur* (van Hees 1997). Development of indeterminate branches increased significantly with decreasing shade in *Prunus serotina*, and short shoots increased significantly with decreasing shade in *Acer rubrum* (Gottschalk 1994). Branches persist longer, if the whole crown is shaded as compared to individually shaded branches in *Betula pubescence* (Henriksson 2001). Leaf longevity varied with the frequency of branch bifurcation in *Picea abies, Pinus sylvestris* and *Abies balsamea* (Niinemets and Lukjanova 2003). Also drought has been reported to change branching, e.g. in two *Populus* species (Rood et al. 2000), in *Hevea brasiliensis* trees (Devakumar et al. 1999), in *Anacardium excelsum* & *Cecropia longipes* trees (Andrade et al. 1998).

Competition drives branch structure and morphology, as branches have the ability to detect competing neighbours through chemical signals (ethylene/ Tscharntke et al. 2001, Pierik et al. 2003, other volatiles/ Dicke et al. 2003) and light quality (Ritchie 1997, Ballare 1999, Smith 2000) even before shading becomes real (Aphalo et al. 1999). This ability is species-specific (Gilbert et al. 2001). Branch spread of *Picea abies* increases with distance from neighbouring trees, whereas branch inclination is affected by crown contact (Deleuze et al. 1996). Wood stability increased through competition in a *Pinus* hybrid (Groninger et al. 2000), and *Fagus sylvatica* responded with increased xylem vessel diameter and density as well as lower hydraulic resistance in sun and shade branches after thinning (Lemoine et al. 2002). The persistence of existing forks was decreased by shading through neighbours in *Quercus petraea* (Collet et al. 1998). In *Populus tremula,* shoot bifurcation decreased rapidly with decreasing light through competition with *Tilia cordata*. The species differed substantially in extension growth and space-filling strategy. Light-demanding *Populus tremula* expanded into new space with a few long shoots, with the shoot length being strongly dependent on photosynthetic photon flux density ($PPFD$). The shoot growth of shade-tolerant *Tilia cordata*, was weakly related to $PPFD$ (Kull and Tulva 2002). Maximum shoot elongation was 3 times higher in *Eucalyptus delegatensis* than in *Eucalyptus pauciflora* in the same environment (Küppers 1994).

Besides that, responses in branch characteristics are species-specific (Gilbert et al. 2001), they are specific to genotypes. The influence of the genotype was shown in the branching pattern and the different response of the branching in *Populus* clones (Ceulemans et al. 1990). In differing climatic zones, foliar characteristics of branches and branching changed in *Abies balsamea* (Gilmore and Seymour 1997) and *Pinus ponderosa* (Carey et al. 1997). In *Fagus crenata,* trees with different leaf sizes showed large differences in canopy structure, particularly in shade-grown saplings. The leaf mass distributions of the large-leaf populations had the maximum foliage mass in the lower canopy, while those of the small-leaf populations had the maximum foliage mass in the top of the canopy. The allometric relations between foliage mass and shoot and branch mass in small-leaved populations were different from large-leaf populations (Hiura 1998).

Although studies on structure and morphology of branches (and stems) are plentiful, studies on the physiology of branches are rare, particularly in relation to light, CO_2, nutrients, age or competition.

Respiration of a suppressed *Chamaecyparis obtusa* tree decreased from year to year, whereas respiration by more dominant trees increased (Yokota and Hagihara 1998). The gas exchange of woody organs is age-dependent in *Populus tremula* (Aschan et al. 2001) and *Fagus sylvatica* (Damesin 2003), and depends on branch diameter (Damesin et al. 2002) as well as the number of living cells (*Pinus cembra, Picea abies*/ Havranek 1981, Stockfors 2000). Stem respiration was related to N content in *Picea abies* (Stockfors and Linder 1998) and in *Pinus taeda* (Maier 2001), and was influenced by drought (Negisi 1978a) and CO_2 treatments (Janous et al. 2000). A detailed study on the respiration in branches of *Fagus crenata* and *Betula ermanii*, at different heights in the crown and along an altitudinal transect, consistently showed higher rates in branches at the upper canopy (Gansert et al. 2002). Respiration responded to thinning treatments in *Abies balsamea* (Lavigne 1987), and depended on plant-internal competition for resources in tomato (*Lycopersicon esculentum*, Shishido et al. 1999).

In general, branch structure and branch physiology are highly variable, within and between plants. Some of above responses to environmental conditions seem to be stable at a given site, but some as e.g. competitive status may still change allometric or physiological responses (cf. Kantola and Mäkelä 2004), which can attribute to the costs of a branch (Morgan and Cannell 1988). The allometric relationship of the biomass of foliage and the woody axes of branches is strong within species ('Kranzberger Forst'/ Grote 2002, Bartelink 1997, Wirth et al. 2004), which agrees with the function of branches modules as a foliage positioning system. Therefore, it is hypothesised that the differences in space sequestration of the foliage (see section 2.1.3.4, Table 6) is reflected and caused by the acclimation of branching pattern:

hypothesis 4 The efficiency of space sequestration by branches increases from the top to the base of the crown in beech, but not so in spruce.

The results on foliar traits in crown space have supported that responses in branches growth are age dependent. The efficiency of space sequestration did not increase in parallel to light, but the efficiency further increased in lower strata without a change in light regime (Figure 19 & Figure 20, page 50). It is hypothesized that

hypothesis 5 the efficiency of space sequestration of beech is more strongly correlated to the relative height in the crown, which is a function of branch age, than to the light gradient in the vertical profile of the stand.

Since the relative annual increment in space, driven by the elongation growth of branch axes, was greater in the sun branches than in the shade branches of beech and spruce (see Figure 13C & Table 6, page 30& 33), it is hypothesized:

hypothesis 6 The branch respiration, being related to branch growth, is higher in the sun than in the shade branches per unit of crown volume.

2.2.2 Material and Methods

The foliated branch volume was approximated section 2.1.2.2 (page 20, Eq. 4, Bartsch 1994).

2.2.2.1 Biomass

Biomass and surface area of the woody axis were approximated non-destructively, based on measurements of their lengths (l) and diameters (d) and through allometric relationships, which were derived from branch samples. Carbon mass was 46 % of dry mass (LECO-CN-2000, partner project B10, cf. Ebermayer 1882).

Beech: During the dormant season, beginning in winter 1998/99, 1999/2000 and winter 2001/02, lengths of all woody axes of the study branches were measured with a metric tape. Diameters were measured with digital callipers (16 ES, Carl Mahr, Esslingen, Germany) at the most recent internodium and the diameter close to the base, where the positions were permanently marked to allow the same positions to be measured in subsequent years. To obtain the biomass, the volumes of the axes (calculated according to Eq. 4 page 20) were multiplied by a wood density of 0.686 g cm^{-3}, empirically approximated from 5 harvested branches (n=145 subsamples, sd=0.136, no difference between sun and shade branches).

Spruce: The lengths of all woody axes of the study branches were measured in 2000 and 2002. The axes were subdivided into three compartments: (a) the main branch axis and strong 2nd order axes, (b) axes attached to either the main axis or strong 2nd order axes, and (c) branching on axes attached to either the main axis or strong 2nd order axes. The mass of the woody axes of the study branch ($Mwood_{branch}$) was calculated as the sum of all its axes (Eq. 23).

$$Mwood_{branch} = \sum_{a\,b\,c} m = \sum \left[V_a \cdot \rho_a + V_b \cdot \rho_b + m_c \right] \qquad \text{Eq. 23}$$

$$\rho_a = \min\left\{ 1.145 \cdot 10^{-3} \cdot \sum \left[V_a , V_b \right] + 0.144;\, 0.75 \right\} \qquad \text{Eq. 24}$$

$$V_b = 0.1281 \cdot l_b + 1.266 \cdot 10^{-3} \cdot l_b^2 \qquad \text{Eq. 25}$$

$$\rho_b = 6.07 \cdot 10^{-2} \cdot l_b^{0.2202} \qquad \text{Eq. 26}$$

$$m_c = \begin{Bmatrix} 1.38 \cdot 10^{-2} \cdot l_c ,\, sun \quad branch \\ 1.12 \cdot 10^{-2} \cdot l_c ,\, shade \;\; branch \end{Bmatrix} \qquad \text{Eq. 27}$$

The woody volume of the main axes (V_a), as approximated through length and diameters (Eq. 4 page 20), was converted to woody mass through an empirical function of wood density

(ρ_a, Eq. 24, n=6, $p<0.01$, $R^2=0.93$). The wood density depended on the total mass of the whole branch, which was approximated by the woody volume of the branch. The wood density was limited to a maximum of 0.75 g cm^{-3} (cf. Trendelenburg 1955). The volume (V_b, Eq. 25, n=205 $R^2=0.948$ $p<0.001$) and the density (ρ_b, Eq. 26, n=205 $R^2=0.65$ $p<0.001$) of axes directly attached to the main axes was estimated from their length l_b. The mass m_c of all other axes was estimated from their length l_c and their position in sun or shade crown (Eq. 27, $n_{sun}=65$, $n_{shade}=40$, $R^2=0.98$ $p<0.001$).

2.2.2.2 Branch surface area

The surface area of the woody axes of the study branch (A, Eq. 28) was approximated geometrically by a frustrum model based on circles (cf. Eq. 4 page 20). The surface area of the main axes (A_a, Eq. 29) was calculated from measured lengths and diameters. The surface area of the axes directly attached to the main axes were estimated from their lengths (l_b) with a quadratic function (Eq. 30, n=205 $R^2=0.937$ $p<0.001$). The surface area of all other axes (A_c, Eq. 31) was approximated by their length (l_c) and the mean radius (r_c). The mean radius (r_c, Eq. 32) was derived from the total volume (V_c) and mass (m_c) and the mean density ($\rho_{b\ mean}$).

$$A = \sum_{a\,b\,c} A \qquad \text{Eq. 28}$$

$$A_a = \sum_{i=0}^{n-1} \pi \cdot \frac{\sqrt{d_{hi} \cdot d_{vi}} + \sqrt{d_{hi+1} \cdot d_{wi+1}}}{2} \cdot \sqrt{l^2 + \left(\frac{\sqrt{d_{hi} \cdot d_{vi}} - \sqrt{d_{hi+1} \cdot d_{vi+1}}}{2} \right)^2} \qquad \text{Eq. 29}$$

$$A_b = 0.4484 \cdot l_b + 4.099 \cdot 10^{-3} \cdot l_b^2 \qquad \text{Eq. 30}$$

$$A_c = \pi \cdot 2 r_c \cdot \sum l_c \qquad \text{Eq. 31}$$

$$r_c = \stackrel{+}{(-)} \sqrt{\frac{m_c}{l_c \cdot \pi} \cdot \frac{\sum V_b}{\sum m_b}} \leftarrow V_c = \frac{m_c}{\sigma_{b\ mean}} \qquad \text{Eq. 32}$$

2.2.2.3 Respiration measurements on branches

CO_2 exchange of woody axes up to a diameter of 10.5 mm was assessed with a portable gas exchange analyser (LI-6400, Li-Cor Ltd, Lincoln, Nebraska, USA) equipped with a chamber that had been developed for spruce shoots (20 mm sample length). Branches with a diameter of 10 to 30 mm were monitored continuously with a gas exchange system, which was stationary and custom made (Figure 17). The system consisted of a sample gas preparation unit, and cuvettes connected to a pumping and an analysing unit:

Sample gas preparation: Ambient air was compressed to 7 bar and CO_2 and most of H_2O vapour removed by an adsorption dryer (KE 30, Zander Aufbereitungstechnik GmbH, Essen, Germany). The dew point was set to -4℃ to avoid condensation in the tubes. CO_2 (Messer-Griesheim, Krefeld, Germany) was added to obtain a concentration of 360 ppm.

Gas exchange cuvettes: Branch respiration cuvettes (Figure 18A&B) were made of two half shells with adjacent walls of 5 mm strong acrylic glass (Plexiglas®, Röhm GmbH, Darmstadt, Germany), connectors of inlet and outlet were of stainless steel. The half shells enclosed the branch, and were pressed together with pipe clamps. The bearing surface was sealed with tape of neoprene foam. At the lower and upper end of the cuvette, branches were coated with sealant (Terostat®-7, Teroson, Ludwigsburg, Germany) and PTFE tape. The branch was pressure-sealed with silicon rubber, softness (shore A) = 25, by tightening the nut on the threaded bolt, which pressed the soft rubber sealing against the cuvette and against the branch. Stem respiration cuvettes (Figure 18C) were also constructed of half-shells of acrylic glass and two adjacent walls. the cuvettes covered either 200 cm² or 600 cm² of the stem surface. Stem surfaces had been brushed to prevent bias by adherent organisms. The cuvettes were fixed with rubber bands to the northern side of the stem, where they had been sealed to the bark with a layer of sealing compound on top of a layer of acrylic gel. Each branch and stem cuvette was pressure-proofed at +20 mbar over-pressure for gas leaks.

Respiration of twigs and shoots was measured with a portable open gas exchange system (Li-6400, Li-Cor). A cuvette was designed to measure light response of gas exchange The body of the cuvette was cut and machined out of a PTFE pole (Teflon®, Röhm GmbH) of 60 mm in diameter. The inside of the chamber was 20 mm long and 30 mm wide and 40 mm deep. The chamber was open at the top and bottom. The bottom, where the shoot was inserted, was closed with a lid with original Li-cor neoprene sealing and Terostat®. The lid was fixed with metal springs. The top was closed with original Li-Cor transparent foil for daylight chambers, which was stuck to the chamber with two sided adhesive tape. The Li-Cor LED-Light source was placed over the foil and fixed with metal springs. Light was generated orthogonal to the shoot axis (Figure 18D, shade shoot of spruce tree 419). Needle temperature was calculated through energy balance (according to the Li-6400 manual). For that purpose a thermocouple was connected and positioned at the gas outlet to the mixing fan.

Analysing unit: The sampling gas was pressed through polyvinyl tubes to the cuvettes, where surplus gas was blown off. From the cuvettes, the sample gas was continuously sucked (membrane pumps, WISA Classic 300, ASF Thomas Industries GmbH, Puchheim, Germany) to the analysing unit. Therefore, the gas pressure inside the cuvette was almost at ambient level.

All tubes to and from the cuvettes were of equal lenght to diminish run-time errors in the analyser. The sampling gas was directed through a mass flow meter (FM 3900, Tylan, Eching, Germany) and an infrared CO_2 gas analyser (BINOS 4b, Leybold-Heraeus, Hanau, Germany). The cuvettes were sampled sequentially (1 reference stem cuvette, 8 stem cuvettes, 1 branch reference cuvette and 12 branch cuvettes) by automatically switching (HP-VEE 5.0, Hewlett-Packard Company, Palo Alto, USA) solenoid valves. The CO_2 gas exchange rate per cuvette R_{cuv} was computed according to Eq. 33. ΔCO_2sam was the difference in the CO_2 concentration of the sampled gas of the branch or stem cuvette to the reference gas of the reference cuvette, ΔCO_2ref was the difference in CO_2 concentration of the reference cuvette to the reference gas, $flow$ was the gas flux through the cuvette. The volume of the molar gas constant (22.414 dm³) was corrected by the approximate temperature (20℃) of the gas in the flow meter.

$$R_{cuv} = \frac{flow \cdot \left(\Delta CO_2 sam - \Delta CO_2 ref\right)}{22.414 \cdot \left(\frac{273.16+20}{273.16}\right)} \qquad \text{Eq. 33}$$

2.2.2.4 Branch and stem temperature

The temperature of the bark was continuously assessed with NTC temperature sensors (Figure 18, SEMI 833 ET, Hygrotec Messtechnik GmbH, Titisee-Neustadt, Germany). The voltage signal was linearised to temperature with a 100 kOhm resistor and electronically recorded (logger 34970 A, Hewlett-Packard Company). The temperature sensors were mounted with artificial resin to the lower side of the study branches and into the cambium of the stems. Missing data were replaced via regressions to air temperature (RFT-2, Mela Sensor Technik GmbH, Greiz, Germany) measured by 16 sensors in the sun and shade crowns of spruce and beech, and of a meteorological station in the vicinity of the site (Bayerische Landesanstalt für Landwirtschaft, Agrarmeteorologische Messstation im Schaugarten Weihenstephan, Germany).

2.2.2.5 Scaling of branch respiration rates

The measured respiration rates of the axes were related to bark temperature, and an exponential relationship was fitted (cf. Bosc 2000) as the basis of annual simulations: Respiration (R_{axes}, Eq. 34) was the sum of maintenance (R_M, Eq. 35) and growth respiration (R_G, Eq. 36, cf. Merino et al. 1982, Gent and Enoch 1983). The maintenance respiration was derived during the dormant season between December and March. R_{M10} and R_{G10} were the normalized respiration rates of maintenance and growth respiration at 10℃, Q_{10} was the factor by which the respiration rate increased with a temperature increase of 10 K and R_{G10max} was the maximum rate of growth respiration at 10℃. The annual course of R_{G10} was parameterised through measurements on beech and spruce branches, and was scaled with the function $f_{ATC}(doy)$ (Eq. 37), based on the day of the year doy. The function $f_{ATC}(doy)$ renders values of 0 before day x_1, linearly increases to the maximum of 1 on day x_2 and linearly declines to 0 on day x_3.

$$R_{axes} = R_M + R_G \qquad \text{Eq. 34}$$

$$R_M = R_{M\,10} \cdot Q_{10}^{\frac{t-10}{10}} \qquad \text{Eq. 35}$$

$$R_G = f_{ATC}(doy) \cdot R_{G\,10\,\max} \cdot Q_{10}^{\frac{t-10}{10}} \qquad \text{Eq. 36}$$

$$f_{ATC}(doy) = \left\{ \begin{matrix} \dfrac{doy - x_1}{x_2 - x_1}, & x_1 \geq doy > x_2 \\ \dfrac{x_3 - doy}{x_3 - x_2}, & x_2 \geq doy > x_3 \end{matrix} \right\} \qquad \text{Eq. 37}$$

2.2.2.6 Data processing and statistical evaluation

Statistical evaluation was performed using SPSS (version 11.0, SPSS Inc., Chicago, IL, USA) and Origin (version 6.0, Microcalc Inc., Northhampton, MA, USA), data management was based on Excel (version 9.0, Microsoft Corporation) and Diadem (version 8.1, National Instruments Corporation, Austin, TX, USA).

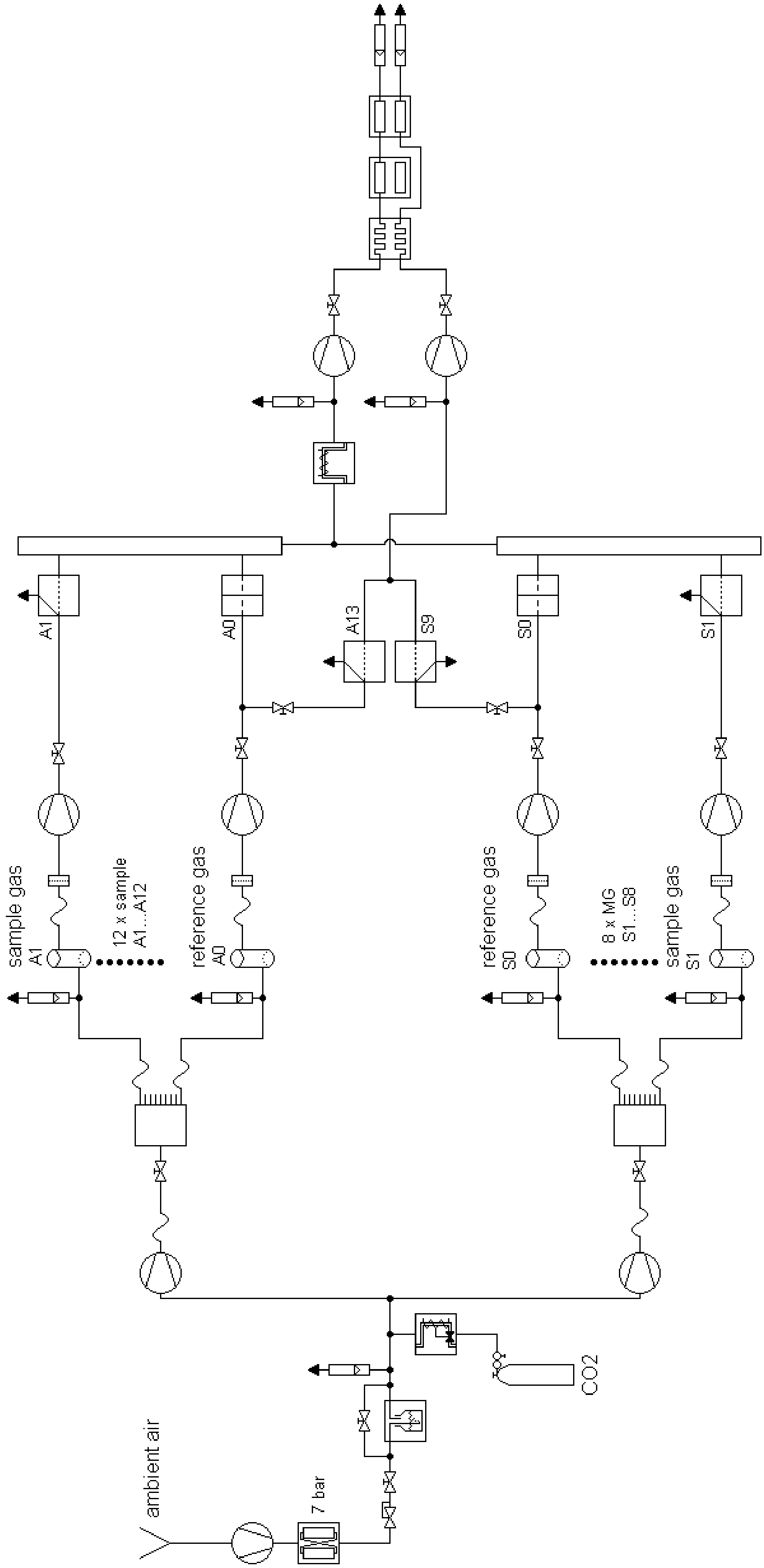


Figure 17: Scheme of branch and stem gas exchange system, which was designed and built by T. Feuerbach. Ambient air is prepared, mixed with CO_2, split into a branch (Ax) and a stem (Bx) circuit, which again have an own circuit for reference and sample gas. Gas from reference and sample cuvettes are analysed with a massflow meter and an infrared CO_2 gas analyser. Further description see text, 2.2.2.3.

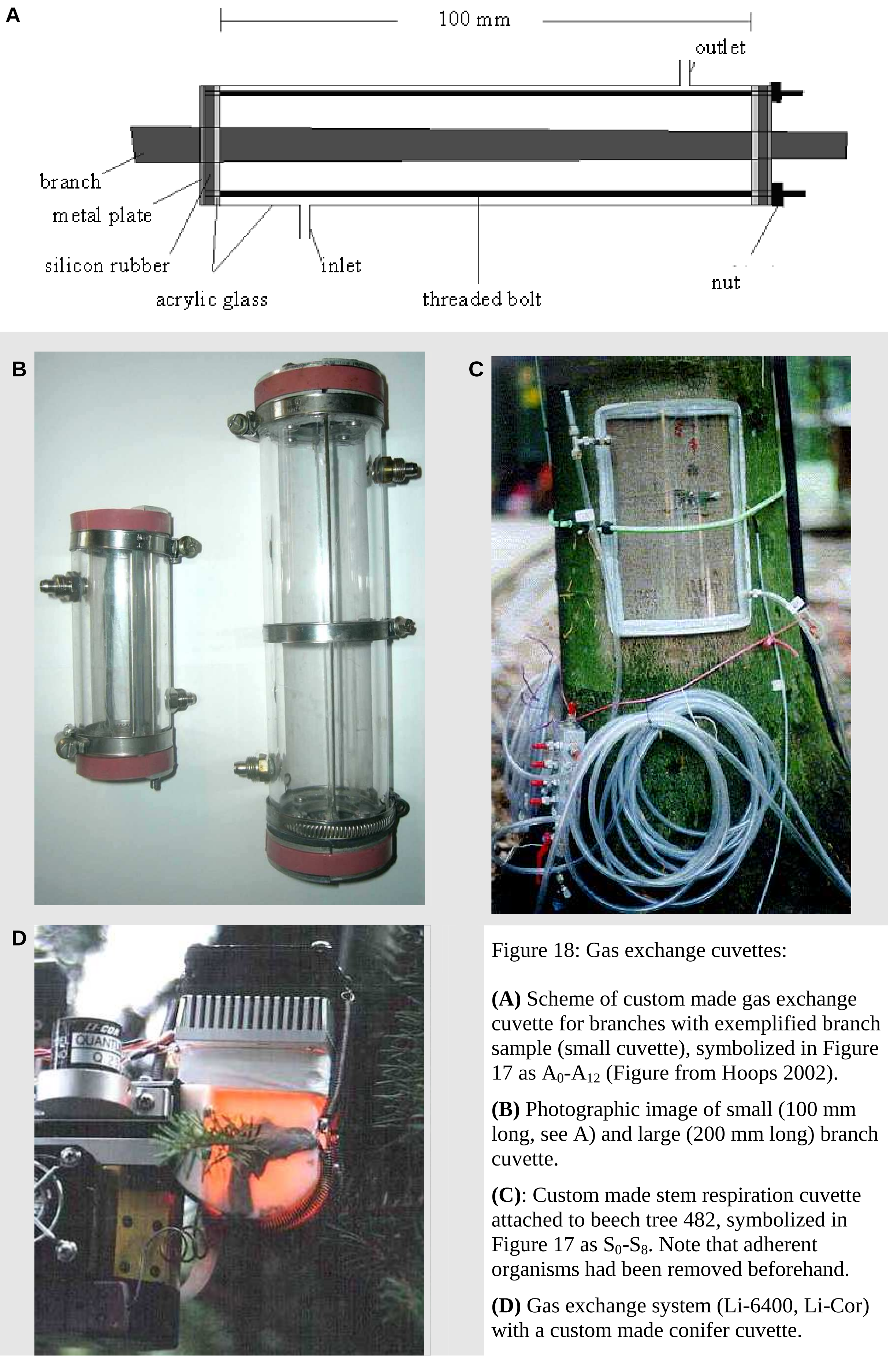


Figure 18: Gas exchange cuvettes:

(A) Scheme of custom made gas exchange cuvette for branches with exemplified branch sample (small cuvette), symbolized in Figure 17 as A_0-A_{12} (Figure from Hoops 2002).

(B) Photographic image of small (100 mm long, see A) and large (200 mm long) branch cuvette.

(C): Custom made stem respiration cuvette attached to beech tree 482, symbolized in Figure 17 as S_0-S_8. Note that adherent organisms had been removed beforehand.

(D) Gas exchange system (Li-6400, Li-Cor) with a custom made conifer cuvette.

2.2.3 Results

2.2.3.1 Space sequestration by woody branch axes

Sun and shade branches of spruce occupied more volume per unit of standing C mass than sun branches of beech (Figure 19, Table 8/ line 1), in contrast to the volume per unit of foliage C mass in spruce (cf. Figure 13A, page 30). Sun and shade branches also tended to occupy more volume than shade branches of beech per unit of standing woody C mass (Figure 19). The difference was significant if the sun branch of beech tree 439 was not included; this branch, although being at the very top of the tree crown, received light typical for shade branches or branches of the intermediate crown zone (see arrows in Figure 19). Tree 439 was therefore rather subordinate in its competitive status, which had changed the allometry of the whole crown (Figure 58, page 112). In beech, foliated volume per woody mass decreased with increasing height in the crown (Figure 19A, $y = 32.5 - 24.8 * rheight$, $R^2=0.22$, $p<0.024$). A similar increase in beech was found for the crown volume per foliage mass (cf. Figure 11, page 28).

The annual C increment of the branch axes scales with light availability (Figure 20B, spruce: $y=408-217 * PPFD_{season}$, $R^2=0.15$, $p<0.053$ beech: $y=83.7-52.9 * PPFD_{season}$, $R^2=0.21$, $p<0.033$), which backs the acceptance of hypothesis 1 in section 2.1.4.1. Spruce occupied more crown volume per annual carbon investment for growth of the axes than beech in the corresponding branch type (Table 8/ line 2). The higher annual space-related investment of beech compared to spruce for growth of the branch axes corresponded to the higher annual space-related biomass investments of beech compared to spruce branches for the foliage of the branches (cf. Figure 13B, page 30). These higher investments allowed higher relative volume increment per season in beech compared to spruce branches (Figure 13C).

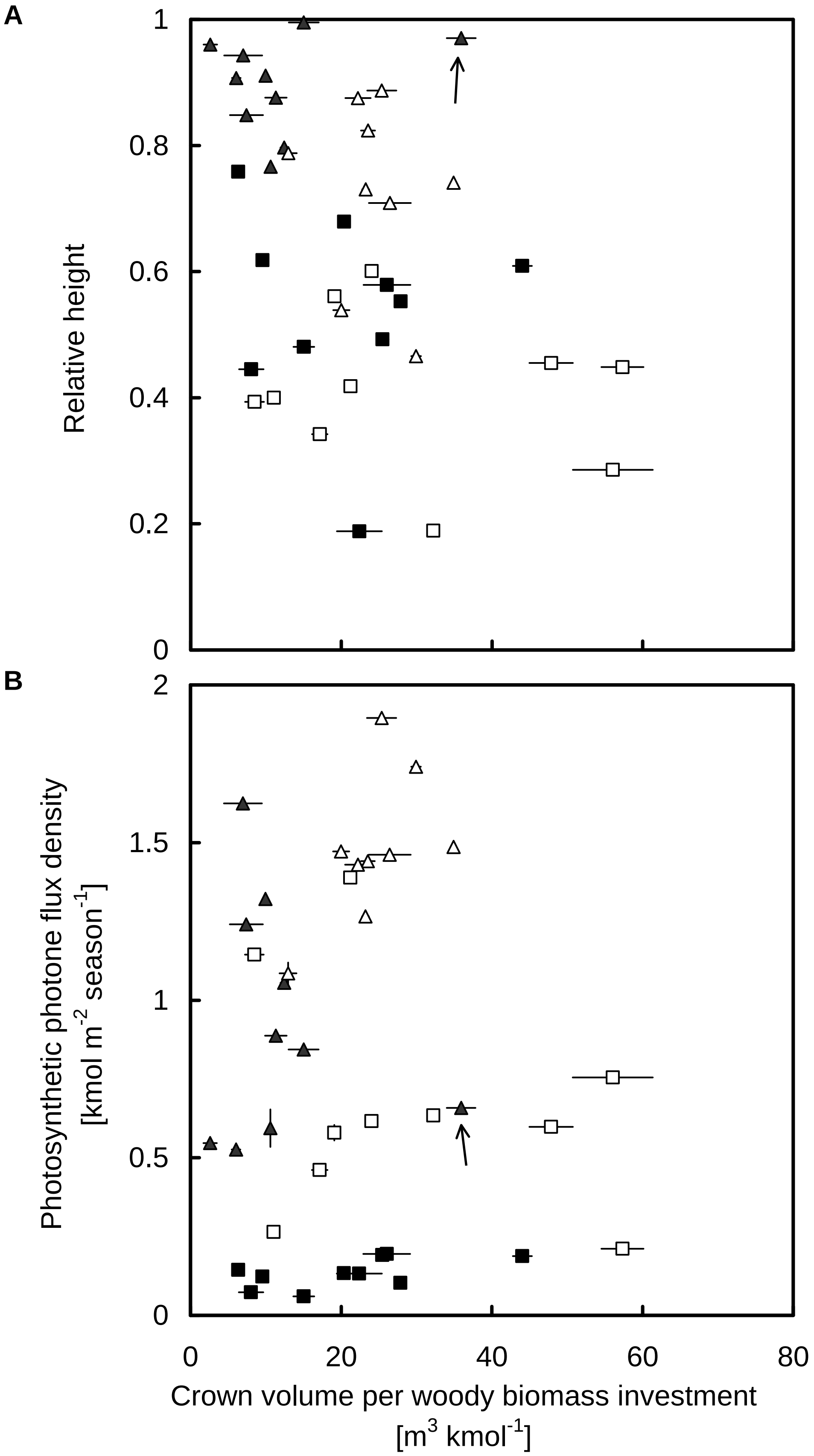


Figure 19: Foliated crown volume per unit of standing C investment of the branch axes:

(A) Along the vertical profile of the foliated crown. Relative height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1).

(B) In relation to the sum of photosynthetic photon flux densities during the concurrent period of their growing seasons (1st June until 30th October), vertical bars denote light range between years.

Depicted are means of the years 1999 to 2000, horizontal bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No bars are present if branch died or broke off. The arrows denote the sun branch of tree 439. See Table 8, line 1 for statistics.

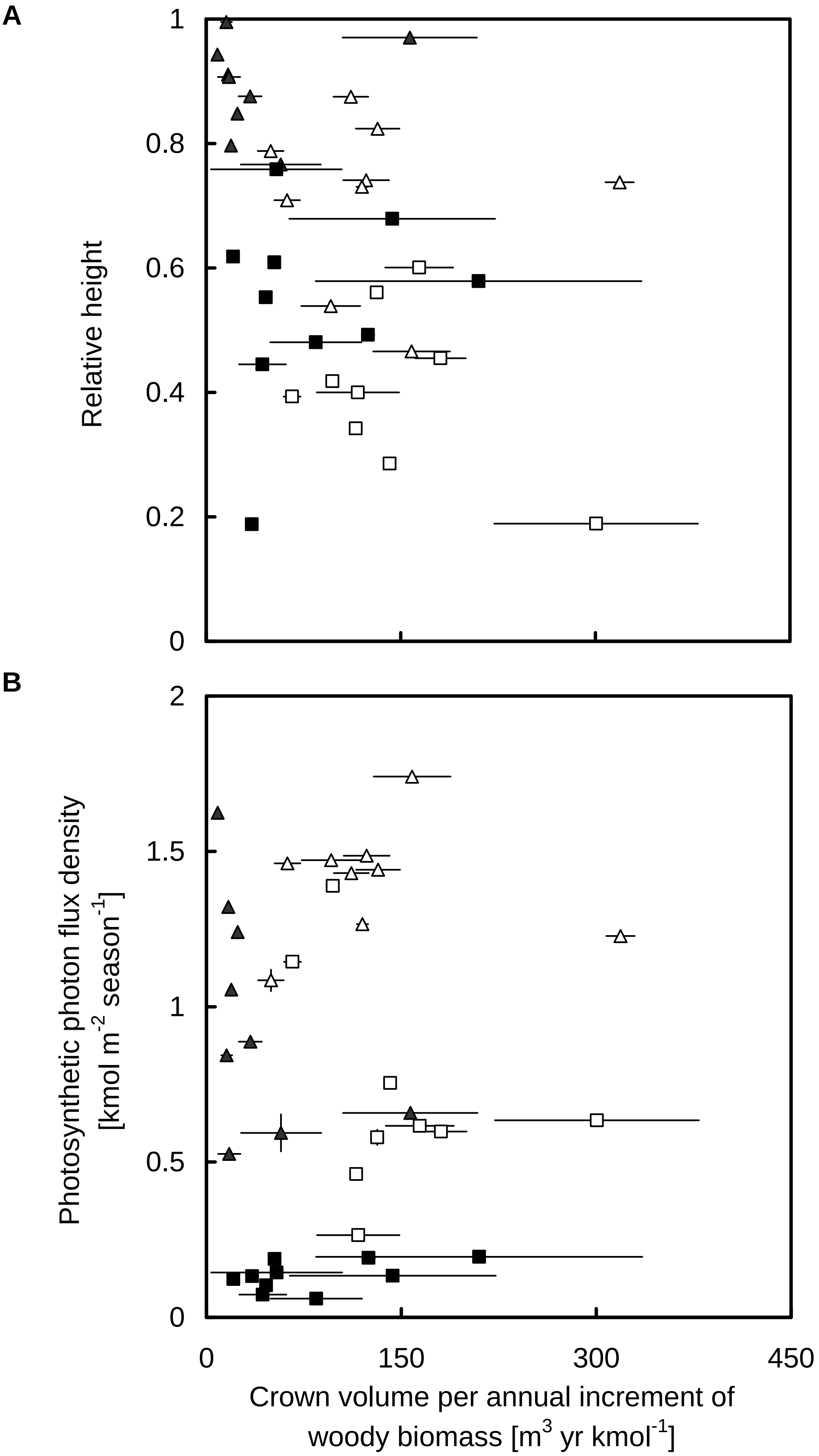


Figure 20: Foliated crown volume per unit of annual C increment of the branch axes:

(A) Along the vertical profile of the foliated crown. Relative height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1).

(B) In relation to the sum of photosynthetic photon flux densities during the concurrent period of their growing seasons (1st June until 30th October), vertical bars denote light range between years.

Depicted are means of the years 1999 to 2000, horizontal bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No data is present if branch died or broke off, within one year of observation. See Table 8, line 2 for statistics.

Table 8: Statistical analysis between (A) species and (B) light environments , “>” denotes higher than , “<“ lower than , and “~” no difference between species or foliage types (Bonferroni, or Tanham if Levene test was significant, p<0.05). ESS = efficiency of space sequestration , ESR = efficiency of “running” respiratory costs for keeping space occupied.

	Foliage parameters	*Figure*	***A*** *Sun*	*Shade*	***B*** *Beech*	*Spruce*
			Spruce Beech	*Spruce Beech*	*Shade Sun*	*Shade Sun*
1	**ESS** (volume vs. standing C investment of axes)	Figure 19	$>^{1}$	$\sim$	$\sim (>^{1,2})$	$\sim$
2	**ESS** (volume vs. annual C investment of axes)	Figure 20	$>^{1}$	$>$	$\sim (>^{1,3})$	$\sim$
3	**ESS** (volume vs. annual C loss of axes)	Figure 34C			$\sim$	
4	**ESS** (volume vs. standing C investment of foliage and axes)	Figure 23	$\sim$	$\sim$	$\sim(>^{1,2})$	$\sim(>^{2})$
5	**ESR** (volume vs. respiration of *axes*)	Figure 21	$<$	$<$	$\sim$	$\sim (>^{2,3})$
6	**ESR** (volume vs. respiration of foliage & axes)	Figure 24	$\sim$	$\sim$	$>^{1} (>^{1,2})$	$\sim$
7	**Carbon balance** of branches vs. volume	Figure 26	$\sim$	$> (<^{4})$	$<$	$<$

[1] sun branch of the subordinate tree 439 is not included in the test, see arrows Figure 19.

[2] significant linear trend with relative height

[3] significant linear trend with light

[4] in terms of the light compensation point of the carbon balnce of the branch, approximated with a logarithmic fit dependent on light, Figure 27

2.2.3.2 Respiratory costs of woody branch axes for crown space

Respiration rates based on surface area and volume

Maintenance respiration of branch axes (R_{M10}), normalized to a temperature of 10℃, of spruce was 2.7 times higher per surface area and 10 time higher per woody volume in sun branches compared to shade branches (Table 9). Maintenance respiration was similar in beech sun and shade branches, but higher in sun branches compared to shade branches in spruce. Growth respiration rates were generally higher in sun branches compared to shade branches, regardless whether based on a surface area or volume.

Table 9: Rates of maintenance (R_{M10}, Eq. 35) and maximum growth respiration (R_{G10max}, Eq. 36) as standardised to branch and stem temperature of 10°C, and a scaling parameter for temperature (Q_{10}, see Eq. 35, Eq. 36), and days of the year limiting the annual course of growth respiration of spruce and beech branches ($x_{1,2,3}$, see Eq. 37).

species	***unit***	***shade branch***		***sun branch***		***all branches***			
		R_{M10}	R_{G10max}	R_{M10}	R_{G10max}	Q_{10}	x_1	x_2	x_3
Picea abies	µmol m^{-2} s^{-1}	0.048	0.12	0.13	0.23	2.45 [1]	95	130	330
Picea abies	µmol m^{-3} s^{-1}	8.0	20	83	164	2.45 [1]	95	130	330
Fagus sylvatica	µmol m^{-2} s^{-1}	0.072	0.48	0.067	0.66	2.61 [2]	100	170	330
Fagus sylvatica	µmol m^{-3} s^{-1}	31	230	41	293	2.61 [2]	100	170	330

[1] Janous et al. 2000, [2] Damesin et al. 2002

In the annual course, growth respiration began and ended at about the same date in both species (see $x_{1,3}$ in Table 9). In both species growth respiration almost linearly increased until a maximum was reached (see x_2 in Table 9), and linearly decreased until the end of the season. However, beech branches took twice as long as compared to spruce branches to reach their maximum rate of growth respiration (R_{G10max}).

Occupied volume and respiratory ‘running cost’ of the axes

Spruce generally occupied more crown volume than beech per unit of respired C of the woody axes inside the foliated crown volume (Figure 21AB, Table 8/ line 4). Although sun and shade branches were not different in spruce and beech (see Figure 21CD for close up of beech), spruce had significant trends with light availability ($y = 425 - 156*PPFD_{season}$, $R^2=0.17$, $p<0.05$) and relative height ($y = 539 - 496*rheight$, $R^2=0.40$, $p<0.01$). The lower space-related respiration costs corresponded with the lower space-related C mass (Figure 19) and the lower annual increment of the axes (Figure 20).

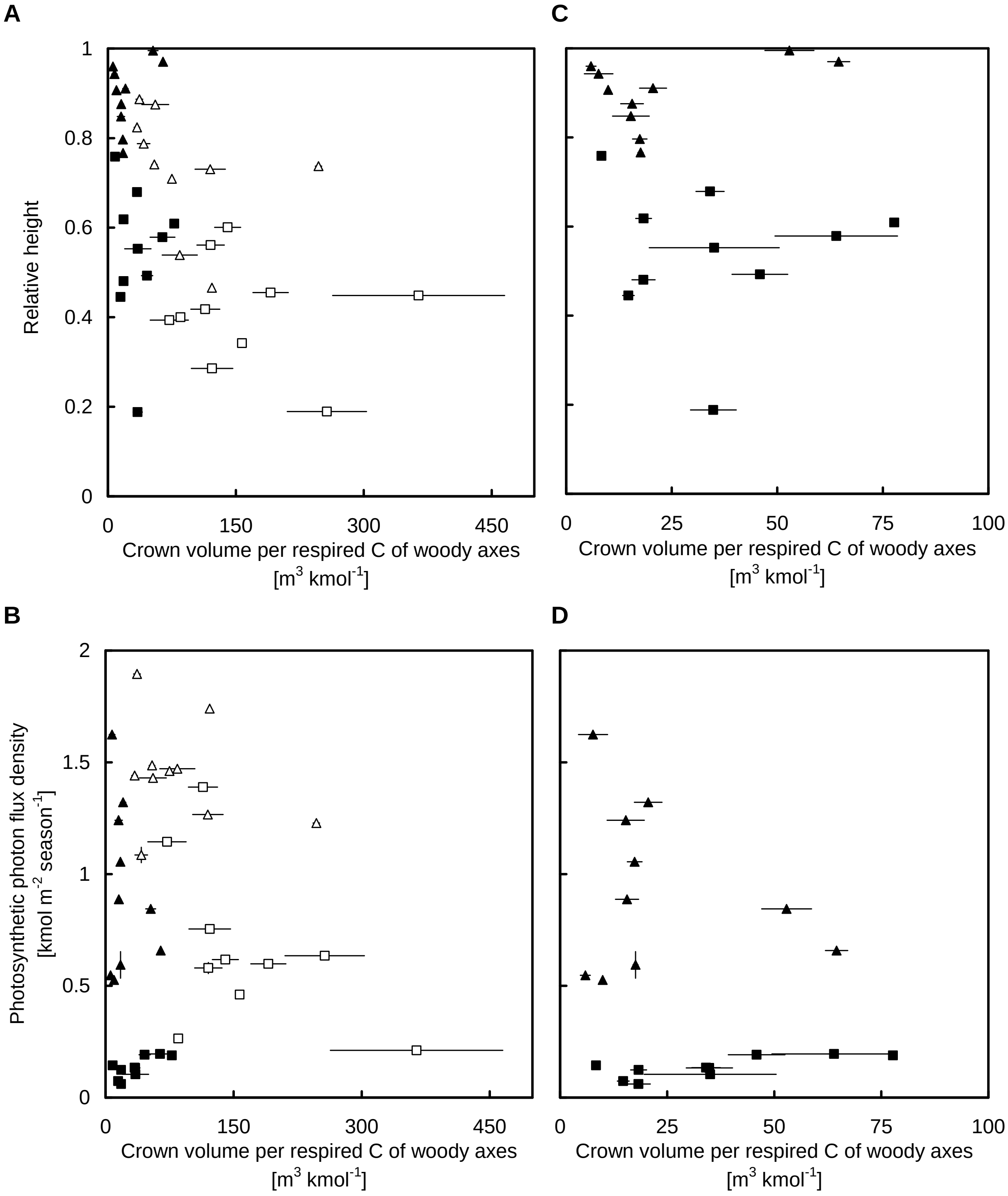


Figure 21: Foliated crown volume per unit of respired C of the woody axes. (A&C) along the vertical profile of the foliated crown and (B&D) in relation to the sum of photosynthetic photon flux densities during the concurrent period of their growing seasons (1st June until 30th October). (C) and (D) are close-ups of beech, same data as (A) and (B) respectively. Relative height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1). Depicted are means of the years 1999 to 2000, bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No bars are present if branch died or broke off.

2.2.4 Discussion

2.2.4.1 Space sequestration by woody branch axes

The efficiency of space sequestration, expressed as crown volume per standing mass of branch axes, was higher in the shade than in the sun branches of beech in this study (Table 8/ line 1, acceptance of hypothesis 4 for beech), which agrees with the findings on crown volume per foliage mass (cf. section 2.1.3.1). In this study spruce shows no difference between sun and shade branches, and no trend with height or light was found (Table 8/ line 1, acceptance of hypothesis 4 for spruce), which agrees with the findings on crown volume per foliage mass in spruce (cf. section 2.1.3.1). The efficiency of space sequestration by the standing axes mass of young *Fagus sylvatica* and *Picea abies* trees was 5.5 m^3 $kmol^{-1}$ and 3.5 m^3 $kmol^{-1}$ in the first year of investigation and 4.3 m^3 $kmol^{-1}$ and 2.8 m^3 $kmol^{-1}$ in the second (Kozovits 2003), which is 2 times and 6 times lower compared to beech and spruce in this study. Apparently short branches are less in need of resources for crown extension, as the construction costs are still low due to the relatively small investment into supportive tissue for the foliage (Falster and Westoby 2003), as well as low gravitational constraints (Sibly and Vincent 1997).

A tree which is unable to growth asymmetrically runs danger to invest resources into shaded or crowded (close proximity of neighbours) branches (Brisson 2001). The efficiency of space sequestration of the woody organs of beech showed a significant linear trend with relative height in the crown but none with light (Table 8/ line 1). This trend corresponds with findings on the branch angle in *Fagus sylvatica,* that linearly decreased from 50° to 10° with the vertical distance from the apex and exponentially with light (Table 3, Figure 64 in Fleck 2001). However, the range in the efficiencies of space sequestration particularly among shade branches was large, and relative height, which was postulated in hypothesis 5 to be a measure of ontogeny, explained only 22 % of the variance in the distribution of the efficiency. The range indicated that the ultimate acclimation of shoots on the branch through self-pruning (e.g. Witowski 1997) and changed growth had not been achieved (Canham 1988, Ballare 1999).

Is the range in the efficiency of space sequestration an effect of ontogeny ? A possible measure of branch age could be expressed in terms of the length between the branch basis on the stem and the beginning of the foliated branch volume. However, neither the height of the branch attachment to the stem nor the length of the leaf-less axis nor the combination of the latter two parameters were related to the efficiency of the space sequestration by the woody mass of the branch. Therefore, ontogeny does not appear to be the cause of the variation. Instead, it appears to be a time-lagged response to shading (rejection of hypothesis 5).

The mean branch angles of *Picea abies* hardly changes (increased from 80° to 90°) along the relative height within the crown of 0.8 to 0 (Mäkinen et al. 2003), but the inclination in branches of competing *Picea abies* increases when affected by crown contact, and branch spread increases with distance from neighbouring trees (Deleuze et al. 1996). Deleuze et al. (1996), therefore, divides competition into two components: (i) direct mechanical contact and (ii) indirect interaction through resource depletion (cf. Figure 1, page 2). The direct interaction of branches was quantified at the stand level and is addressed in section 3.1. In this study, the linear trend of the efficiency of space sequestration with height or light is considered to be a response to the indirect interaction of the trees. A steady increase or decrease of a morphological parameter with height or light in the crown is not a necessity, and other approximations may be necessary (e.g. Schmid et al. 1994). For example, the crown space per individual branch increases with decreasing density in developing stands (Pretzsch 2002). The decrease in density can be reflected in the larger size of the branch as a response to higher light availability. In *Picea abies,* the diameter of branches had their maximum in the upper third of the crown, where they had originated with competitors at greater distance compared to branches in lower canopy strata (Mäkinen et al. 2003).

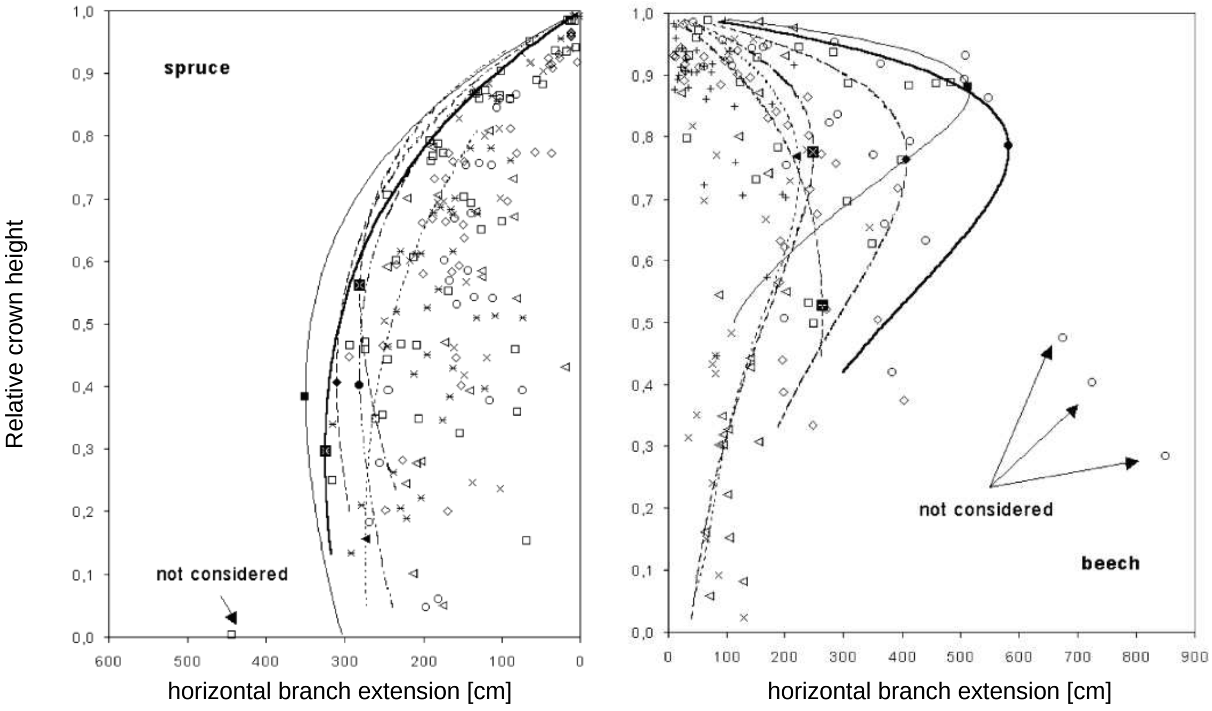


Figure 22: Simulated crown radius (lines) and calculated horizontal branch extension (symbols) at their relative height within the crown of spruce (left) and beech (right). Six open symbols are used for six harvested sample trees of each species. One symbol of each tree is solid to indicate the largest branch extension that is used to fit the crown shape function (from Grote and Reiter 2004).

Elongation of the main branch axes of spruce is maximal at about mid-crown height in the 'Kranzberger Forst' (Figure 22, cooperation with partner project C3, Grote and Reiter 2004). However, the mean branch diameter of *Pinus sylvestris* increased from the top of the crown to a maximum at whorl 14 and remained unchanged down to whorl 20 (Mäkinen and Makela 2003).

The question arises as to whether shaded branches can regain their vigour in ameliorated light regimes, or whether their age (hypothesis 5) impedes such processes. There is evidence that conifers are constrained by age. Total closure of the canopy of *Picea abies* stands after thinning will typically take 10 to 15 years if canopy height is about 20 m, however, complete closure will not be achieved again after thinning in old stands, where height growth has almost ceased (Nielsen 1995). In tall compared to short trees of *Pseudotsuga menziesii, Abies amabilis, Abies grandis* and *Tsuga heterophylla* production of new shoots was low. The negative effects of physiological aging and increased size are more important in determining crown extension than are local light conditions, whereas in short trees, the allocation to shoot elongation in the upper-crown is important for crown expansion and survival (Ishii et al. 2003). Main stem diameter, internodal lengths and diameters at branch nodes were the most consistent and reliable markers of maturation in *Pseudotsuga menziesii* (Ritchie and Keeley 1994). For broadleaved species rather the opposite to conifers in terms of gap closing capacity has been reported. Although approaching maturity, *Fagus sylvatica* was shown to be able to close gaps rapidly in contrast to *Picea abies* (Assmann 1970, Larson 1992, Pretzsch 2003). The limited ability of *Picea abies* to respond to heterogeneous light environment (cf. Figure 12B) is also contrary to expectations of Avalos and Mulkey (1999). The latter authors found a high degree of plasticity of *Stigmaphyllon lindenianum* to heterogeneity in the light environment in terms of space sequestration (allocation to plant modules as a function of opportunity for resource access).

2.2.4.2 Respiration of woody branch axes

Growth respiration of spruce and beech was higher in sun than in shade branches regardless of expression per unit of surface area, wood volume, or crown volume (Table 8/ line 2, acceptance of hypothesis 6). The respiration rates of spruce and beech are well within the range of published data: Shade branch respiration rate of the deciduous conifer *Larix* was 0.5 µmol m^{-2} s^{-1} at 10°C in July (Matyssek and Schulze 1988), which was similar to beech (0.55 µmol m^{-2} s^{-1} at 10°C), but much higher than in spruce (0.17 µmol m^{-2} s^{-1} at 10°C) in this study. Regardless of CO_2 regime, respiration of *Picea abies* branches from the intermediate crown (0.135 µmol m^{-2} s^{-1} at 10°C, Janous et al. 2000) was similar to spruce shade branches in this study. Twigs of young shade (20% sunlight) and sun grown (100% sunlight) *Fagus sylvatica* had the same respiration rate of 0.77 µmol m^{-2} s^{-1} at 10°C (Wittmann et al. 2001), whereas beech sun branches of this study had 33 % higher values than the shade branches. The difference between spruce sun and shade branches was 112 % on an area basis. Although this difference is much higher than in beech, it is similar to findings in *Betula ermanii* and *Fagus crenata*, which differed by about 80% from upper (0.30 µmol m^{-2} s^{-1} at 10℃) towards lower (0.55 µmol m^{-2} s^{-1} at 10℃) branches (recalculated means from July of both species from Gansert et al. (2002) assuming an Q_{10} of 2.5, see Eq. 36). Respiration of the high nutrient treatment compared to the low nutrient treatment was 4 to 6 times higher at the same relative growth rate of the stem in young *Betula pendula* (Matyssek et al. 2002a). The fertilized *Betula* plants had increased 10-fold in size compared to the unfertilized treatment, therefore absolute growth increment of stem biomass was also higher (Maurer and Matyssek 1997). This explains the differences in respiration, as growth is proportional to the respiratory production costs (Poorter and Villar 1997). No significant variation of soil nutrient supply on the study site ‘Kranzberger Forst’ is known for individuals among each species (pers. comm. Dr. Göttlein, partner project B10, Schuhbäck 2004).

Kozovits (2003, partner project B5) reported space-related efficiencies of respiration rates of the woody organs. The rates ranged between 840 and 310 m^3 $kmol^{-1}$ C in young *Picea abies* and between 500 and 340 m^3 $kmol^{-1}$ C in young *Fagus sylvatica* during the first and second year of the chamber study. The efficiencies of young *Picea* and *Fagus* trees had decreased drastically after the first year, but were still 4 times higher than beech. The efficiencies of the young trees might continue to decrease, due to an increase in supportive woody tissue. This means that at first, age promotes similarity of space related respiration rates in young trees and branches of old trees. However, when trees exceed a certain size the increasing proportion of respiration by the stem and non-foliated branch sections will increase in trees, particularly as stems have a higher surface area based rate than branches (Negisi 1974).

Axes of different age classes and, therefore, also of different diameters have varying respiration rates when they are based on surface area or mass. In *Pinus densiflora,* the respiration rate based on branch surface area showed a slight increase with increasing branch diameter, whereas the respiration rates based on dry or fresh mass linearly decreased with increasing diameter on a double logarithmic scale (Negisi 1974). In contrast, young twigs of *Fagus sylvatica* and *Populus tremula* have higher respiration rates than older twig parts. In part, the higher rates may be attributed to morphology, as current year twigs have high gaseous conductance through stomates, that are transformed into lenticells in the next season (Sitte et al. 2002).

On the other hand, light reduces respiration (Marsham 1759, Pfanz and Aschan 2000, Pfanz et al. 2002, Aschan and Pfanz 2003), most strongly in the younger internodes (Aschan et al. 2001, Wittmann et al. 2001). Respiration measurements with a portable gas exchange analyser (Li-Cor, see Figure 18) on thin branch axes in have shown in the sun crown of beech that shoots with a diameter of up to 4 mm (current year shoots) have high dark respiration rates 2-3 µmol m^{-2} s^{-1}, which are reduced by 2-3 µmol m^{-2} s^{-1} in high light (2000 µmol m^{-2} s^{-1}) through refixation (cooperation with Dirk Hoops, Hoops 2002). Previous-year and older shoots up to a diameter of 9 mm had dark respiration rates of 1 µmol m^{-2} s^{-1} and a refixation in high light of about 50 %. The rate measured with the stationary gas exchange system (cf. Figure 17) was 0.73 µmol m^{-2} s^{-1}, which was mid-way between dark respiration and respiration at ‘maximum’ refixation rate. Therefore, the error by not accounting for the influence of age and light when scaling up respiration rates of whole branches in beech was rather small. Branches of *Pinus densiflora* also had no trend in respiration rate (0.3 µmol m^{-2} s^{-1} at 10℃) between 0.5 cm and 2 cm of branch diameter (Negisi 1974), so that the calculated respiration rates of beech appear plausible. This is even more the case in the study branches of spruce. Photosynthesis was assessed on the whole-shoot basis and throughout the annual course (see Figure 18, and methods section 2.1.2.5, cf. Agren et al. 1980). Therefore respiration and refixation of the spruce axes, that were part of foliated shoots, was most accurately included in the calculations of the annual gas exchange of the shoot (model PSN6, section 2.1.2.5).

Recently, uncertainties for respiration measurements with stem and branch cuvettes have been reported. The effect of aqueous transport of CO_2, in the xylem sap from the soil water to the leaves, on gas exchange of leaves (Levy et al. 1999) and the bark (McGuire and Teskey 2002, Teskey and Mcguire 2002) is currently under debate. The concern that CO_2 efflux from the stem was influenced by movement of the xylem water was already expressed by Boysen-Jensen (1933), cited in Negisi (1978b): "... decrease of the rate of CO_2 release from the bark of intact …“ stems “… might be related to transpirational losses, as part of the respiratory CO_2 in the wood dissolved in the transpiration stream and was transported to the leaves ...". The phenomena of daytime decrease in CO_2 efflux was confirmed in *Pinus densiflora* and *Magnolia obovata* trees (Negisi 1972, Negisi 1978a, Negisi 1979). The decrease in efflux was strongest at the stem base, so that refixation through bark photosynthesis can be ruled out (Foote and Schaedle 1976b, Foote and Schaedle 1976a, Foote and Schaedle 1978, Cernusak and Marshall 2000, Aschan et al. 2001). Teskey and Mcguire (2002) conclude the fact that the respired CO_2 in the transpiration current diffuses to the atmosphere at a different location in the tree, from where it was generated, may explain the large variation in reported respiration rates. Heterogeneity of the permeability of the bark layer causes additional variation in CO_2 efflux from the bark. Latter authors conclude that transport of CO_2 in the xylem may lead to overestimated respiration rates in some tissues and underestimated respiration in other tissues. Their reasoning that the gaseous regime of the soil determines the gaseous partial pressures in the stem, might also explain the differences in the decrease of O_2 during the growing season in stems (Eklund 2000) even if the stem was theoretically not respiring at all. Improved assessment of respiration (proposed as a combination of measurements of sapflow, CO_2 and O_2 concentration in the stem/ Teskey and Mcguire (2002), CO_2 efflux from the stem, CO_2 concentration and pH of the soil) incorporated into a reliable flux calculation concept, may in the near future become state of the art to account for potential variation. However, as shown in the beginning of this section, measurements of this study with published data agree well across species, climate and branch size. This shows that with a small number of samples was sufficient to compensate expected variation of CO_2 efflux.

2.3 Synthesis across foliage and axes

2.3.1 Space sequestration in foliage and axes

Sun branches of spruce had tended to have lower space-related investments per unit of standing C mass of foliage and axes compared to beech (Figure 23) and beech shade branches tended to occupy more volume per C mass of foliage and axes than sun branches (Figure 23), which is in analogy to the space-related separate investments of foliage and axes (cf. Figure 13A/ page 30 and Figure 19/ page 50). Spruce compared to beech branches had a higher efficiency of space sequestration based on C mass of foliage and axes in the sun crown, but spruce and beech were similar in the shade crown (Figure 23B). The efficiency of space sequestration based on the C mass of foliage and branches was weakly related to the relative height in both species (Figure 23A, Table 8/ line 4, page 52). In beech, the maximum efficiency of space sequestration based on the C mass of foliage and branches tended to increase with decreasing light availability as indicated with the dotted line in Figure 23B.

In general, spruce did not respond in space sequestration to a decrease in light availability, whereas beech shows such a response reflected by an increase in the efficiency of space sequestration in more shaded branches.

In spruce and beech, responses of the foliage to the environment are rather fast compared to the responsiveness of the whole branch structure. For example, enzymes (Hampp 1994), pigments (Hansen et al. 2002), secondary metabolites (e.g. induction of defence in an individual - through efflux of volatile organic compounds of neighbours attacked by herbivores - even before contact with herbivores, Karban 2001, Tscharntke et al. 2001), photosynthetic pathways (Naidu and De Lucia 1997) are continuously acclimated to the environment of the current season. Leaf structure is mainly determined by light availability (cf. Annex A) during the previous season in plants with determinate growth (SLA during the season/ Naidu and De Lucia 1997, during and prior to season/ Kimura et al. 1998, Uemura et al. 2000). In fact, shoot growth is directed according to ‘anticipated’ environmental conditions even in advance of changes in the imminent environment (Aphalo et al. 1999, Ballare 1999). However, it takes time until previously generated branch axes - on average - reflect the new (usually more shaded) current environment, as each of the internodes did rather individually acclimate to the prevailing environment in the past (Sprugel 1987, but see Sprugel et al. 1991, Henriksson 2001). The slow responses of the structure of branch axes to progressive shading are self-pruning (*Pinus sylvestris*, Witowski 1997), a more horizontal extension of the foliated volume (*Quercus robur* & *Fagus sylvatica,* Fleck 2001), shorter internodal lengths of new branch growth (*Populus tremula* & *Tilia cordata*, Kull and Tulva 2002), or less bifurcation (*Acer saccharum*, Canham 1988). *Fagus sylvatica* and *Fagus grandifolia* also show variation in the branch angle of the main axis (Canham 1988, Fleck 2001). *Picea abies* increases needle longevity in the shade, which is coupled to reduced branching and extension growth (Niinemets and Lukjanova 2003). Shade branches of *Pinus sylvestris* in a closed stand had lower elongation of internodes than sun branches. However, shade branches of trees which had been exposed to canopy gaps, elongation growth of their shade branches was inhibited compared to shade branches beneath a closed canopy within the same stand (Stoll and Schmid 1998).

All above changes in branch growth and morphology are gradual. Although foliar morphological characteristics proceeded in their response to shading (cf. Annex A). The corresponding change in their spatial arrangement, mediated by the branch structure, can be time-lagged and somewhat buffered. The latter was indicated in beech, but not so in spruce. Possibly, the time lag or buffer functions as a mean of preventing over-reactions to exceptional temporal variation at the site, and to warrant an economic growth form with a low fraction of respiratory tissue and growth investments per carbon gain of the plant. Only few species have developed large variation in growth form which appear economic e.g. in *Pinus mugo (*Rothmaler 1995), but less so in e.g. *Pinus cembra* (Ellenberg 1996). On the other hand, delayed self-pruning and, therefore, the preservation of the axes’ architecture once achieved at a given time may be advantageous to exploit future canopy gaps (Connell et al. 1997, see section 5: general discussion) or to sustain a high leaf area index that shades competitors (Hagemeier 2002).

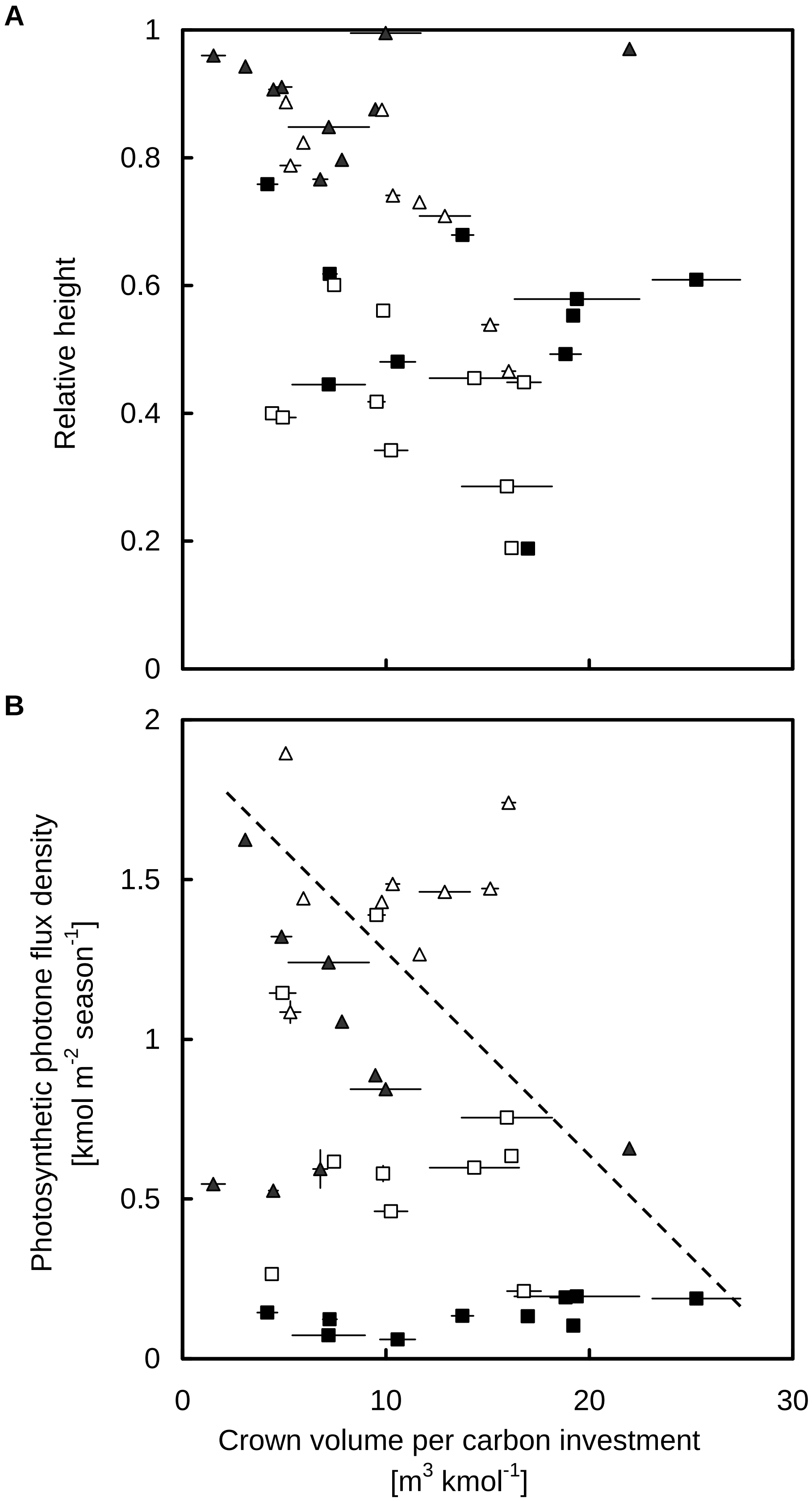


Figure 23: Foliated crown volume per unit of biomass of the foliage *and* woody axes in beech and spruce.

(A) Vertical profile through the foliated crown. Relative height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1).

(B) in relation to the sum of photosynthetic photon flux densities during the concurrent period of their growing seasons (1st June until 30th October).

Depicted are means of the years 1999 and 2000, bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No bars are present if branch died or broke off. The hatched line indicates the upper limit of crown volume per invested biomass of beech as depending on light availability.

2.3.2 Annual respiratory costs of foliage and axes for space occupation

The foliated crown volume per unit of respiration of foliage and axes did not show major differences between beech and spruce, but a tendency for beech shade branches was indicated to occupy a larger crown volume per unit of respired carbon (Figure 24). This tendency in beech shade branches corresponded to the trend in space-related C mass of their axes. If the sun branch of tree 439 was not considered (the branch had very low light availability compared to the relative height in the canopy, see Figure 19, section 2.2.3.1 & 4.1.5), then beech shade branches were significantly more efficient than beech sun branches and showed a linear trend with relative height ($y = 33.1 - 26.0*rheight$, $R^2=0.3$, $p<0.001$, Table 8/ line 6). These results were similar to the results on the space-related respiration of the foliage (see section 2.1.3.3), which was mainly due to the fact that foliar respiration compared to woody respiration was substantially higher (about 5 times in beech) in the foliated volume, and because foliage and axes proportionally correlated with each other in an allometric relationship (Figure 44 page 97). Comparable ratios of foliar to woody respiration were found for *Abies amabilis* (Brooks et al. 1991), where the respiration of the foliage of a shoot was about 10 times higher than the respiration of the woody organs of the shoot, and the mass ratio of foliage to wood of a shoot was of similar magnitude.

In the main growing season, foliage respiration of *Abies amabilis* decreased to ‘zero’ in the lower crown, whereas upper foliage respiration rose in accordance with air temperature (Brooks et al. 1991). The latter authors argue that a very low respiration rate indicates a high carbohydrate deficit of the foliage of shade branches during times of high temperature in summer. If carbohydrate reserves are running low, respiration of the foliage and of woody organs may indeed be decoupled from photosynthesis and reduced in relation to photosynthetic capacity and temperature. This issue was not incorporated into the photosynthesis model nor the calculations of branch respiration (cf. sections 2.1.2.5 & 2.2.2.5) and may lead to overestimation of respiration.

However, the respiration of the foliated shoots of spruce and leaves of beech was measured several times during the growing season and always showed good agreement with electron transport capacity (Figure 25), also for the low capacities of the shade branches. Therefore shade branches were apparently not limited in carbohydrates. This is important as respiration rates of the foliage were coupled to the electron transport capacity, J_{max}, , in the gas exchange model applied in this study (Eq. 22, Table 5, pages 25 & 26). Foliage respiration was about 20 % - 25 % of the gross C gain in a young *Fagus sylvatica* forest, which is lower as compared to this study (Granier et al. 2000), where the fraction was about 30 % of gross C gain.

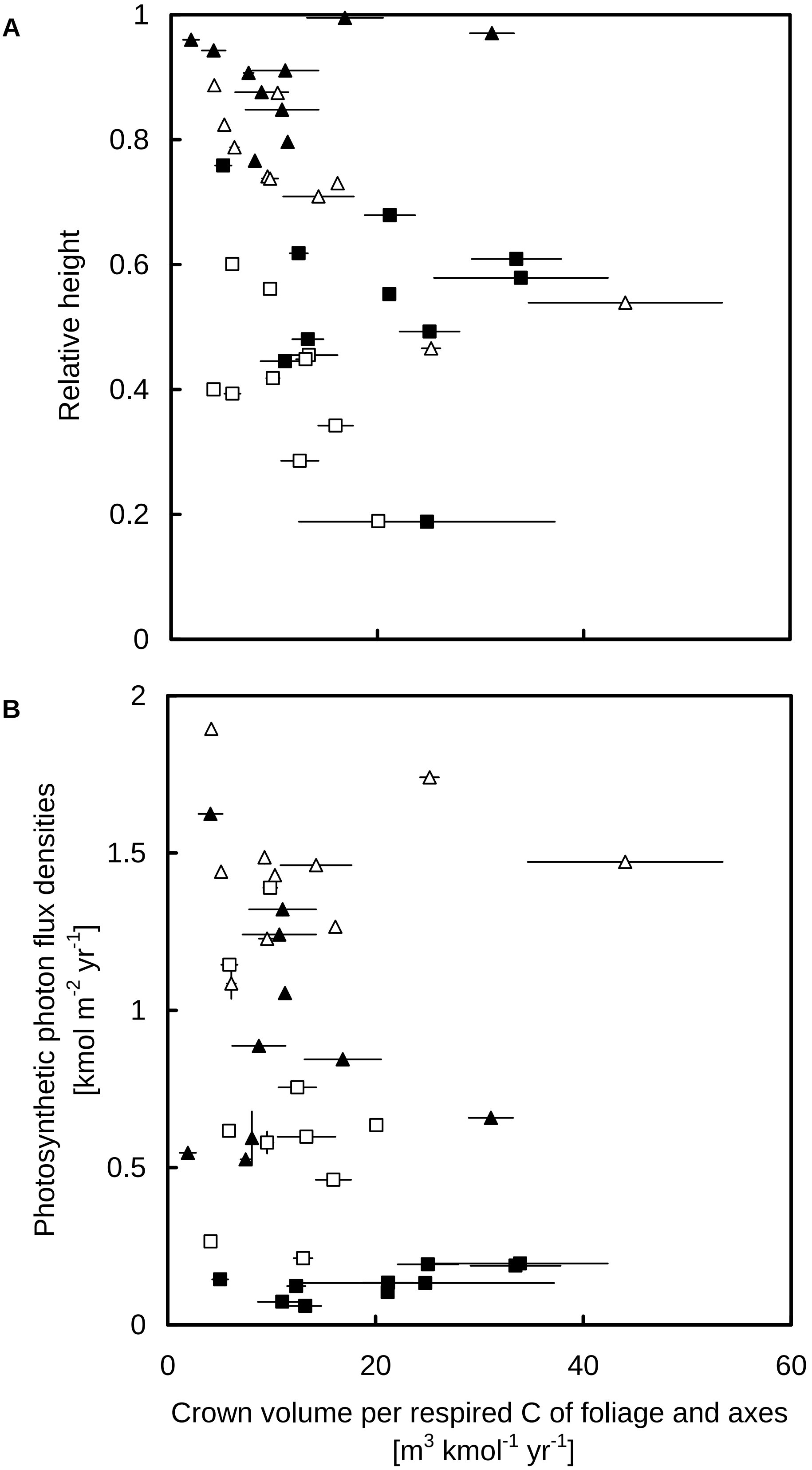


Figure 24: Foliated crown volume per unit of respired C of the foliage *and* woody axes in spruce and beech.

(A) Vertical profile in the foliated crown. Relative height is the vertical distance normalized between the base of the crown (=0) and the tree top (=1).

(B) in relation to the sum of photosynthetic photon flux densities during the concurrent period of their growing seasons (1st June until 30th October).

Depicted are means of the years 1999 to 2000, bars represent the range between the years in beech (closed symbols), spruce (open symbols), sun branches (triangles) and shade branches (squares). No bars are present if branch died or broke off.

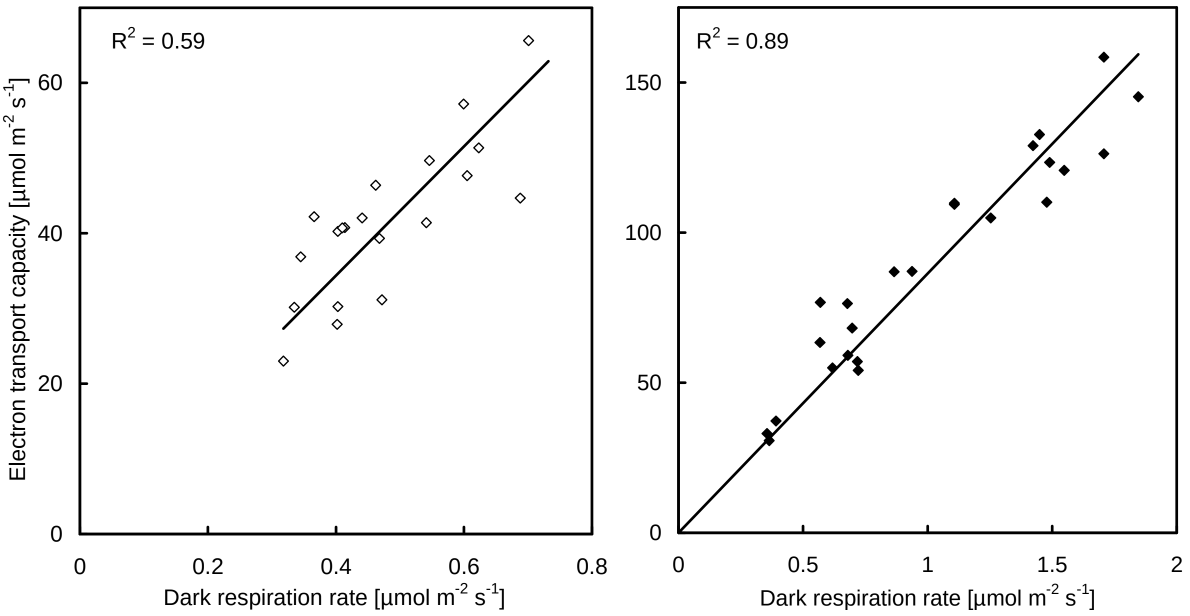


Figure 25: Electron transport capacity and dark respiration rate in shoots of spruce (left, open symbols) and leaves of beech (right, closed symbols). The lines denote linear regression forced through the origin (see Table 5). Rates are based on all-sided needle area in spruce (i.e. projected needle area * 2.6, cf. Annex B) and projected leaf area in beech.

2.3.3 Annual carbon balance of branches

The annual carbon balance (CB) of axes and foliage at the branch level (Eq. 38) was calculated as the gross carbon gain (C_{gain}, Figure 14, page 31) minus investments into respiration (R_{fol}, Figure 15A, page 32) and growth (G_{fol}, Figure 13B, page 30) of the foliage, and minus investments into respiration (R_{axes}, Figure 21, page 54) and growth (G_{axes}, Figure 20, page 51) of the axes. Volatile organic compounds were not accounted for in the balance due to their low contribution in the CB (see Kesselmeier and Staudt 1999).

$$CB = C_{gain} - \left(R_{fol} + G_{fol}\right) - \left(R_{axes} + G_{axes}\right) \qquad \text{Eq. 38}$$

2.3.3.1 Carbon partitioning in study branches

Study branches of spruce and beech generated a similar surplus of assimilated carbon per unit of volume in the annual carbon balance (CB) within the sun crown, 200 mol m^{-3} yr^{-1} (see ‘Export’, Figure 26AC). Foliar respiration was the main sink for carbon in both species (compare grey and black section of pie) and was proportionally higher in the shade branches. The fraction of carbon that was allocated to woody organs for growth and respiration was twice as high in beech compared to spruce. Nevertheless, the proportions between the fractions of growth and respiration of woody organs (bars, Figure 26) was quite stable within a species and between species, except that the respiratory fraction was somewhat higher in beech.

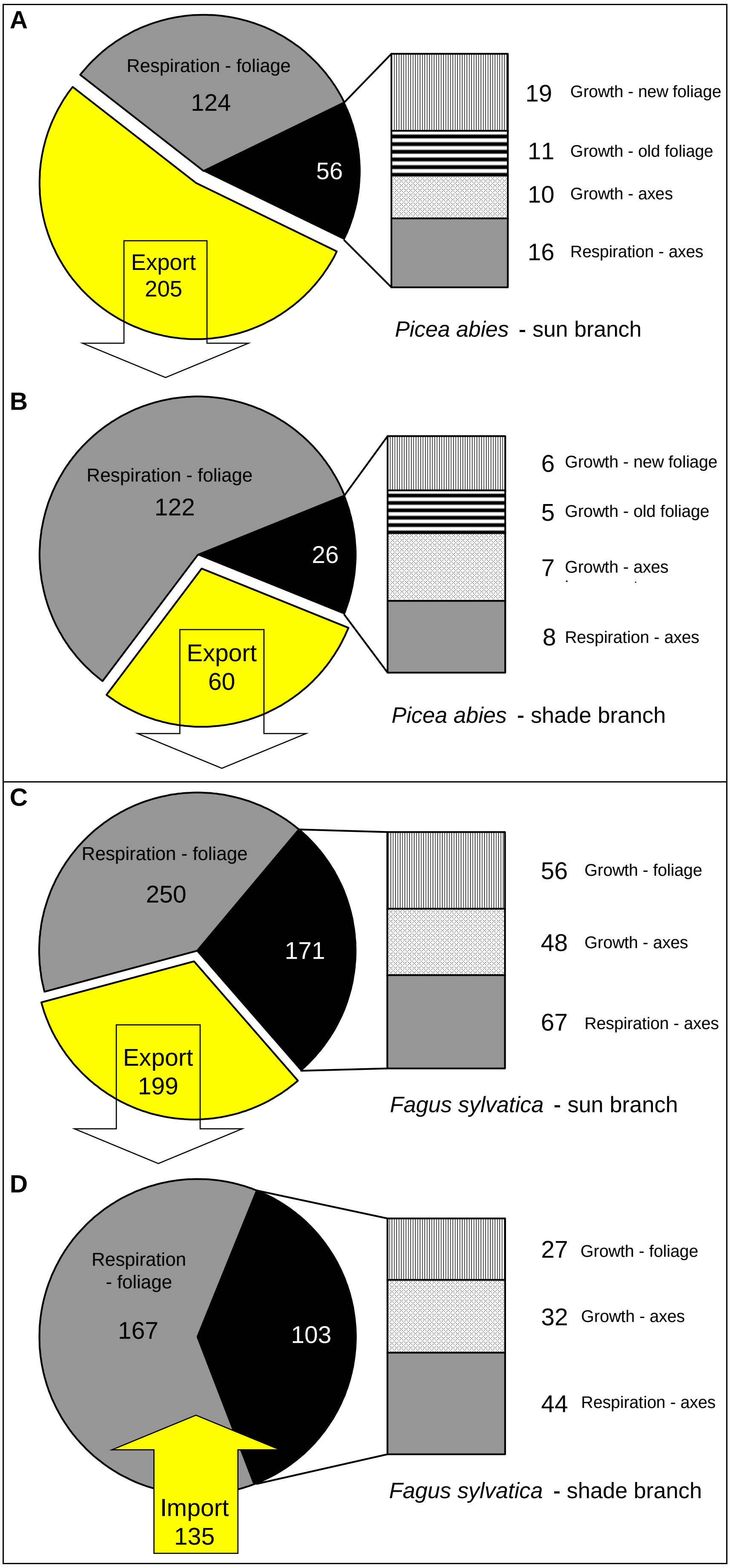


Figure 26: Carbon balance of study branches. Top panel: spruce (A) sun & (B) shade branches, lower panel: beech (C) sun & (D) shade branches, n=10 per crown type and species, shown are mean values of years 1999 and 2000. Bars present detailed C partitioning within the black section of the pie chart. Numbers denote crown space related carbon portions of the gross carbon gain, in mol m^{-3} yr^{--1}. 'Export' denotes the fraction that may be allocated from the foliated part of the branch to the reserves, the non-foliated branch section, the stem and the roots. 'Import' denotes the carbon demand, that was not covered by the carbon gain of the branch.

Although the *CB* of single shade branches of spruce was negative (cf. Figure 27B), spruce shade branches on average still generated a surplus of carbon, which was a quarter to a third of the surplus of sun branches (Figure 26B). However, the carbon gain of beech shade branches from the lower edge of the crown base did not cover the C demand. A very large portion (50 %) of the carbon demand (see 'Import', Figure 26D) had to be drawn from other resources, i.e. from other less light-limited sun and shade branches. The vertical distribution of *CB* of the study branches was related to light availability in section 2.3.3.2, and scaled to the stand level in section 2.3.3.3.

2.3.3.2 Carbon balance of study branches as dependent of light

In both spruce and beech, the *CB* of the *foliage* reflected a linear relationship with light (Figure 27A, spruce: $y=269.8*PPFD_{season}-110.3$, $R^2=0.47$, beech: $y=441.0*PPFD_{season}-116.2$, $R^2=0.70$). A higher number of study branches in beech displayed a negative balance (cf. Figure 16, page 34). The foliage of branches of spruce had a higher light compensation point in the *CB* and had a lower slope between *CB* and increasing light availability (Figure 27A).

When the carbon cost of the growth increment of axes and the respiration of the axes were included in the *CB* (Figure 27B), then spruce and beech were more similar to each other, and the relation with light availability was rather logarithmical than linear (spruce: $y=138.1*\ln(PPFD_{season})+147.4$, $R^2=0.44$, beech: $y=156.5*\ln(PPFD_{season})+218.9$, $R^2=0.33$). The light compensation point of the branch *CB* of spruce was still higher than in beech, but the *CB* of branches of a light availability lower than 0.3 kmol photons m^{-2} yr^{-1} had a similar relationship. However, not all of the investigated shade branches of spruce were in such severely light-limited crown positions as compared to beech (see relative height, e.g. Figure 23).

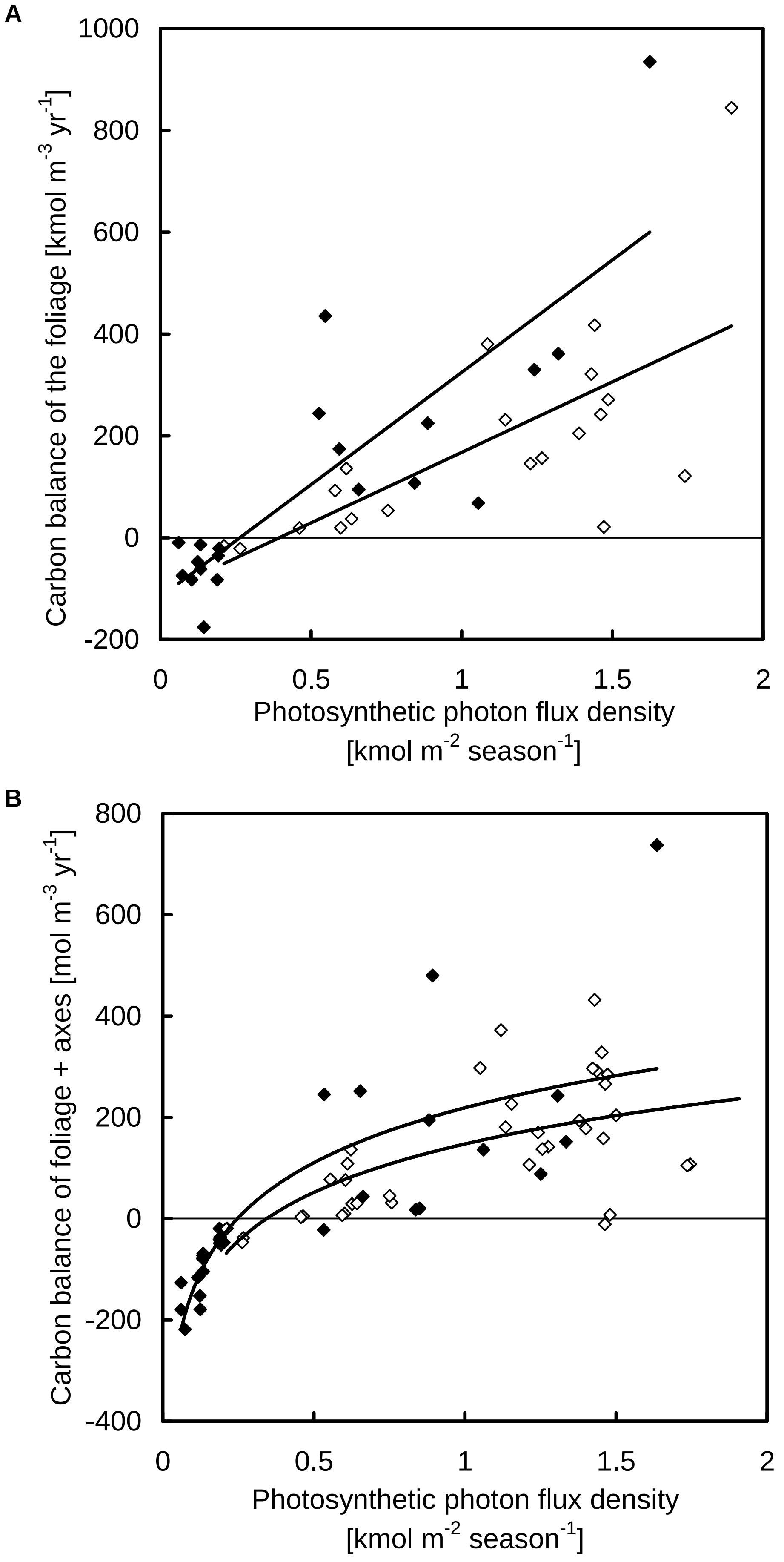


Figure 27: Light availability and carbon balance of the (A) foliage of study branches, and (B) of the foliage *and* the axes within the foliated volume.

Spruce (open symbols) and beech (solid symbols) in years 1999 and 2000. Solid lines denote linear regression, the solid horizontal line represents the transition between positive and negative balance (i.e. level of ‘compensation’ in the carbon balance)..

2.3.3.3 Carbon balance of branches scaled to the stand level

The annual gross carbon gain and the annual carbon balance of branches were scaled to the stand level: The space-related C gain and *CB* were weighted with the fraction of sequestered canopy space within the vertical profile of the stand (Figure 12A, cf. Annex C). C gain and *CB* were expressed as a function of the relative height in the crown (Table 10).

Table 10: Parameters for approximation (SPSS Inc.) of annual carbon gain and annual carbon balance in the vertical profile of the crown (*rheight*, 1=top, 0=crown base), model $y = a * rheight^b + c$.

	species	*a*	*b*	*c*	R^2
Carbon gain	*Picea abies*[1]	473.4	1.133	0	0.38
	Fagus sylvatica[1]	432.1	1.678	0	0.42
Carbon balance power function	*Picea abies*[1]	483.4	2.118	-33.45	0.59
	Fagus sylvatica[1]	431.4	1.960	-195.9	0.33
Carbon balance linear function	*Picea abies*	471.8	1	-131.6	0.53
	Fagus sylvatica	612.9	1	-366.2	0.13

[1] regression shown in Figure 28

The annual (gross) carbon gain per unit of projected ground area of the stand was 160 mol C m^{-2} yr^{-1} for spruce and 105 mol C m^{-2} yr^{-1} for beech (cf. Figure 28). The annual balance per unit of projected ground area in spruce (57 mol C m^{-2} yr^{-1}) was 67 % higher compared to beech (34 mol C m^{-2} yr^{-1}), if the vertical distribution was approximated with a power function (Table 10, cf. Figure 28). If the vertical distribution was approximated linearly (Table 10) then the *CB* of spruce (51 mol C m^{-2} yr^{-1}) was 10 % higher than beech (47 mol C m^{-2} yr^{-1}), but the determination coefficients were lower. The discrepancy between the approaches are explained by the variance in the horizontal layers within the stand. This variance is caused by the heterogeneity of the three dimensional structure of the individual trees of the stand and the inherent heterogeneity in microclimate of light and temperature (cf. Figure 12B, page 29). However, $PPFD_{season}$ alone explained part of the variance (cf. Figure 27B) so that on the other hand space-related branch morphology (section 2.2.3.1 & 2.3.1) caused variation through the amount of biomass per volume and also through the relationship of photosynthetically productive to respiring biomass. The biomass per volume further depended on the size of the branch and on the size of the tree; this issue is covered in section 4.1.4 & 4.1.5. Altogether, the scaling approach returns a result which represents on average the given study trees. Further estimates within specific individual trees or the whole stand require the application of an explicit three dimensional model on the scale of individual tree crowns. The geometric crown model needs an adequate number of layers and sections, as was presented by partner project C3 (model BALANCE, Grote and Pretzsch 2002, Grote and Reiter 2004). The BALANCE model simulates, within crown sections, light climate depending on the biomass distribution in the stand. The biomass distribution is dependent on tree size and crown extension and the biomass of the neighbours (cf. section 4.1.2, Figure 50). The results of this study may validate modelled results, providing that the position of the study branches can be assigned to the corresponding crown section, and providing that the relationship between the foliated volumes of the branches and the foliated volume of the crown section of the model is known (see section 4.1.3).

Negative balances

No substantial negative balances are depicted in beech in the vertical profile of the foliated crown (Figure 28B), although Figure 26 & Figure 27 clearly show that all study branches from the crown base had a negative *CB*. The optical measurements of leaf area density did not measure or resolve leaf area below a relative height of 0.6 in the canopy of beech, which was on average 3.5 m from the tree top (see Annex C). Only few branches prevailed below 3.5 meters and certainly had a small influence on the vertical distribution of leaf area in the stand. However, most shade study branches of beech were chosen below a relative height of 0.6. As a consequence, the negative *CB* of the shade branches had a minor effect on the annual *CB* of the stand level of beech. The measured leaf area index of beech was 5.8 m^2 m^{-2} in this study. The mean leaf area index for beech in the literature review given in Annex C was 6.25 m^2 m^{-2}. If this 0.45 m^2 m^{-2} difference in leaf area index, was attributed to shade branches, then the carbon balance of beech decreases by 3 mol C m^{-2} yr^{-1}, which was 6 % to 9 % of the *CB*. It seems like a small fare for these shade branches with a negative balance. However, an annual deficit of on average 7.5 % corresponds to a deficit of one annual carbon balance every 13 years.

Although less branches with a negative *CB* were found in spruce, a considerable crown region in the vertical profile was affected by these negative *CB*. Moreover the negative *CB* were weighted with a substantial amount of foliage. Compared to beech, the reduction of the *CB* on the stand level through branches with a negative balance was at least twice as high in spruce, as could be expected from the high proportion of biomass in the lower crown of spruce (left section of Figure 28A). The light compensation point of the *CB* of the study branches in spruce coincided with the dieback of foliage towards the crown base, as denoted with the horizontal line in the depicted spruce crown in Figure 28A.

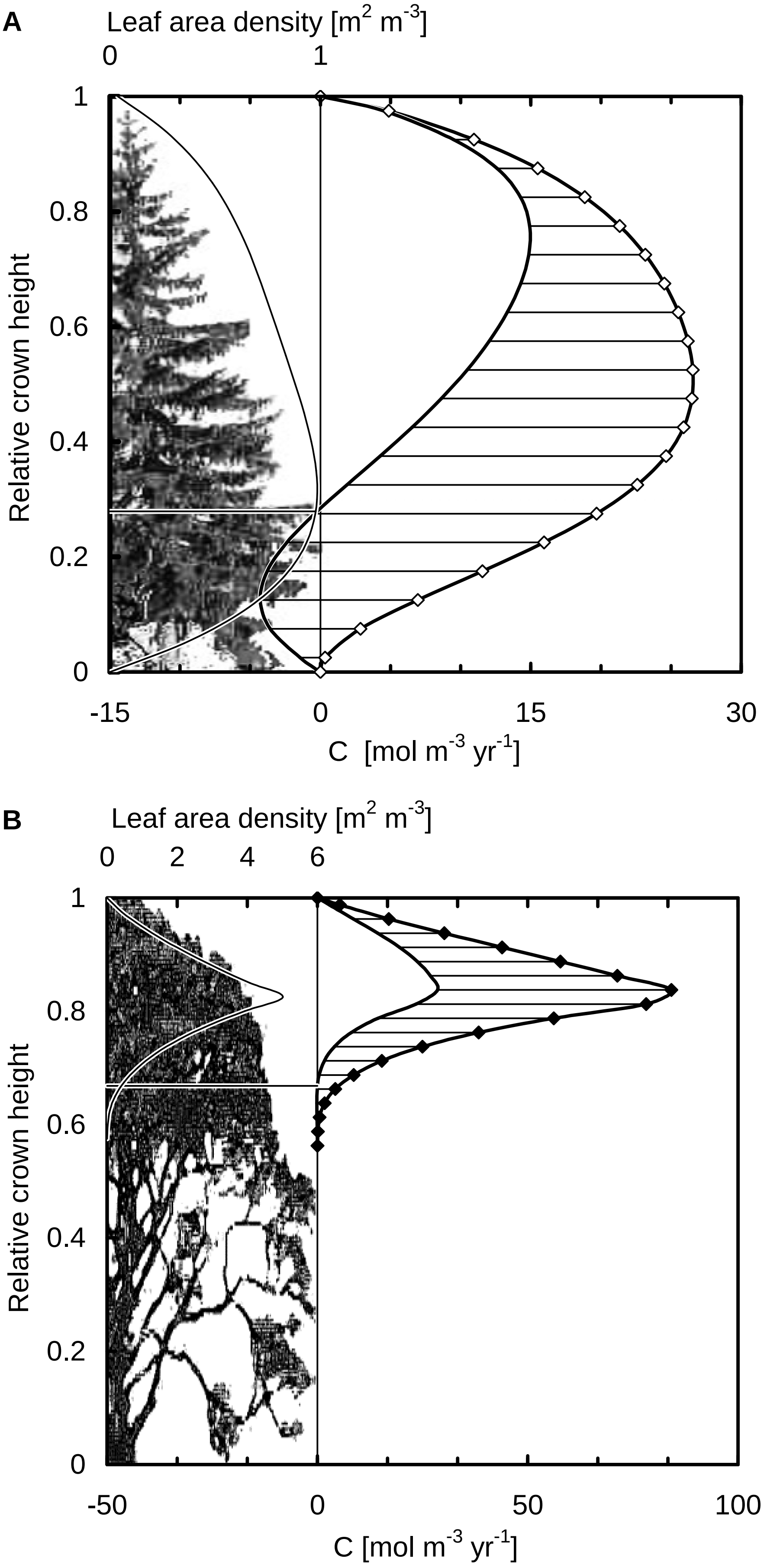


Figure 28: Vertical distribution of the projected leaf area density (thin line in left section of figure), carbon gain (strong line with symbols) and the carbon balance (strong line without symbols). Figure (A) represents spruce, figure (B) beech. Depicted are non-linear regressions (see Table 10) for the study branches in the years 1999 and 2000. The hatched area denotes the amount of carbon invested into growth and respiration of the foliated part of the branches, the white area enclosed by the carbon balance and the zero axis denotes the amount of carbon exported from these branches, and the hatched area left of the zero axis in spruce denotes a negative balance, i.e. the amount of carbon that needs to be imported to the study branches during one year. The horizontal line in the left section of the figures marks the mean height, below which the carbon balance of branches was negative.

2.3.3.4 Discussion

- ***Carbon gain of forest stands***

The gross carbon gain of branches scaled to the stand level is identical to the gross primary production at the stand level (carbon uptake through photosynthesis without respiratory C release, cf. Valentini et al. 1996) as derived from eddy flux analysis and modelling. The results from this study were indeed similar to published data of gross primary production in *Fagus sylvatica* and *Picea abies* in temperate forests (Table 11), with beech at the 'Kranzberger Forst' being within the range and spruce slightly above the range of published data.

Table 11: Annual gross primary production (GPP) of forest ecosystems [mol C m^{-2} ground yr^{-1}]. Temperate sites, marked with bold letters, are similar in climate to the study site 'Kranzberger Forst'.

Ecosystem	***Site***	***Country***	***Species***	***GPP***	***Source***
Boreal evergreen coniferous forest	Norunda	Sweden	*Picea abies* *Pinus sylvestris*	141	Falge et al. (2002)
Boreal evergreen coniferous forest	Flakaliden	Sweden	*Picea abies*	60.3	Falge et al. (2002)
Cold temperate evergreen coniferous forest	**Weidenbrunnen**	**Germany**	***Picea abies***	**110**	Falge et al. (2002)
Temperate evergreen coniferous forest	**Tharandt**	**Germany**	***Picea abies***	**151**	Falge et al. (2002)
Temperate evergreen coniferous forest	**Kranzberger Forst**	**Germany**	***Picea abies***	**160**	This study
Temperate broadleaved deciduous forest	**Hesse**	**France**	***Fagus sylvatica***	**101**	Granier et al. (2000)
Mediterranean broadleaved deciduous forest	**Central**	**Italy**	***Fagus sylvatica***	**101**	Valentini et al. (1996)
Temperate broadleaved deciduous forest	**Hesse**	**France**	***Fagus sylvatica***	**105**	Falge et al. (2002)
Temperate broadleaved deciduous forest	**Kranzberger Forst**	**Germany**	***Fagus sylvatica***	**105**	This study
Temperate broadleaved deciduous forest	**Soroe**	**Denmark**	***Fagus sylvatica***	**106**	Falge et al. (2002)
Temperate broadleaved deciduous forest	**Hesse**	**France**	***Fagus sylvatica***	**125**	Granier et al. (2000)
Temperate broadleaved deciduous forest	**Vielsalm**	**Belgium**	***Fagus sylvatica***	**126**	Falge et al. (2002)
Temperate broadleaved deciduous forest	**Hainich**	**Germany**	***Fagus sylvatica*** ***Fraxinus excelsior***	**130**	Knohl et al. (2003)

- ***Carbon balance of branches &***
  Allocation to respiration of axes and growth of axes and foliage

Carbon allocation to plant organs are most commonly compared by means of fractions of *net* C gain so that the allocation of assimilated carbon to the respiration of the foliage during daytime and night can not be derived. One has to caution as night-time respiration is sometimes given separately and is not included in the seasonal *net* C gain (e.g. Tranquillini 1963, Benecke and Nordmeyer 1982). Using the annual *gross* C gain as the basis of allocation patterns would render studies more comparable, particularly as the largest fraction of C demand - the respiration of the foliage - could be analysed across studies.

The *CB* of beech sun branches in this study was similar to branches of the deciduous conifer *Larix decidua x leptolepis* (Table 12A). The *CB* of beech branches was 10 % lower than in large trees and 20 % lower than in small trees (partner project B5) of *Fagus sylvatica* (Table 12B). The negative balance of the beech shade branches can not be expressed based on fractions of the *net* C gain.

The *CB* of spruce branches in this study were 80 % higher than in small trees of *Picea abies,* but similar to the aboveground *CB* of small trees (~0.1 m height) of *Pinus cembra* (Table 12A). The shoot of *Pinus cembra* is reported to resembled a short upright branch rather than a tree (Tranquillini 1959). The *CB* of the spruce branches of this study was well within the range and close to the mean (69 %) of the *CB* of coniferous trees (Table 12B), with the exception of a *Pinus cembra* tree which was 95 years old and grew at the timberline (Wieser et al. pers. comm.).

Table 12: Carbon balance of branches expressed as fraction of net carbon gain (net carbon gain minus investments for growth of foliage & axes and respiration of axes - divided by the net carbon gain) of (A) individual branches and (B) the whole crown without the stem.

Species	**A** ***Shade branch* [%]**	***Sun branch* [%]**	***Source***	**B** ***Crown* [%]**	***Source***
Picea abies		44[1]	Kozovits 2003	83	Matyssek (1985)
Pinus cembra		73	Tranquillini (1963)	37	Wieser et al. pers. comm.
Pinus pinaster	31		Bosc (2000)		
Pinus sylvestris	14		Witowski (1997)	68	Agren et al. (1980)
Pinus contorta				71	Benecke and Nordmeyer (1982)
Larix decidua* x *leptolepis	26	58	Matyssek and Schulze (1988)	65	Matyssek and Schulze (1988)
Larix decidua				62	Matyssek (1985)
Larix leptolepis				67	Matyssek (1985)
Nothofagus solandri				59	Benecke and Nordmeyer (1982)
Fagus sylvatica		67[1]	Kozovits 2003	61	Lebaube et al. (2000)
Picea abies	**70**[2]	**79**[2]	This study	**63**[3]	This study
Fagus sylvatica		**54**[2]	This study	**43**[3]	This study

[1] small trees, age 2-3 years [2] based on the foliated branch section [3] based on the whole branch

The *CB* of the study branches at ‘Kranzberger Forst’ (Table 12A) should be slightly higher than published data, because only the fraction of the foliated branch was included in this study (i.e. without respiration and growth of the unfoliated branch sections). This is not the case in the literature review given in Table 12A&B, containing *CBs* of the foliated and unfoliated sections of branches. In the following, an estimate of additional investments for the unfoliated branch sections is given for the branches of this study: The growth of the unfoliated branch section is similar to growth of ‘coarse branches’, which was 1.5 % to 2.9 % of the net C gain in a mixed forest stand of *Fagus sylvatica* and *Quercus petraea* (Terborg 1998, Hertel and Leuschner 2002) and 2.6 % in *Larix decidua* x *leptolepis* (Matyssek and Schulze 1988).

Table 13: Allocation to growth of the foliage and to growth and respiration of the axes expressed as fraction of net carbon gain and on a whole-crown basis. Ratios between these carbon investments are given.

Species	**Growth foliage [%]**	**Growth axes [%]**	**Ratio: growth of foliage to axes [-]**	**Respiration axes [%]**	**Ratio: respiration of axes to growth of axes [-]**	**Source**
Acer campestre	14.0	34.0	0.4			Küppers (1985)
Crateagus macrocarpa	10.5	28.5	0.4			Küppers (1985)
Prunus spinosa	10.0	45.0	0.2			Küppers (1985)
Ribes uva-crispa	8.0	46.0	0.2			Küppers (1985)
Fagus sylvatica & Quercus petraea	10.0	4.2	2.4			Terborg (1998), Hertel and Leuschner (2002)
Nothofagus solandri	14.8	12.0	1.2	8.6	0.7	Benecke and Nordmeyer (1982)
Heliocarpus appendiculatus	32.5	42.9	0.8			Timm (1999)
Ochroma lagopus	34.2	40.0	0.9			Timm (1999)
Guarea glabra	38.2	38.8	1.0			Timm (1999)
Billia colombiana	27.4	42.6	0.6			Timm (1999)
Calatola costaricensis	18.2	55.0	0.3			Timm (1999)
Salacia petenensis	7.6	69.3	0.1			Timm (1999)
Larix decidua	16.0	8.3	1.9	4.6	0.6	Matyssek (1985)
Larix decidua x leptolepis	16.0	7.5	2.1	5.5	0.7	Matyssek (1985)
Larix leptolepis	15.0	6.4	2.3	4.8	0.8	Matyssek (1985)
Picea abies	8.0	6.4	1.3	3.1	0.5	Matyssek (1985)
Pinus cembra	6.9	17.9	0.4	35.6	2.0	Wieser et al. pers. comm.
Pinus contorta	8.1	6.7	1.2	8.3	1.2	Benecke and Nordmeyer (1982)
Pinus pinaster	18.6	19.4	1.0	23.9	1.2	Bosc (2000)
Pinus sylvestris	18.3	7.7	2.4			Küppers (1994)

On the crown scale, the ratio of C investments for growth of the foliage to growth of the axes was on average 0.83 for broadleaved species and 1.13 for coniferous species for the examples listed in Table 13. This amounts to about 10 % of the net C gain for branch growth, whereof a fraction of 50 % was allocated to the unfoliated branch sections. The fraction of net C gain for the growth of the unfoliated branch section is twice as high compared to the growth of ‘coarse branches’ (>7 cm diameter), which was 1.5 % to 2.9 % of the net C gain in a mixed forest stand of *Fagus sylvatica* and *Quercus petraea* (Terborg 1998, Hertel and Leuschner 2002) and 2.6 % in *Larix decidua* x *leptolepis* (Matyssek and Schulze 1988). The respiration of branches ranged between factors of 0.5 and 2 of their C demands for branch growth in the examples listed in Table 13, and between 1.0 and 1.6-fold in this study. Together, growth and respiration of the unfoliated branch segments comprise a C investment between 9 % to 14 % (mean 11.5 %) of the annual net C gain per unit of ground area. The subtraction of this C investment from the *CB* at the stand level should support comparability with the data given in Table 12B.

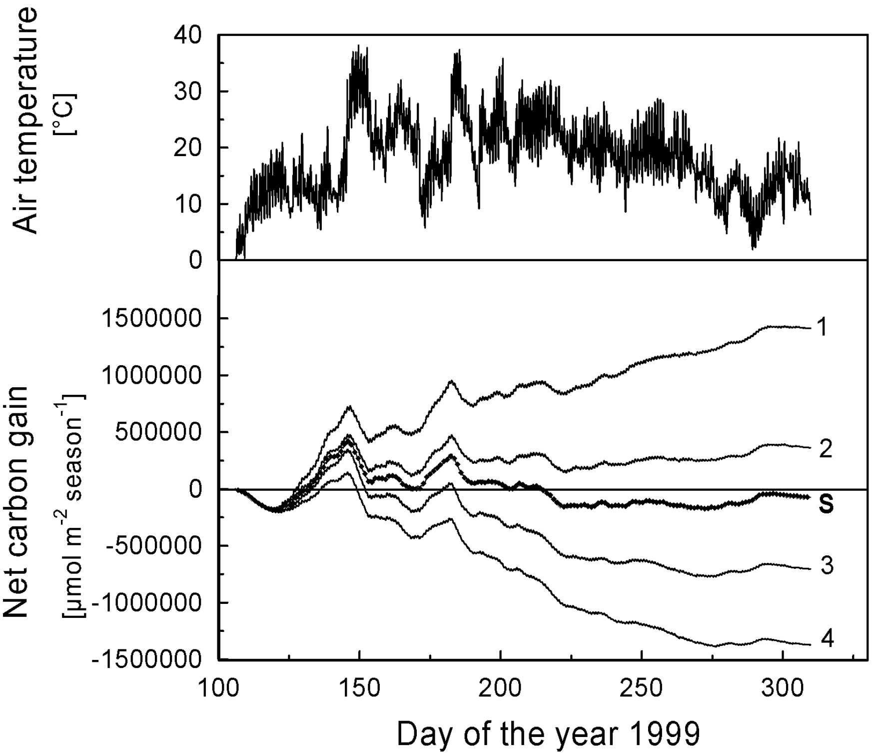


Figure 29: Annual course of air temperature and cumulative net carbon gain of a shade branch of beech (study tree 399) during year 1999. Numbers right of the lines denote the branch sector from distal (1) to proximal (4) position, ‘S’ denotes the mean net carbon gain (average of line 1 to 4) for the total foliage of the branch. Rates were calculated based on microclimate in 10-minute intervals.

Besides being affected by differences between species, individual age and size, the *CB* is substantially influenced by the prevailing climate. Ecosystem respiration has been found to be highly sensitive to changes in temperature on an annual basis (Lindroth et al. 1998), whereas gross primary production appears to be largely temperature-independent for a broad latitudinal range (Valentini et al. 2000). For example, in trees of *Eucalyptus globulus*, the canopy net photosynthesis was reduced from 175 mol C m^{-2} yr^{-1} at optimum sites to 142 mol C m^{-2} yr^{-1} at cold and wet sites and to 58 mol C m^{-2} yr^{-1} at dry and warm sites (Battaglia et al. 1998). Bosc (2000) showed that the climate can greatly affect the annual *CB* of branches in *Pinus pinaster* (one branch even showing a negative balance during a dry year). The mean annual temperature during this study was 1.3°C to 2.3°C above the mean long-term annual temperature (Table 1, page 7). Colder years may therefore increase the *CB* of branches so that a continuous negative balance for strongly shaded branches not necessarily needs to result. An example of the annual course of a beech shade branch is given in Figure 29. At the end of the season, the distal sectors (cf. Figure 9, page 11) of the branch (lines 1&2) have a net carbon uptake, whereas in the proximal sectors (lines 3&4) respiration of the foliage exceeds carbon gain. The mean cumulative carbon gain (S) is slightly negative after day 220, but remains close to zero until the end of the season. The carbon gain strongly depended on temperature and may have been positive, if temperatures had been lower. Hence, keeping branches alive despite the necessity of carbohydrate import into such branches so that they may regain a positive balance in colder years, could be an advantage for the future sequestration and occupation of canopy space and to sustain a high leaf area index.

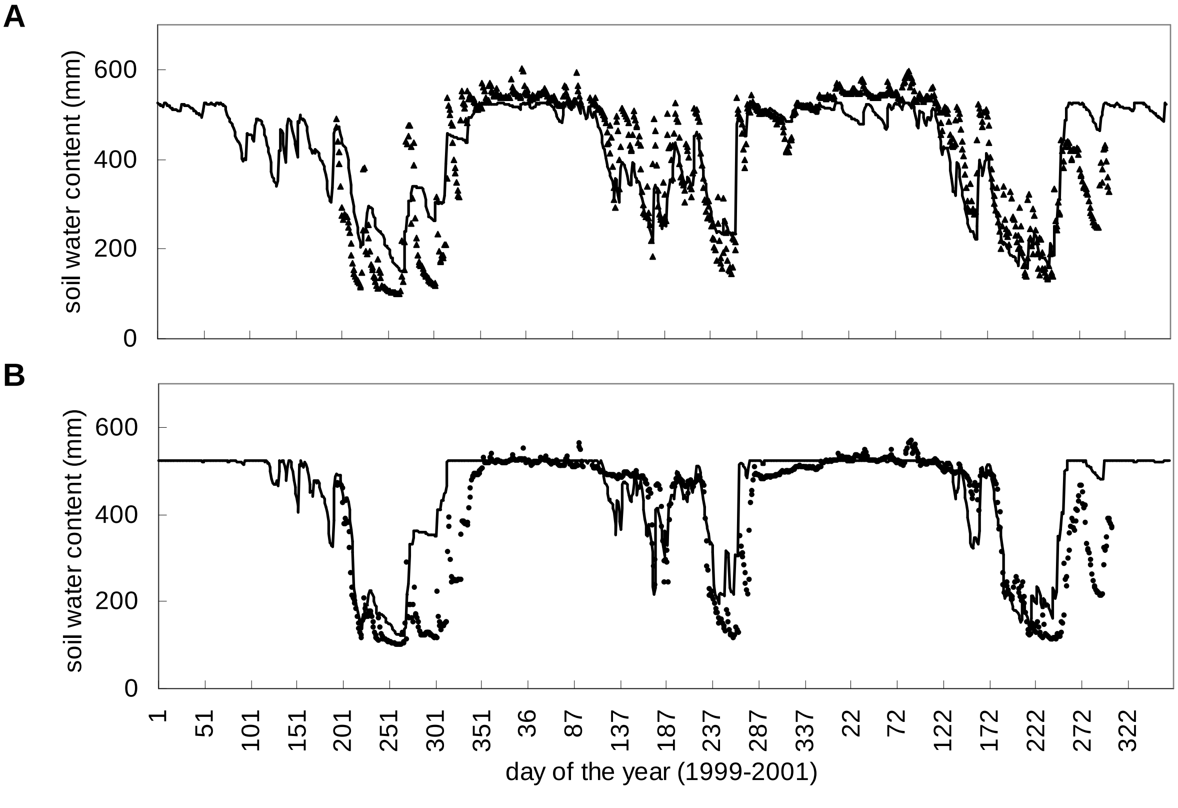


Figure 30: Soil water content beneath crowns of (A) *Picea abies* and (B) *Fagus sylvatica* in the ‘Kranzberger Forst’ of year 1999 through 2001. Symbols denote measured data, the line denotes simulated soil water content by the model BALANCE (adapted from Grote et al. 2003, partner project C3).

The gas exchange model that was applied for the foliage in this study does not incorporate effects of water limitation. Dry years as in 1976 and 2003 (Pretzsch et al. 1998, Schmidt 2004) have a high potential for ‘negative C balances’, as the reduced stomatal conductance (Matyssek et al. 1991, Lu et al. 1995) and photoinhibition (Werner et al. 2001b, Werner et al. 2001a) will inhibit CO_2 uptake into the intercellular air space, which makes CO_2 a limited resource to photosynthesis. However, the water status at the study site was not limiting for spruce or beech during 1999 throughout 2001 (Figure 30).

• *Negative carbon balances of branches and branch autonomy*

In section 2.1.4.4, page 37ff, the carbon balance was discussed on the level of the foliage. It was found that all shade branches of beech, but only two shade branches of spruce had a negative *CB*. It was concluded that this was a difference between these species. The completion of the *CB* by including the C investments for axes and scaling of the *CB* in the vertical profile of the crown showed that also a considerable portion of branches with a negative *CB* were prevalent in the lower quarter of the spruce crown.

The negative *CB* of shade branches in beech and spruce contradicts postulations that branches are carbon autonomous (Sprugel 1987), and that the maintenance of a positive *CB* of branches is a general principle in trees (Matyssek and Schulze 1988). Bosc (2000) reports that the *CB* of the oldest branches of *Pinus pinaster* was more or less zero, but was never strongly negative. The latter author agrees with Witowski (1997), who investigated the lowermost shade branches of *Pinus sylvestris*, in that branches die once their costs to produce and develop their structure are not covered by their own carbohydrate production or their reserves. Study branches of Witowski (1997) had died between the end of July and end of August, soon after their current *CB* had become negative. However, the latter author did not analyse the *CB* of the previous year(s) in his study branches, which might already have been negative without the branches having died.

At the stand level, this study is consistent with other studies regarding C gain (cf. Table 11). A study on a mixed *Fagus sylvatica* and *Quercus petraea* stand (Terborg 1998) has reported *net* C gain per unit of ground area (122 mol C m^{-2} yr^{-1}, *Fagus sylvatica*) that had been scaled from leaf gas exchange to the crown and stand level. No negative balances were reported in the study by Terborg (1998). However, results at the stand level of that study exceed published data of *gross* C gain of *Fagus sylvatica* (cf. Table 11).

Approximate light limit for negative balances and affected species

In Figure 27 (page 68), the light compensation point of the *CB* is indicated for both species. The light compensation points - of 12 % and 16 % relative to the study branch with the maximum light availability - correspond to a relative light level of about 8 % - 12 % compared to above the canopy. Such a light level apparently is a rather common threshold, measured as the light level on the forest floor, for the persistence of foliage in light demanding trees, e.g. *Pinus laricio* 9 %, *Olea europea* 10 %, *Pinus sylvestris* 10 %, *Betula pendula* 11%, *Betula verrocusa* 11 %, *Populus tremula* 11 %, *Quercus penduculata* 11 %, *Sorbus aucuparia* 12 %, *Fraxinus excelsior* 13 % (Büsgen and Münch 1929, Lerch 1991, Larcher 2001, Sitte et al. 2002). These listed tree species can be expected to perform similarly to beech and spruce on a branch basis, due to the great similarity in *CB* and allocation across a wide range of species (Table 12 & Table 13). On average, it is unlikely that these trees display negative *CBs* at the branch level. *Thus, at least most of their branches are indeed carbon autonomous* (sensu Sprugel 1987). Tests of branch autonomy should therefore be designed at relative light availabilities below this threshold of ~10 % compared to above the stand, otherwise the potential of a tree to sustain branches with a negative CB may not be revealed, e.g. branches of young *Juglas regia* trees were shaded to 33 % of incident *PPFD* (Lacointe et al. 2004). Branch autonomy remained unviolated during the main growing season after leaf and shoot development.

However, many trees form stands with lower light availability than 10 % in the lowermost crown layer, e.g. *Quercus robur* 4 %, *Picea abies* 3.6 %, *Acer platanoides* 1.8 %, *Fagus sylvatica* 1.6 %, *Buxus sempervirens* 0.9 % (Lerch 1991). If branches are sustained in a very light-limited environment, there must be an advantage or benefit, from an economic point of view, for the 'permanent' occupation of space, e.g. the mentioned storage of nutrients, a decoy for insects, shading of neighbouring competitors, or a sit-and-wait strategy for incidental canopy gaps or other, which favour these shade-tolerant tree species to be dominant in late successional stages of stand development (Bazzaz 1979, Bazzaz and Pickett 1980, Ellenberg 1996). Possibly the occupation of space with unproductive branches lasts long before an actual C gain can be expected or a loss of C or nutrients prevented.

Why were negative *CBs* not as common in shade branches of *Picea abies*? Potential conflicts with measurements and model assumptions.

Besides the high heterogeneity in the light climate of lower branches of spruce due to the stand structure, there were more ways for the C gain to become low:

Potential influence of leaf and shoot inclination

Particularly the long and old lateral twigs on spruce branches show a hanging habitus (inclination ~0°) on a branch. Photosynthesis was measured with a leaf inclination orthogonal to the light source (inclination ~90°, Figure 18). This means that photosynthesis is overestimated (Figure 31) particularly in the shade crown, where most lateral twigs have inclinations close to 0°. Lower rates of photosynthesis decrease the *CB*. The inclination of the foliage of beech shade branches is about close to 90°. It can be expected that spruce photosynthesis is overestimated in the shade crown compared to beech.

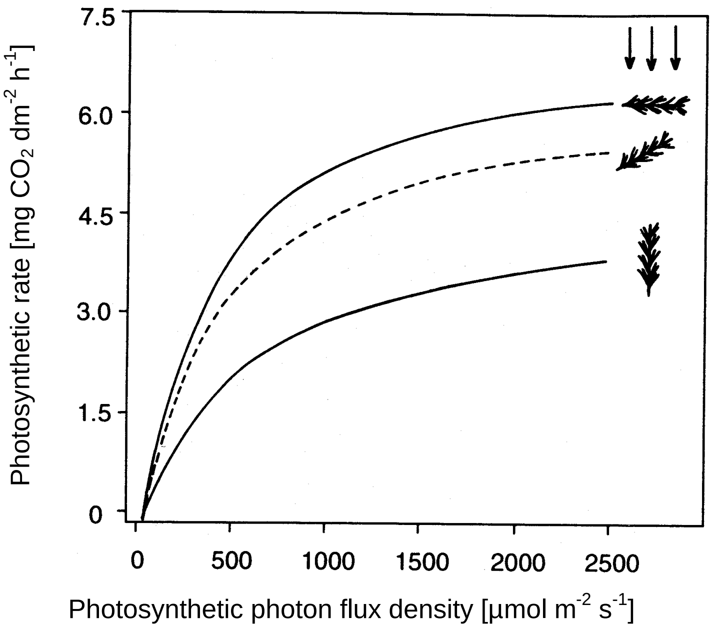


Figure 31: Photosynthetic rate of *Pinus sylvestris* depends on shoot inclination (0°, 45°, 90°) to the radiation beam (From Stenberg et al. 1995).

Influence of cold temperature during winter

Picea abies continues to assimilate in the cold season, as long as air temperature is not too low (e.g. Parker 1953). Under cold stress during winter the Q-cycle (Crofts 2004) is not able to maintain a H^+ /e ratio of 3 for ATP synthesis (ratio is suggested to be flexible, Cornic et al. 2000), as was indicated in measurements of maximum photosynthesis (at ambient CO_2) in October for *Picea abies* (Matyssek 1986). Minimum temperatures below -3℃ determined the *CB* of the next day. A rapid temperature increase at the end of February showed that spruce needles had a positive *CB* after 3 days and had largely recovered compared to rates during the main growing season after 9 days of warm temperatures (Matyssek 1984, Figure 33/ Matyssek 1985, Pinus sylvestris/ Strand and Öquist 1985). Pisek and Kemnitzer (1968) showed for trees of *Abies alba* that preceding frost between -2℃ to -18℃ reduced photosynthesis most in October, less in December and least in March. They also reported an increased respiration dependent on the severity of preceding frost during March, which was thought to be one of the reasons for the slow recovery of net photosynthesis. Thus, it can be expected that in this study the photosynthesis of spruce is overestimated in the shade crown during winter due to a time-lag of regeneration and/or induction of the photosynthetic system (October until March), and that in late winter respiration may even be underestimated.

The presented reasons for an overestimation of C gain in spruce are in agreement with the findings that the gross primary production of spruce at the stand level was slightly above the range of published data (cf. first paragraph of this section). In general, it is likely that shade branches of spruce have a slightly lower C gain, therefore a lower *CB*, and may be more similar compared to beech in their *CB* than shown in Figure 26 & Figure 27.

3 Disturbance of space-related investments and gains

3.1 'Direct interaction' of tree crowns and self-pruning

3.1.1 Introduction

Adjacent crowns of adult trees hardly touch or grow into each other (Figure 32 and Figure 33). Two kinds of observations exist, one relating this phenomenon to directed growth, the other to mechanical damage from antagonistic tree movement during wind. The abiotic environment, e.g. light quality, has proven to direct growth in herbaceous and woody plants (Gautier et al. 1997, Gilbert et al. 2001), and also biotic chemicals, such as ethylene (Pierik et al. 2003), have shown to direct growth of neighbours. However, mechanic injury of spruce branches resulted from contact with neighbouring spruce trees (Schulze et al. 1977). Kramer et al. (1988) reported that amongst spruce, pine and beech trees growing at the forest edge, beech crowns suffered most from wind and had the highest decrease in average stand height, whereas spruce had the lowest.

3.1.2 Methods

Branch loss was estimated on the experimental plot by means of ten square nets of 1.5 m and 2 m length positioned on the forest floor. Four nets were placed beneath spruce and six beneath beech, overall covering 33 m². Dry mass (Sartorious Type 1413, Göttingen, Germany) was determined after oven-drying the branches at 60℃ to constant weight. Measurements started on 16 Dec 1999 and sampling dates were 12 Jan 2000, 11 Jul 2000 and 15 Dec 2000. Diameter classes of branches smaller than 0.5 cm and between 0.5 and 1.5 cm were regarded separately for spruce and beech. After storms in December 1999 and July 2000 losses of life biomass were also documented, so that the costs related to competitive interference between tree crowns could be estimated for the stand for those storms. Biomass loss of study branches (Figure 38) was determined through assessments as described in section 2.2.3.2.

3.1.3 Results

Beech had about 3 times higher losses of branch biomass than spruce at the stand level (Figure 34A). Most of the lost woody biomass were axes with diameters less than 15 mm (Figure 34B). This was not only due to self pruning. Crown abrasion, when sequestrated crown volumes collided during wind, caused a considerable amount of branch loss and injury. Obvious signs of branch fractures and foliage loss (Figure 35/ boxes and circles) along the edge of neighbouring crown regions. These are symptoms of *intense competitive interference between tree crowns* (Leuschner 1999, Figure 1, page 2) and occur among individuals of the same species (Figure 35/ upper left & right, lower left) and between individuals of different species (Figure 35/ lower right, Figure 36, Figure 37).

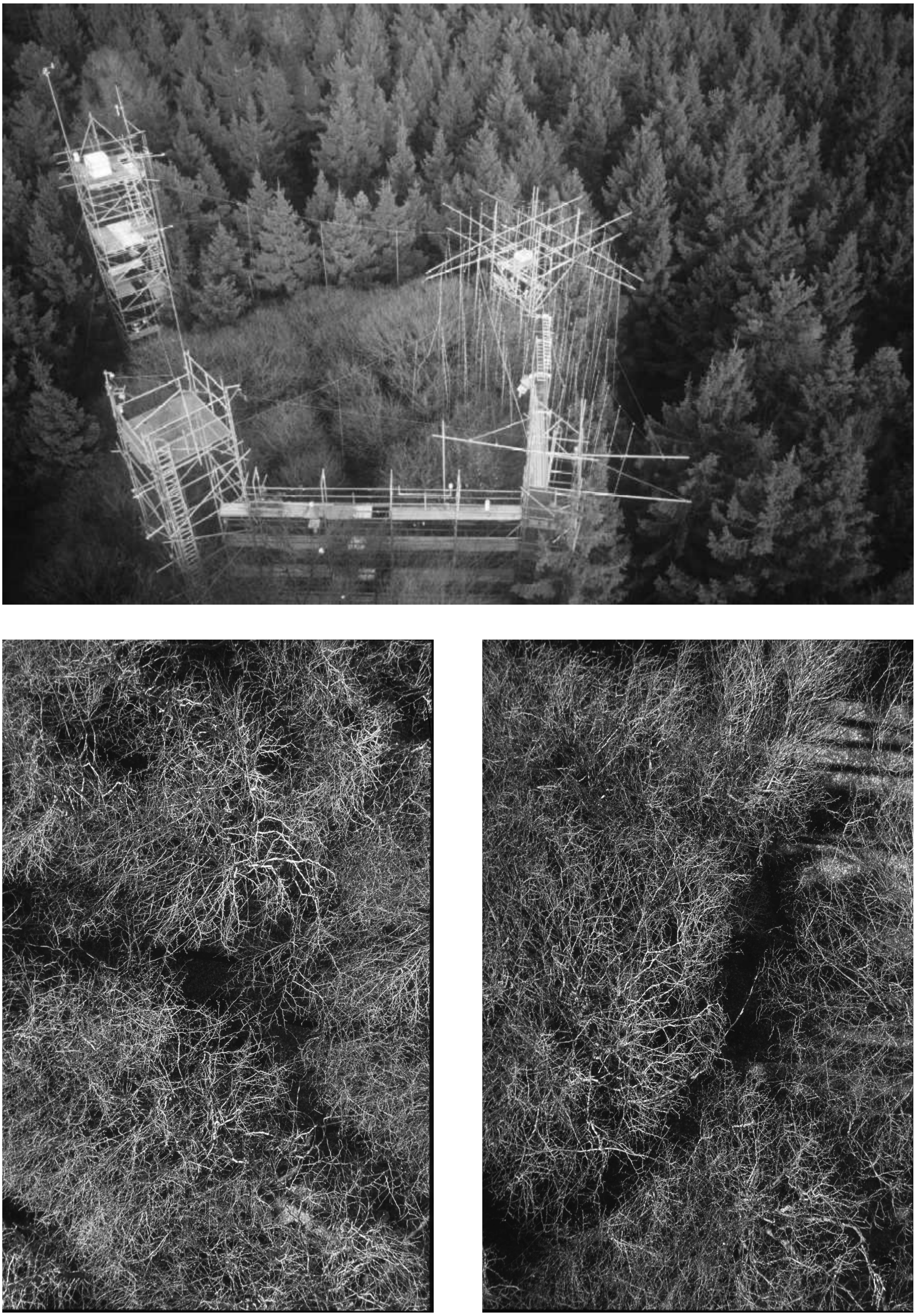


Figure 32: Gaps between tree crowns. Top – View of the study site, note gap fraction between spruce trees. Lower left and right – close up of beech tree crowns viewed from above, note that individual crowns hardly intermingle, this phenomenon is termed ‘crown shyness’.

The costs of competitive interference of beech compared to those of spruce were 2.5 times higher in terms of biomass losses of live branch axes per unit of stand area, as was estimated through litter sampling after storms (Figure 34C). The largest fraction of live biomass were shade branches (>99%). The buds attached to lost beech branches through a severe storm in winter (low pressure system “Lothar”) were equivalent to a leaf area loss of 0.15 m^2 m^{-2}. The leaf area loss was certainly higher as injured and singly lost buds were not assessed. The relationship of lost biomass in spruce and beech was about the same for life (Figure 34 bottom) and dead biomass (Figure 34 upper left). The space that had been lost according to the loss of life biomass of the axes, however, was about similar in both species (cf. Figure 19, page 50).

Self-pruning of beech twigs (lateral axes) was found at an early stage of branch development. Self-pruned of twigs began at proximal positions in sun branches of beech and continued in shade branches (Figure 38/ ‘Self-pruning’ is termed ‘twig loss’, as some twigs may have been broken off through interference with other branches. The major fraction nevertheless, was lost through self-pruning). About the same fraction of biomass was lost in shade and sun branches of beech, which reduced costs of biomass maintenance and increase efficiency of space sequestration at the branch level (cf. Figure 11, page 28, Figure 15A, page 32). Beech eventually had a more horizontally extending branch volume in shade branches compared to sun branches (cf. Figure 45, page 101). However, planar branch growth of spruce only occurred in shade branches at the crown base. Spruce tended to develop new shoots on the dorsal side of the main axis in these very shaded branches. The new shoots displayed planar growth and pendulous axes below these new shoots tended to die back, similar to shade branches of beech. The planar growth is indicated at the proximal branch position in the illustration of the spruce shade branch of tree 483 (Figure 45, page 101).

Figure 33: Crown shyness between beech. Close-ups of Figure 32, viewed from above (left) and from below (right). Pictures were taken in winter.

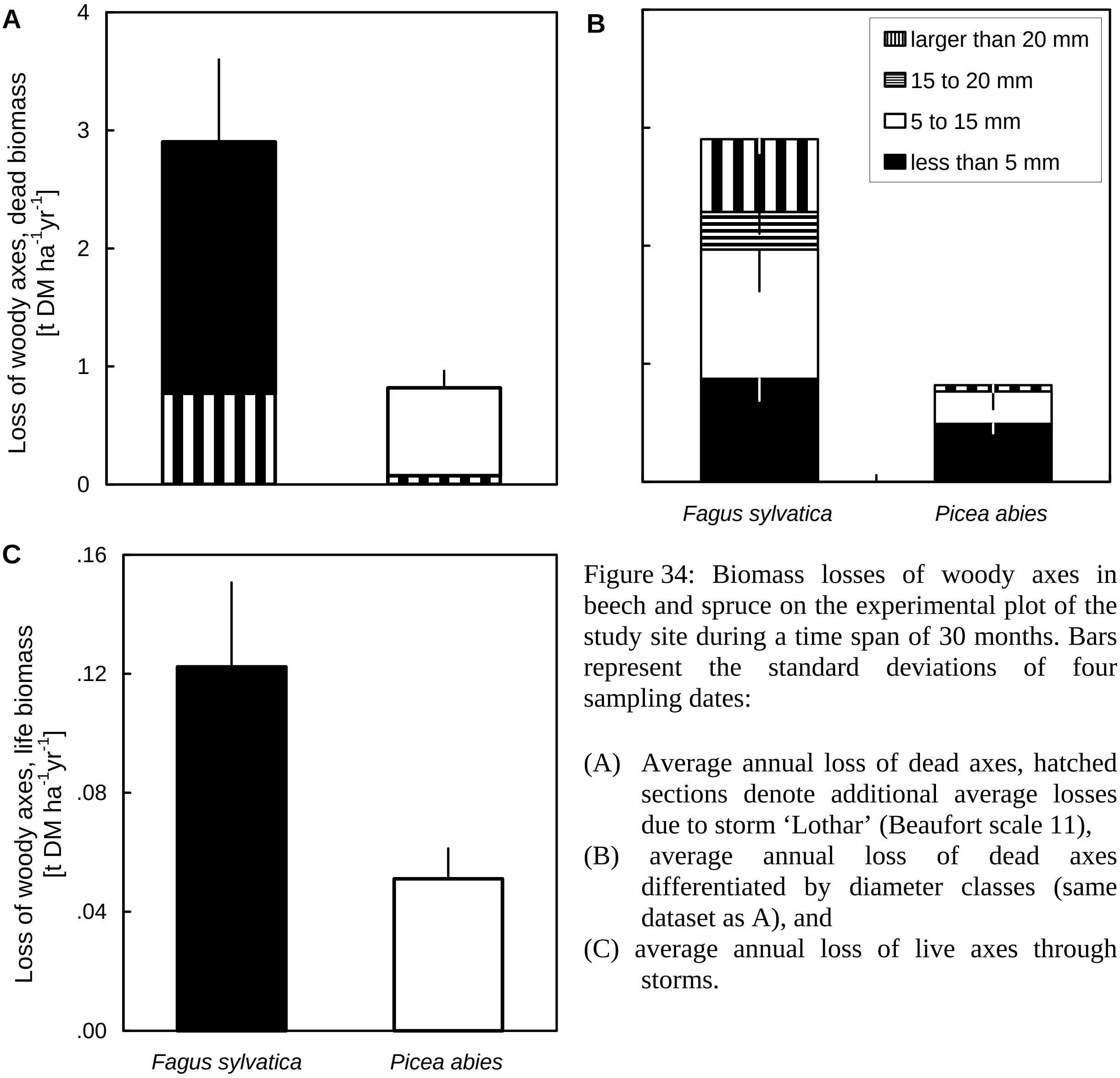


Figure 34: Biomass losses of woody axes in beech and spruce on the experimental plot of the study site during a time span of 30 months. Bars represent the standard deviations of four sampling dates:

(A) Average annual loss of dead axes, hatched sections denote additional average losses due to storm ‘Lothar’ (Beaufort scale 11),

(B) average annual loss of dead axes differentiated by diameter classes (same dataset as A), and

(C) average annual loss of live axes through storms.

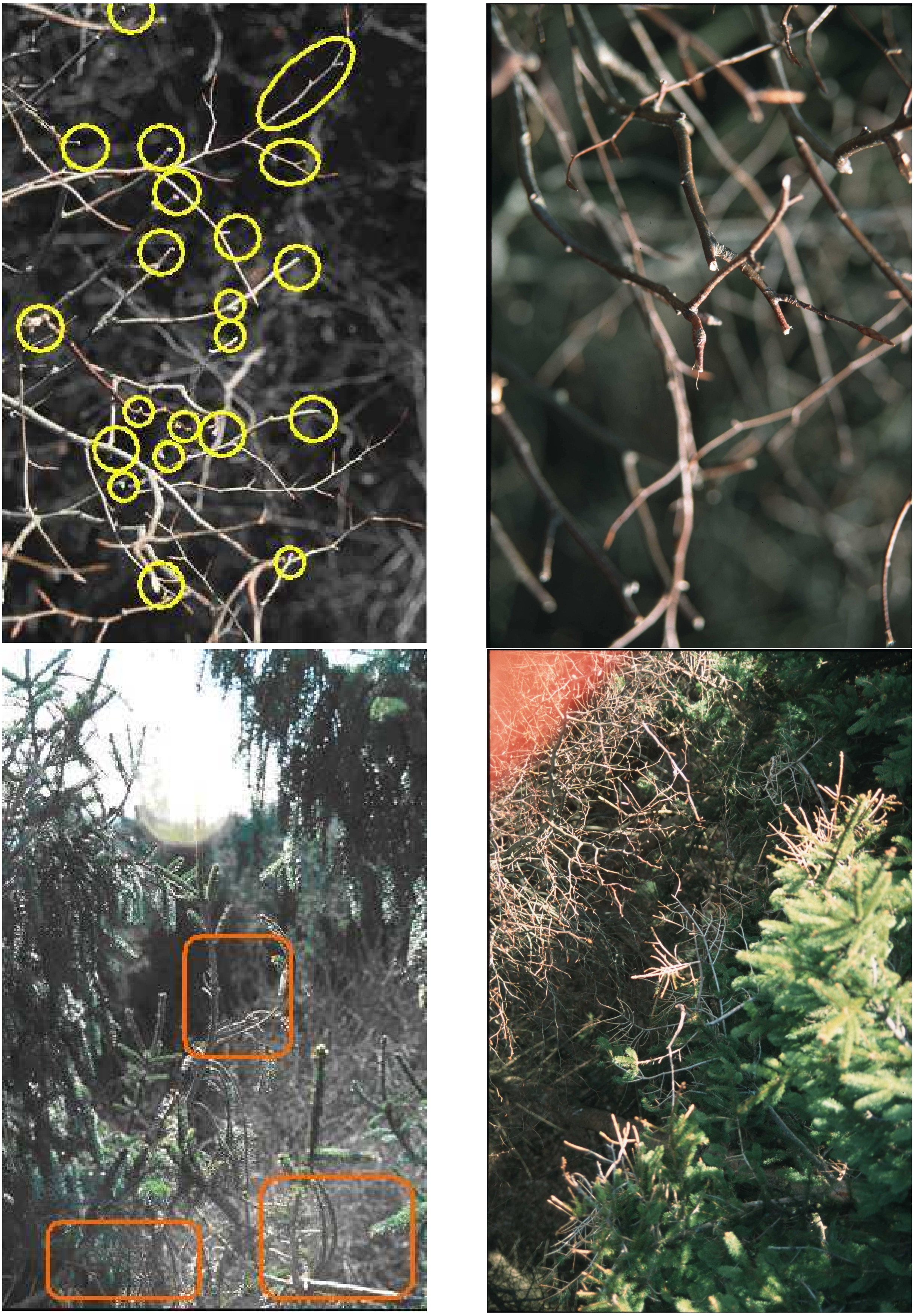


Figure 35: Crown abrasion between neighbouring trees: between beech (upper left and right/ circles denote sites of branch fractures), between spruce (lower left/ boxes denote sites of foliage abrasion and branch fracture), and between neighbouring spruce and beech (lower right). Pictures were taken in winter.

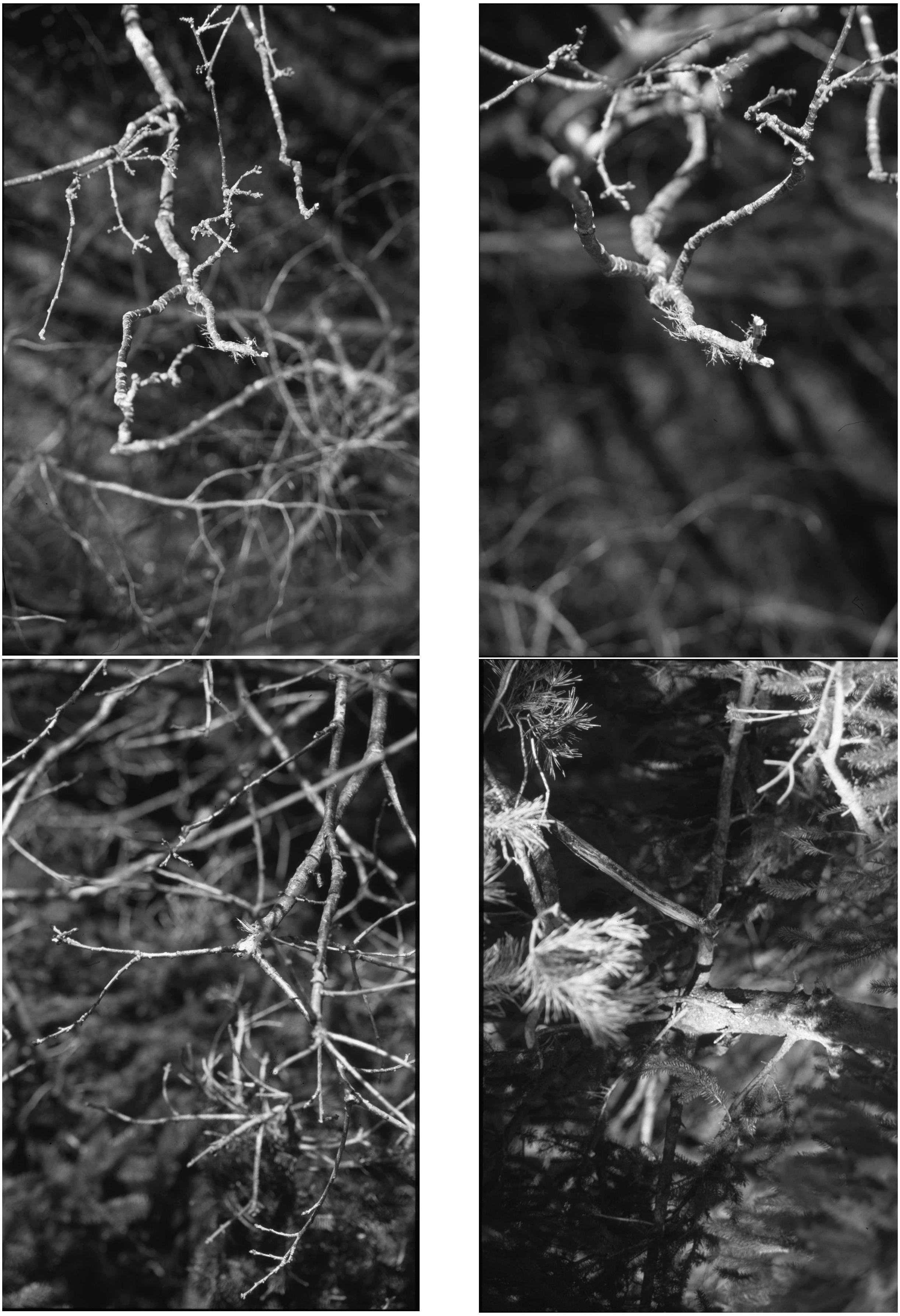


Figure 36: Crown abrasion between neighbouring trees: oak (upper left/ with beech as neighbour, upper right/ close up of upper left), between spruce and oak (lower left), and between spruce and pine (lower right). Pictures were taken in winter.

Figure 37: Crown abrasion between neighbouring trees: pine (left/ with spruce as neighbour), and between spruce and larch (right). Pictures were taken in winter.

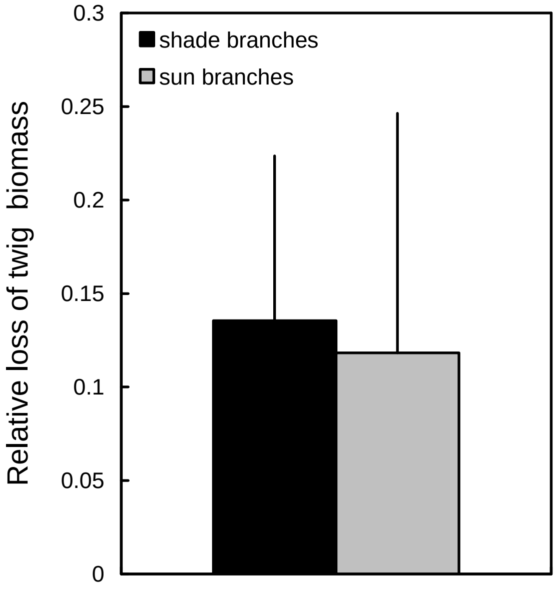


Figure 38: Biomass loss of twig axes (lateral axes) from sun and shade study branches of beech (see legend). The fraction is expressed as the lost biomass in relation to the standing woody biomass of the preceding dormant season. Mean values of 1999 and 2000, bars denote standard deviation among study branches, n=10 per light regime).

3.1.4 Discussion

Fagus sylvatica is more susceptible to wind damage compared to *Picea abies* trees (Kramer et al. 1988). The lost biomass in beech at ‘Kranzberger Forst’ was 3 times higher than in *Fagus sylvatica* stands of varying age (Table 14, Möller et al. 1954), which may be due to the high plant density and strong competition among beech at the study site (cf. Figure 7, page 8).

Table 14: Average annual branch, leaf and root loss and characteristics of beech stands of differing age (data from Möller et al. 1954).

Age [years]	***Stems*** [n ha^{-1}]	***Basal area*** [m² ha^{-1}]	***Aboveground increment*** [t ha^{-1}]	***Branch loss [0.8% of aboveground woody biomass]*** [t DM ha^{-1}]	***Branch loss, fraction of gross primary production*** [%]	***Branch loss, fraction of net primary production*** [%]	***Leaf loss*** [t ha^{-1}]	***Root loss*** [t ha^{-1}]
8			4	0.5	3.6	4.8	2.1	0.1
25	3800	17.7	8	1	4.5	5.7	2.7	0.2
46	960	23.2	8	1	4.3	5.3	2.7	0.2
85	260	26.9	6.2	1	4.6	5.9	2.7	0.2

Being able to sequester canopy space is important to access resources. However, being able to keep that space occupied is constrained by neighbours and can require carbohydrate import in shade branches (see Figure 26 & 28, page 66f). To keep the investment costs relatively low, it can be postulated that the carbon gain should be maximized within the physiological and morphological plant-specific range. Therefore, a planar growth of shaded branches should be of advantage, as light can be intercepted with a minimum of self-shading within the branch. This may be achieved by self-pruning of ‘dorsal’ and ‘ventral’ axes. The self-pruning decreases the mass of the whole branch, which on the one hand reduces respiratory costs. On the other hand costs for lignification, which compensates the tension and compression caused by the own mass of the branch, are reduced (Sibly and Vincent 1997).

Having to lose previously sequestered space to or due to an interfering neighbour can determine competitive success in trees, for example: The foliage area distribution is dependent on the mixture of species and degree of species dominance as was simulated for *Picea abies* and *Pinus sylvestris* (Moren et al. 2000); *Pinus sylvestris* seemed to have intruded into the lower crown of *Picea abies*. However, at the study site ‘Kranzberger Forst’ inspection showed more intense ‘crown shaping’ through branch injury in pine compared to neighbouring spruce. *Pseudotsuga menziesii* is faster in height growth than *Abies grandis*, but *Abies grandis* eventually catches up. When *Abies grandis* approached the height of *Pseudotsuga menziesii*, then height growth of *Pseudotsuga menziesii* was slowed down, due to crown abrasion. The strong branches in the shade crown of *Pseudotsuga menziesii* broke all terminals of *Tsuga heterophylla* off and prevented any transition to dominance. The same abrasion effect was observed, where *Quercus rubra* suppressed *Tsuga canadensis* (reviewed by Larson 1992). The phenomenon has recently received more attention; tree swaying, crown interaction and crown injury was studied in *Picea sitchensis* (Milne 1991, Milne 1995), *Pinus contorta* (Rudnicki et al. 2003), *Pinus strobes* (Leal and Thomas 2003), and several hardwood species (Muth and Bazzaz 2003). Besides immediate injury through breakage of twigs and branches, whole-shoot hydraulic conductance, conductance per unit pressure gradient and leaf specific conductance in *Fagus sylvatica* were negatively correlated with the number of bud scars per unit length (Rust and Hüttl 1999). Negative feedback mechanism were proposed by which stress-induced changes in shoots (e.g. through abrasion) can cause a lasting reduction of vigour.

Two or more species must share resources, in particular space, differently, if they are to avoid competition and to coexist on a site, which was termed ‘Competitive Production Principle’: Two species have reduced competition in mixtures compared to monocultures (Kelty 1992). Higher productivity of mixed forest stands has globally been observed for a number of species (Table 15; page 91). Besides the species mixture, the stratification of the stand was important (Table 16, page 91). The light demanding species was at the top of the canopy, which allowed transmittance of a relatively high fraction of light (cf. section 2.3.3.4, page 77) to the shade-tolerant species in the lower canopy. Once these light-demanding and shade-tolerant tree species competed for space in the same crown layer, then a higher productivity through “job sharing” is no longer given (cf. Pretzsch 2003). In monocultures *Picea abies* can be 10 % to 100 % more productive in stemwood biomass than *Fagus sylvatica*. The mixture of the two species is even more productive if beech occupies the understorey. If the species share the same canopy stratum, yield of *Picea abies* was less than in the monoculture (Assmann 1970). This was confirmed for *Fagus sylvatica* and *Picea abies* in a transect through Germany. No higher yield, but lower yield was found for *Picea* in mixture with *Fagus* compared to *Picea* monocultures (Pretzsch 2003).

Therefore, space is object of competition and a resource that determines competitive success. Tree swaying is a natural phenomenon by which crown space can be released through injury or loss of branches through crown abrasion. Depending on the growth form or physical branch characteristics, tree species can ‘suffer’ to a varying degree from injuries due to crown abrasion. In the case of spruce and beech, although similar losses of space may be encountered in both species, beech may be more severely affected. The sequestration of new space with potentially more favourable light conditions in higher strata of the canopy predominantly depends on branch elongation in beech, but not so in the monopodial growth form of spruce, where the stem and not the branches directly contributes to height growth.

Thus, the ability to ensure access to space of high light conditions is less constrained in spruce compared to beech through crown abrasion due to direct interaction of neighbouring tree crowns.

Table 15: Mixtures that improved yield of the stand compared to monocultures of at least one of the species (Kelty 1992).

Species 1	***Species 2***	***Country/continent***
Pinus densiflora	*Chamaecyparis obtusa*	Japan
Pinus sylvestris	*Picea abies*	Europe
Quercus, Acer, Betula	*Tsuga canadensis*	northeast USA
Pseudotsuga menziesii	*Tsuga heterophylla*	northwest USA
Agathis australis	main canopy species	New Zealand
Araucaria husteinii	hardwood species	Papua New Guinea
Eucalyptus saligna	N_2-fixing *Albizia falcataria*	Hawai

Table 16: Stratified mixed forest stands of two species. Mixed stands consistently showed greater yields than monocultures of the less shade-tolerant species and (where comparison was possible) than the more shade-tolerant species (from Assmann 1970):

Mixed stand Upper canopy species	***Mixed stand Lower canopy species***	***Monoculture for comparison***
Pinus sylvestris	*Picea abies*	only upper canopy species
Pinus sylvestris	*Fagus sylvatica*	
Quercus petraea	*Fagus sylvatica*	
Larix decidua	*Fagus sylvatica*	both species
Picea abies	*Abies alba*	

3.2 Response to elevated ozone

3.2.1 Introduction

Plants respond to ozone in multiple ways and scales (reviews on trees by Matyssek et al. 1997, Samuelson and Kelly 2001, Matyssek and Sandermann Jr 2003). The response depends on ozone uptake (Skärby et al. 1987, Wieser and Havranek 1993, Baumgarten et al. 2000, Mikkelsen et al. 2000, Bortier et al. 2001, Wieser et al. 2003b, Matyssek et al. 2004, Nunn et al. in preparation), competition (Kozovits et al. 2004), species (Matyssek et al. 2002b, Schaub et al. 2003), plant age (Grulke et al. 1996, Wieser et al. 2000, Grulke and Retzlaff 2001, Wieser et al. 2003a), foliage age (Polle et al. 2000, Wieser et al. 2000), nutrition (Landolt et al. 1997, Maurer and Matyssek 1997, Maurer et al. 1997). Known chronic responses to elevated ozone can be premature leaf loss, reduction of gas exchange, and altered resource allocation to roots, shoots and foliage, which changes the allometry of plants. Allometric relationships have shown to be rather conservative in herbaceous species (e.g. *Arabidopsis thaliana* & grass species/ Müller et al. 2000, Stoll et al. 2002), and also in woody species (e.g. *Prunus dulcis*/ Heilmeier et al. 1997). Nevertheless, changes in allocation through ozone in *Betula pendula* (Matyssek et al. 1992) and interspecific competition altered allometric relationships of foliage and shoot & axis biomass in young *Fagus sylvatica* trees (Kozovits 2003). In the following, senescence, leaf gas exchange, and the allometric relationship of foliage and axes were investigated in terms of response to elevated ozone. The aim of the ozone fumigation was to reduce the available resources through a reduction of carbon gain. Ozone was not applied as an air-pollutant, but as an ecophysiological tool to experimentally invoke changes in carbon allocation within trees.

3.2.2 Methods

3.2.2.1 ‘Free-air’ ozone fumigation system

A novel system for continuous and controlled free-air fumigation of mature tree canopies with ozone (Figure 6, page 8) started operation in May 2000. Within a volume of 2000 m^3 which comprises the neighbouring crowns of five beech and five spruce trees (cf. Figure 3, page 5), the ozone (O_3) levels prevailing at the forest site are increased to a “2 x ambient” O_3 regime (Table 17), up to maximum levels of 150 ppb O_3. The system was designed by the partner project B2, Chair of Bioclimatology, Technische Universität München, Germany (Werner and Fabian 2002).

Ozone is produced by a commercial ozone generator (Ozonia-CSI). To prevent formation of oxides of nitrogen, the ozone generator is operated with oxygen rather than air. With a commercial oxygen generator ambient air is purified to 90% oxygen, after passing over a dryer and subsequent filter for volatile organic compounds. A system of 130 PTFE tubes fitted to a mixing tank was used to conduct an ozone & air mixture directly into the canopies of the trees of interest. These tubes are fixed to a 1 m x 1 m grid above the canopies. Every tube is equipped with 45 calibrated outlets, 33 cm apart from each other, providing a constant flow of about 0.30 l min^{-1} each. Experiments and calculations have shown that from the outlet a steep gradient from enriched to twice ambient conditions already occurred within 5 cm. Therefore, the fraction of fumigated volume around the outlets that is markedly exposed to higher than twice ambient conditions is less than 0.2 % of the fumigated canopy. This fumigation system ensures an experimentally enhanced and chronic whole-tree exposure to ozone while avoiding – in the absence of plant enclosure in chambers/cuvettes – physiological bias through micro-climatic artefacts (as prevailing in conventional fumigation studies). The advantage is the applicability to adult trees as growing in naturally structured forest stands (Karnosky et al. 2001).

In the growing season a twice ambient ozone concentration was achieved for year 2000 (Figure 39, Table 17 SUM0). 'Critical levels' (AOT40) were increased by factor 4 to 5 (see Fuhrer 1994, Skärby and Karlsson 1996). The two dimensional distribution of the ozone "cloud" within the experimental plot, was quite limited to the target canopy and the ozone concentration rapidly decreased with distance from the fumigation system (Figure 40).

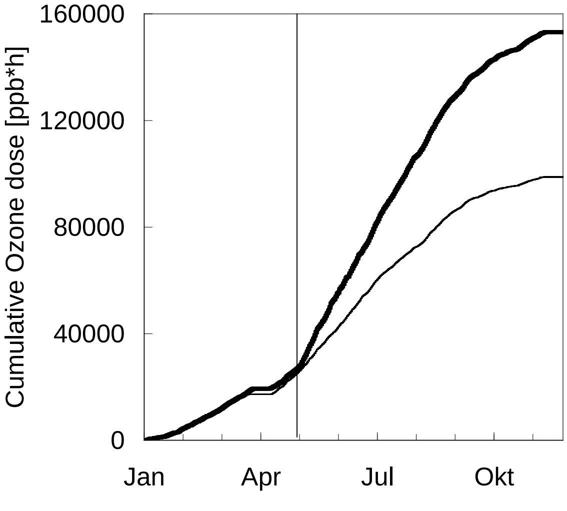


Figure 39: Annual course of cumulative ozone dose in the sun crown during the first year of fumigation in 2000, which was started just before May (vertical line). The thin line is based on the ambient ozone concentrations, whereas the thick line denotes the experimentally enhanced 'twice' ambient ozone dose (Figure by partner project B2.)

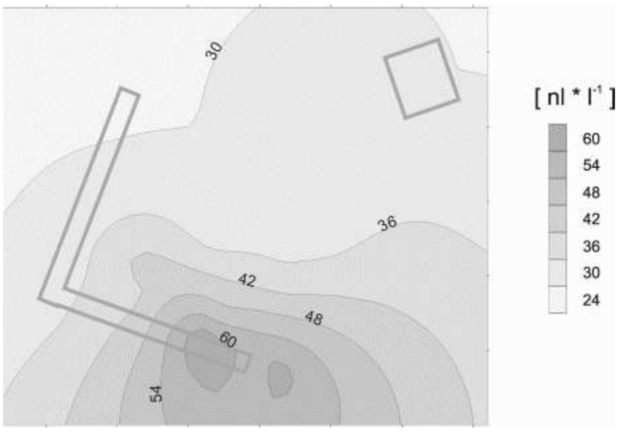


Figure 40: Extension of the experimental ozone regime in the sun crown. In addition to ambient ozone concentrations, the "free-air" fumigation experimentally increased the O_3 regime. Ozone distribution was assessed by passive samplers, isobars were created by the method of Kriging. Frames represent the scaffoldings. (From Nunn et al. 2002, cooperation with project B2).

Table 17: SUM0 (accumulated exposure to ozone per year) and AOT40 (accumulated exposure to ozone per year above a threshold of 40 ppb O_3 and 50 W m^{-2} of global radiation) of ambient ($1xO_3$) and twice ambient ($2xO_3$) ozone treatment, for the years 1999 to 2002 of the beech and spruce study branches in the sun and shade crown. Standard deviations of beech resulted from different lengths of the growing season. (From Nunn 2004, cooperation with partner project B2).

Ozone treatment	*Branch type*	*SUM0 [µl l^{-1} h]*				*AOT40 [µl l^{-1} h]*			
		1999[1]	*2000*	*2001*	*2002*	*1999*[1]	*2000*	*2001*	*2002*
beech									
$1xO_3$	***shade***	124.4 +/- 1.2	139.4 +/- 1.4	131.5 +/- 3.2	123.2 +/- 5.2	10.1 +/- 0.2	15.4 +/- 0.1	15.0 +/- 0.3	16.0 +/- 0.5
$2xO_3$	***shade***	117.1 +/- 1.4	201.0 +/- 10.9	191.2 +/- 1.4	180.7 +/- 1.5	13.4 +/- 0.1	59.9 +/- 1.3	48.3 +/- 0.2	48.0 +/- 0.4
$1xO_3$	***sun***	124.7 +/- 2.1	140.2 +/- 0.7	136.4 +/- 2.1	126.4 +/- 1.1	10.2 +/- 0.1	15.4 +/- 0.0	15.0 +/- 0.3	16.3 +/- 0.3
$2xO_3$	***sun***	122.5 +/- 2.2	221.5 +/- 2.1	256.2 +/- 4.8	234.0 +/- 3.0	13.6 +/- 0.3	62.4 +/- 0.0	70.9 +/- 0.7	67.2 +/- 0.5
spruce									
$1xO_3$	***shade***	217.9	212.9	217.5	211.1	13.0	16.4	16.5	18.7
$2xO_3$	***shade***	197.2	278.3	282.4	271.6	16.4	62.0	51.1	52.7
$1xO_3$	***sun***	217.9	212.9	217.5	211.1	13.0	16.4	16.5	18.7
$2xO_3$	***sun***	211.3	303.7	345.2	328.3	16.4	65.5	74.1	72.6

[1] control year without ozone fumigation

3.2.2.2 Autumnal senescence

Autumnal leaf senescence was estimated as the discoloured or shed leaf area in proportion of total foliage area of the study branches (using nets for assessing the shed leaves). The dates of 50% leaf senescence of branches (discoloured or shed foliage area) were calculated using a non-parametrical, sigmoidal fit (*Boltzmann,* ORIGIN 6.0, Microcal Inc., USA, cf. Eq. 18, page 25).

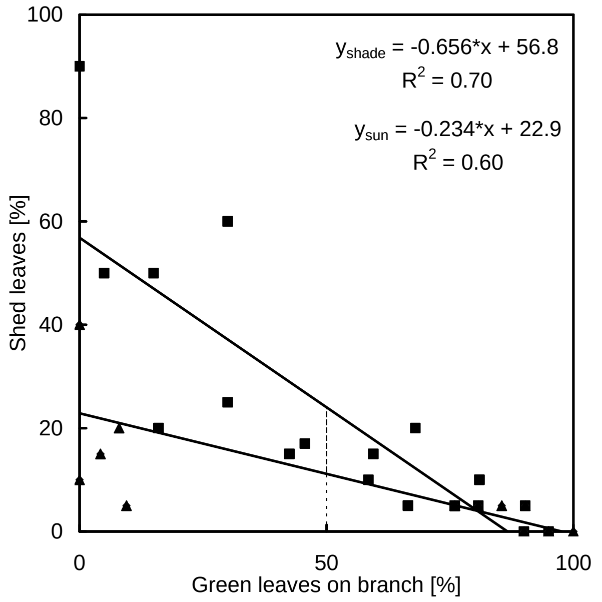


Figure 41: Relationship of the proportion of green and shed leaves in the beech study branches during 1999 and 2000. Triangles denote sun and squares denote shade branches, n=10 per branch type. Lines represent linear regression, equations and coefficient of determination are given in figure. Dotted line indicates 50 % senescence.

The results correspond to the ‘colouring of leaves’ (BBCH94 / Meier 1997, 50 % coloured: Rötzer 2001), though already fallen off leaves (BBCH95 / Meier 1997, 50 % fallen off: Rötzer 2001) bias the estimate (Figure 41). The bias will vary e.g. according to prevailing winds. If half of the leaves on a beech branch were still green then a proportion of 24 % and 11 % of the leaves in shade and sun branches respectively, had already been shed in the study branches (Figure 41).

3.2.3 Results and Discussion

3.2.3.1 Autumnal senescence, leaf abscission

The foliage of beech on the study site showed early autumnal senescence after the first season of twice ambient ozone fumigation (Figure 42, Nunn et al. 2002, significant differences in the length of the growing season compared to the control, Nunn, in preparation). However, these differences were far less distinct and restricted to the shade crown in the second season, and not present in the third season (Figure 42).

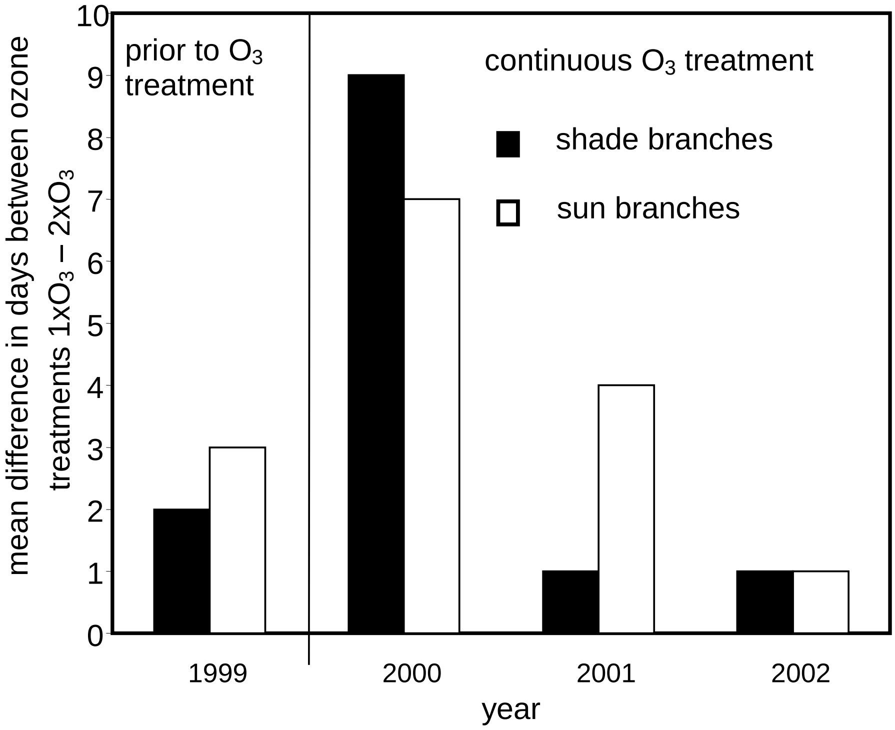


Figure 42: Temporal differences in autumnal senescence of sun and shade study branches in beech given prior (1999) and after 1 to 3 seasons (2000-2002) of twice ambient ozone fumigation (n=5 per treatment of ozone and sun and shade branch). Data of year 2001-2002 from Nunn, in preparation).

Rspense of foliage to the first year of fumigation is different from further years, as in the first year of fumigation the foliage developed from buds, that had not been formed in elevated ozone concentrations (Roloff 2001). Thus the foliage had adapted to elevated ozone concentrations after one season of fumigation. The change in ozone exposure had apparently had been memorised (Sandermann et al. 1990) in the buds, which had been developed in elevated ozone. This agrees with findings on *Fagus japonica*, in that leaf properties were largely influenced by current year *PPFDs*, whereas characteristics of shoot gross morphology were determined by previous year *PPFDs* (Kimura et al. 1998). Young beech trees in a chamber study showed early leaf loss in twice ambient ozone, but this effect could almost be compensated if CO_2 was also elevated (Kozovits 2003, partner project B5). Leaf abscission was enhanced in ambient and elevated ozone regimes compared to charcoal filtered air in young *Fagus sylvatica* and *Populus nigra* (Bortier et al. 2000). The acclimation to ozone in terms in the length of the growing season, suggests that beech may be more susceptible to injury through ozone, if the the variability of ozone is high between the growing seasons.

3.2.3.2 CO_2 gas exchange

In sun and shade branches of beech, no effect of ozone on the CO_2 gas exchange was found, exemplified for the maximum electron transport capacity, J_{max} in shade and sun foliage (Figure 43AB).

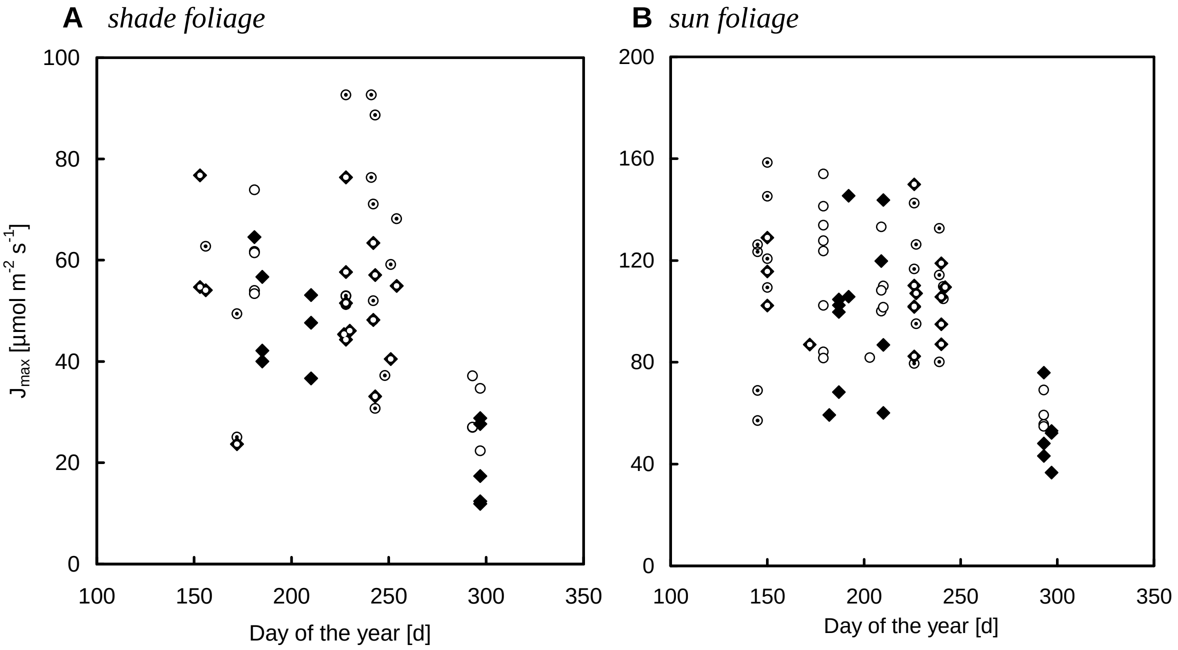


Figure 43: The maximum electron transport capacity (J_{max}) in (A) shade and (B) sun foliage of beech before (1999, plain symbols) and during first year (2000, dotted symbols) of ozone treatment. Circles denote the control group and diamonds the fumigated group of trees, n=5 trees per treatment.

Published data does not reveal a uniform picture of gas exchange response to ozone, even for the same species: (i) Ozone had no effect on the CO_2 gas exchange in seedlings of *Picea abies* (Leverenz et al. 1999). (ii) However, ozone reduced photosynthesis dependent on - the nutrient treatment (Lippert et al. 1996) and duration of treatment (second year of elevated O_3/ Nunn et al., in preparation) in *Picea abies*, time of the year in *Fagus sylvatica (*latter part of the season, August & September/ Paludan-Müller et al. 1999), plant age in *Sequoiadendron giganteum* (Grulke and Miller 1994), depended on species in *Prunus serotina* > *Fraxinus americana* > *Acer rubrum* (Schaub et al. 2003). (iii) Reductions of gas exchange, were reported for young plants of *Fagus sylvatica* (Grams and Matyssek 1999, Bortier et al. 2001), *Picea abies* (Kronfuß et al. 1998), *Betula pendula* (Matyssek et al. 1991). (iv) In current year shoots of young *Picea abies,* growing in mixture with young *Fagus sylvatica*, the ozone treatment increased CO_2 gas exchange during the second season of fumigation (partner project B5, Kozovits 2003). Regarding the effects of ozone on senescence, it may be expected that ozone affects leaf gas exchange during the second year of fumigation, as leaf characteristics could have been set differently in the buds, which were developed under elevated ozone conditions (Kolb and Matyssek 2001, *cf.* *SLA* Annex A 3.1).

3.2.3.3 Branch allometry

No differences in the allometry of the biomass of axes and foliage were found between branches that had been exposed to twice ambient ozone for one season (Figure 44).

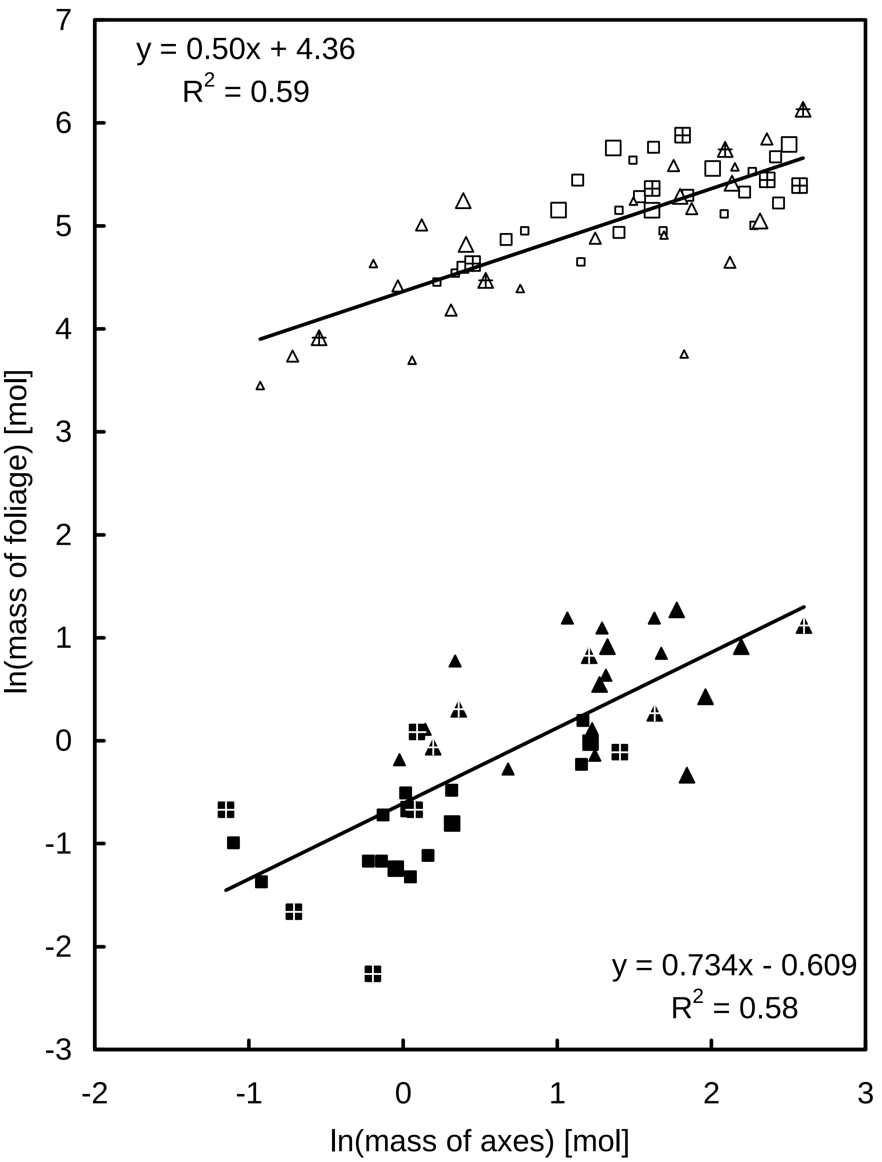


Figure 44: Allometric relationship of C mass of foliage and woody axes (logarithmic scale).

Open and closed symbols denote spruce and beech, triangles and squares denote sun and shade branches. The size of the symbol denotes the year: small-1998 (spruce only), medium-1999 and large-2000. Symbols marked with '+' represent branches treated with twice ambient ozone. Lines denote linear regression, equations and coefficients of determination are given in the upper left corner for spruce and the lower right corner of the figure for beech.

Differences of branch growth of *Populus tremula* in elevated ozone were time-shifted to the second year of the experiment (Matyssek et al. 1993). Shoots are grown mainly from previous year reserves, which are at least partially drawn from a central pool of carbohydrates in the stem (Sprugel and Hinckley 1990). Shoot axes could be fully developed, before injury due to chronic ozone exposure in the current year affects the plant. However, leaves of *Fagus sylvatica* have been reported to be rather sensitive to ozone stress during development (Polle et al. 2001), and model evaluations showed that the defence capacity of leaves of young *Malus* (“Golden Delicious”) trees was lowest during leaf development and senescence (partner project C2/ Gayler et al. 2004). If shoots depend on carbon gained by current year foliage as plants with indeterminate growth, then high ozone concentrations during leaf development may affect shoot development, as at that time, defence may be low in leaves and altered C partitioning is likely.

In summary, adult trees of this study showed no reduction in gas exchange rates between ozone treatments. No differences in the characteristics of the branch axes in response to elevated ozone were detected after one season of fumigation. Still, exciting insights can be expected in the second and following seasons of fumigation, when effects on leaf level and increasingly at the branch and whole tree level take effect (Kolb and Matyssek 2001).

4 Comparative analysis of space-related concepts

4.1 Comparative analyses of volume

4.1.1 Introduction

Growth form of species is highly variable, as well as the species-specific shape of the individual plant. The assessment of that shape by means of geometrical approximation of the shape's volume as given by – cubes, cuboids or voxels (e.g. Whitehead et al. 1990, Hendrich 2000), cylinders (e.g. Falge et al. 1997), layers (e.g. Monsi and Saeki 1953) or outlines (Hagemeier 2002) has been done repeatedly. A simplification seems necessary as the geometrical shapes, that plants develop during their life cycle, are complex and usually hard to approximate or parameterise through simple methods (Riedel 2000, cf. Grote and Reiter 2004, review by Godin 2000). Therefore, the space or volume that plants actually grow in, has seldom been the basis for ecological studies, although many plant models, that depict the plant structure, are currently functioning in a three-dimensional way. One common problem in approximating the volume of plant structures is, that the space occupied by the structure does not have clear and distinct enveloping boundary areas. A typical example is the foliated space of a branch. Hence, the shape of the geometrical model applied (cf. Figure 46 to Figure 49) and also the size of the integrated volume have been submitted to considerable variance and imaginativeness. This complicates comparison among different studies.

In the following the geometrical model of this study, advantages of the method applied in this study and a comparison to approaches of selected studies will be given with emphasis being on the branch level. The model of the study at hand is termed 'frustrum model' for simplification. The role of size for the outcome at different scales is discussed. Size is known to have significant effects on the outcome of analyses (Weiner 1996). Müller et al. (2000) have shown ways to process data affected by variation in size of the plant or plant parts. A method to enable comparison of measured and modelled results is presented.

4.1.2 Selected geometric models

- **This study- 'frustrum model'**

A novel method for the measurement of crown volume was developed based on frustra and applied to the study branches (see Figure 45, Eq. 4 page 21, Grams et al. 2002), as well as to the spruce trees of partner project B5 by Alessandra Kozovits (see Figure 47, Kozovits 2003). In Figure 45 the measured crown volumes are reconstructed symmetrically around the main axis.

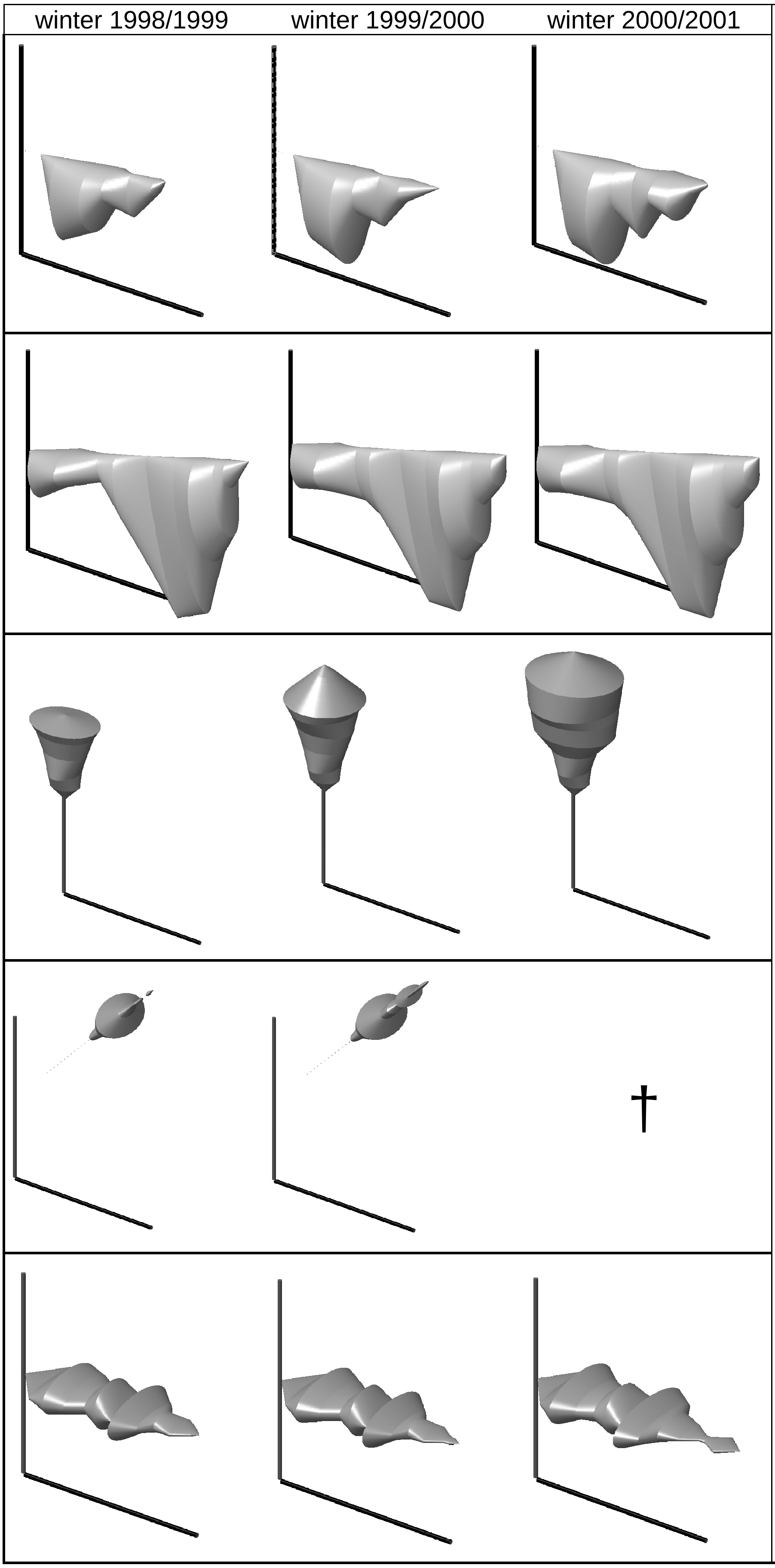


Figure 45: Three dimensional illustration of the crown volume occupied by selected study branches from the beginning (left figure in a row) through to the end of the study (right figure in a row). The figures were developed with the software CATIA (version 5.1, Dassault Systemes, Dassault, Suresnes cedex, France) in close cooperation with C. Schweigert. The volume was reconstructed from measurements of the horizontal and vertical extension of the foliage along the main axis. The geometric model are frustra based on ellipses (cf. Eq. 4, page 21). The base of the study branch is located in the middle of the upright reference axis. The Reference axes scale to 1 m. The cross denotes death of the study branch.

The following study branches are presented, from top to bottom: sun branch of spruce374, shade branch of spruce 483, sun branch of beech 412, shade branch beech of 443, shade branch of beech 412.

The symmetry is a simplification. In order to represent the deviation of the centre of the foliage extension the measurement of 4 lengths (horizontal and vertical range of the foliage in relation to the main axis) instead of 2 lengths (horizontal and vertical diameters) is necessary. The cross-sectional area would be a construct of four quarter ellipses instead of one ellipse, i.e. more measurements as well as calculations are necessary. However, the area and, therefore, the absolute volume remains exactly the same, which justifies the simplification. The main axis is a straight line, which was quite in accordance with the observations in the field. Large lateral axes to the main axis were enveloped separately with the ‘frustrum model’ and the volumes summarized, to avoid inclusion of non-foliated space.

The advantages of this method compared to existing methods are that,

(i) measurements are readily perform with a simple metric tape
(ii) calculations are basic and could be performed with an ordinary calculator in the field
(iii) the geometric model is universally applicable to plants with shoots and foliage
(iv) the geometric model is flexible to account for irregular shoot, branch or crown habit
(v) costs are low.

• Küppers (1985)

Küppers (1985) was the first to combine the physiology and the architecture of woody plants with the volume sequestered by their foliage. His volume model is constructed at the scale of single shoots. The volume is approximated for the foliated section of the woody axis through a cylinder with a circular base which has the radius of the mean orthogonal distance between the leaf tip and the shoot axis (Figure 46). This model is special case of the ‘frustrum model’ (Figure 45), i.e. the diameters of the ellipses at the base of the shape (cf. d_{vi} and d_{hi} in Eq. 4, page 21) are all of the same length.

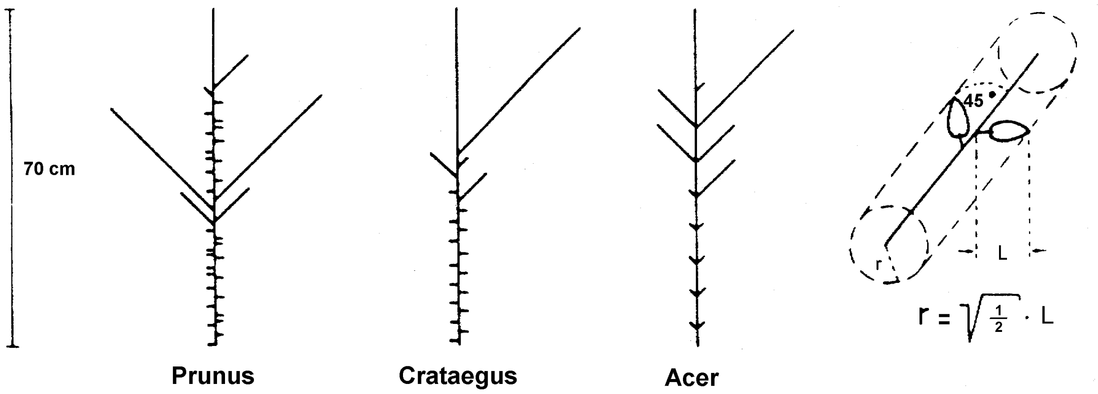


Figure 46: Geometric model used to approximate the shoot structure and the foliated volume of *Prunus*, *Crataegus* and *Acer* in a hedgerow study. L is based on the mean length of the leaf, and r is the computed radius for the cylinder, which envelops the foliated volume of the branch (Figure from Küppers 1985).

If leaves tend to be more horizontally orientated as is the case in beech shade branches as well as spruce shade shoots and shade branches then a base with elliptical shape should be preferred. The difference of the study by Küppers (1985) compared to the frustrum approach of this study was the application of the model to segments, which enclosed smaller volumes.

- **Kozovits (2003)**

In partner project B5 the crown and branch volume of young spruce and beech trees was analysed in a chamber study. The geometric approach was at the branch scale for beech, where cuboids approximate the foliated volume (Figure 47A). The shape is different from the frustrum model, but was suited to approximated the volume with a minimum of measurements, given the irregular branch shape. How can modelled volumes be compared ? The orthogonal cross-section represents a rectangle, whereas the cross-section of the frustrum model is an ellipse. An ellipse has a 21.5 % [1-(π/4)] smaller area than the rectangle (Figure 47C), therefore the volume of the cuboid is also 21.5 % larger. Less quantifiable deductions in volume become a problem, if the distal end of the cuboid was shaped as a pyramid in analogy to the 'frustrum model'. Approximations indicate that, if the tip was approximated with a pyramid, then the volume can be reduced by another 10-15 %.

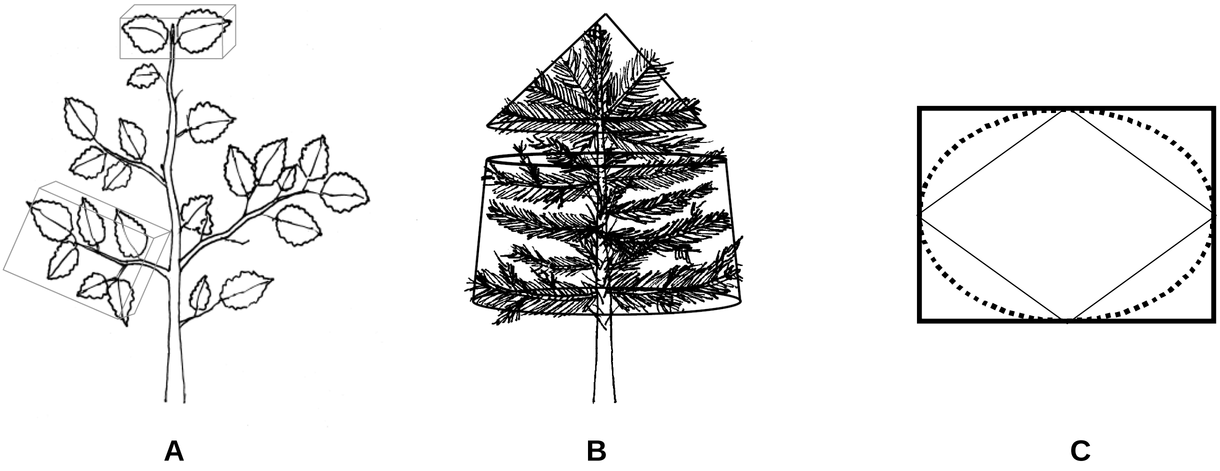


Figure 47: Geometric models to approximate the foliated volume. These methods were applied to **(A)** juvenile *Fagus sylvatica* and **(B)** *Picea abies* grown in containers in a chamber study. **(C)** represents three possible cross-sectional area calculations based on measurement of height and width of the foliated volume or 'leaf cloud', thick line: rectangle (cf. Figure 47A), dotted line: ellipse (this study & Figure 47B & Grams et al. 2002), thin line: polygon (cf. Figure 48A&C). Figures A&B from Kozovits 2003, partner project B5.

In total, if the same shoot or branch was approximated with a cuboid and the 'frustrum model', then the 'frustrum model' would render a volume, which is about 30 % to 35 % smaller. This is because the 'frustrum model' can better account for the shape of the branch. For spruce a model, comprised of one frustrum and one cone, was applied (Figure 47B), which is identical to the 'frustrum model'. No deviations are expected.

- **Fleck (2001)**

In a study by Fleck (2001), the crown volume occupied by branches of beech and oak was analysed. The geometric model was a polyhedron based on the absolute position of beginning and end of 5 parallel axis (Figure 48A).

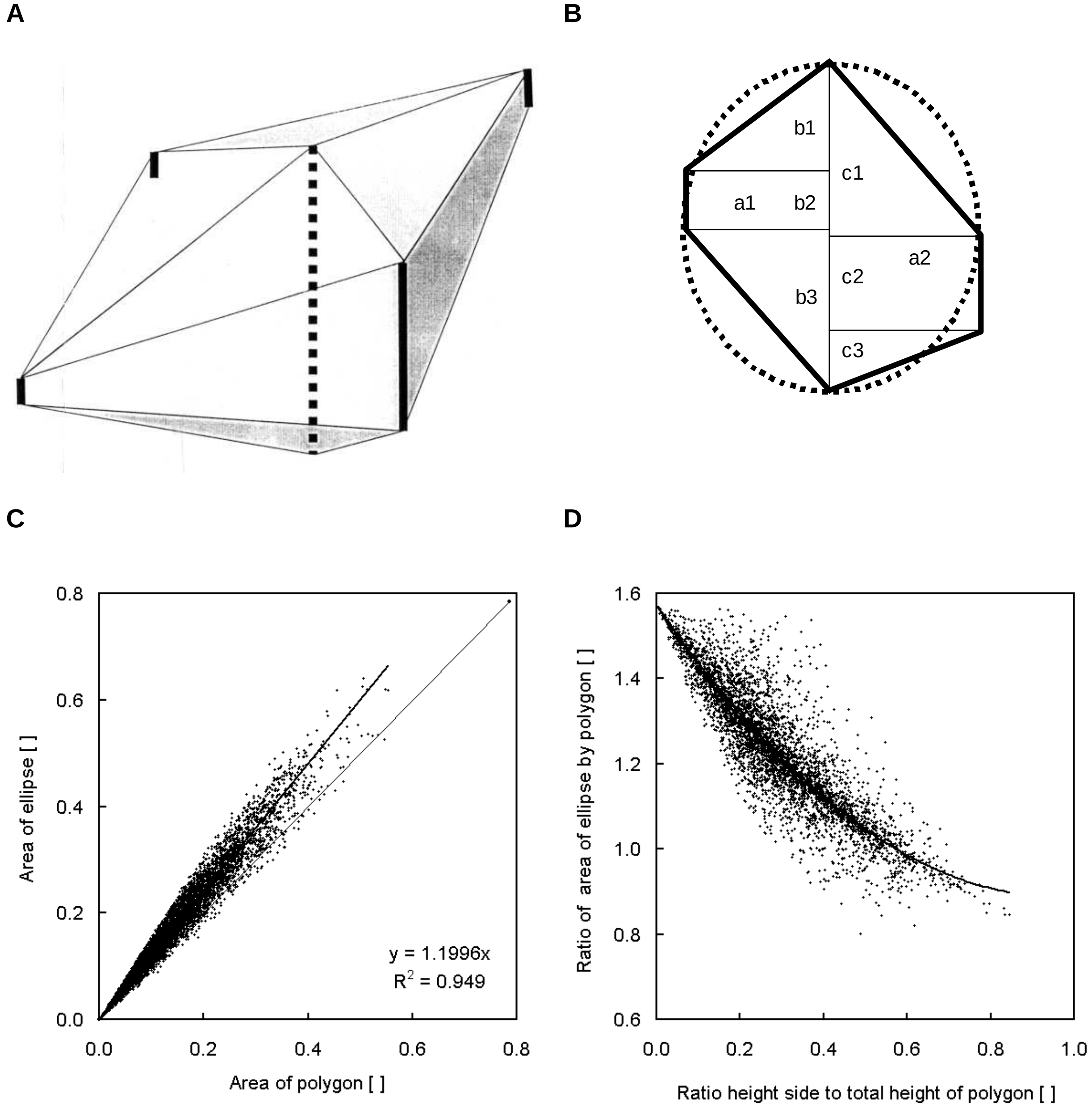


Figure 48: **(A)** Geometric model of the volume approximation applied for branches of *Fagus sylvatica* and *Quercus petraea*. The polyhedron is constructed from 5 vertical axes, denoted as solid and dotted thick lines. **(B)** Cross-section of the polyhedron and the ‘frustrum model’, represented through a polygon and an ellipse with the same height and width. **(C)** Simulation of the area ratio (=conversion factor) which was derived for randomly generated lengths of the axes (a1,a2,b2,c2). **(D)** The deviation from the mean ratio (slope of regression) in (C) was largely explained by the ratio of the mean side lengths to the central axis (figures A&B from Fleck 2001).

The relation, in cross sectional area of the ‘frustrum model’ compared to a polyhedron, is more complex as compared to a cuboid (compare Figure 48B and Figure 47C). A general example of the cross-section of the polyhedron orthogonal to the branch axis is given as a polygon in Figure 48B. The lengths as well as starting and end point of the bordering side axes (b2 & a1, c2 & a2), and the length of the central axis (b1+b2+b3) of the polygon’s cross-section were randomly generated (Microsoft Excel 9.0). The side and central axes of the cross-section are denoted as bold and dotted line in Figure 48A respectively. The random generation of the length of these axes revealed that the mean and the median of the ratio from the cross-sectional area of the polyhedron and the ellipse of the ‘frustrum model’ was about 1.2 (Figure 48C, standard deviation 0.146). Most of the deviation from the mean ratio could be explained by a second ratio of the mean length of the side axes to the central axis (Figure 48D, $y= 0.7756x^2 - 1.4375x + 1.5708$, n=5000 runs, $R^2= 0.81$). The random distribution is irrespective of the absolute size, but does not precisely reflect the species-specific shapes (cf. spruce and beech branches in Figure 45) that also varied in sun and shade crown (see sun and shade branches in Figure 45, and in Figures 19&20 by Fleck, 2001). If the ratio of the side axes to the central axis (Figure 48) is known for the plant or species-specific shape, then a conversion from the volume based on the polygon to the equivalent volume based on the ‘frustrum model’ may be performed. However, the necessary measurements to enable the construction of the polyhedron are difficult to perform with simple inexpensive tools. The calculation is also rather complex. In addition, the polygon model is incapable to account for the irregularities of the branch shape in the same quality as the ‘frustrum model’. Thereby, a higher fraction of non-foliated volume is incorporated into the polyhedron compared to the ‘frustrum model’.

- **Cermak (1990)**

Cermak (1990) has established the approximation of ‘leaf clouds’ (Figure 49), which has been applied to several tree harvests and used in up-scaling studies (e.g. Cermak et al. 1997, Cermak 1998). The leaf cloud is approximated as an ellipsoid. Therefore, the cross-section orthogonal to the main branch axis is identical to the ellipse of the ‘frustrum model’. The distribution of volume along the main branch axis is expected to be higher in the ‘leaf cloud’ approach’, as the stepwise approximation of the extension of the ‘leaf cloud’ by 10-30 cm intervals as in the ‘frustrum model’, can not be performed by a single ellipsoid. Therefore, more gap fraction is incorporated into the ‘leaf cloud’ compared to ‘frustrum model’, in particular, if branches are large and irregularly foliated.

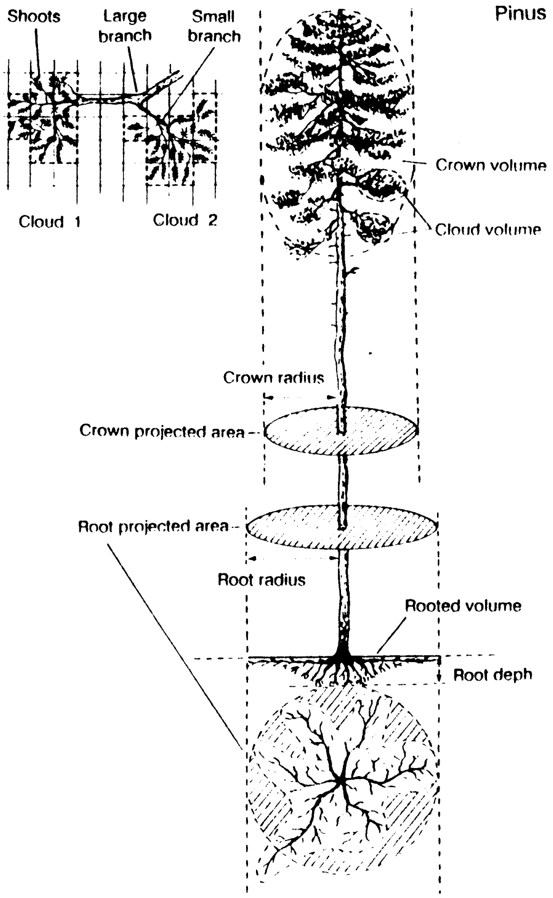


Figure 49: Approach used to assess the foliated volume of branches (“leaf clouds”) in *Pinus sylvestris*. The geometrical shape to approximate the leaf cloud is an ellipsoid (figure from Cermak et al. 1997).

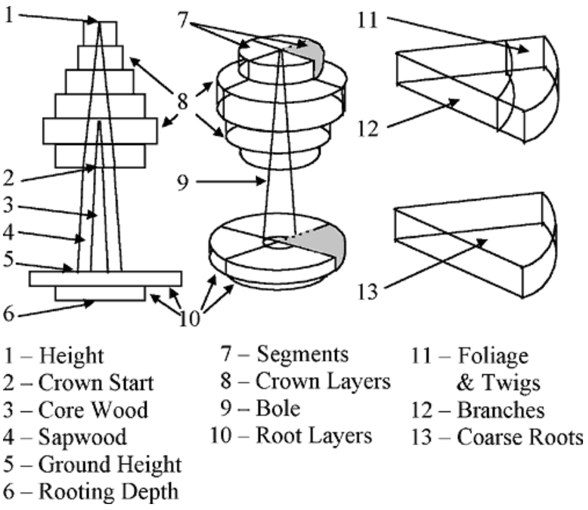


Figure 50: Geometric model of the tree structure, implemented in the stand growth model BALANCE. The trees are divided into stem, branches, coarse roots, fine roots and reserves. Branches, foliage, and fine roots are distributed around the stem in disks (8). Each disk is further divided into 8 segments (7). Within the crown, a foliated (11) and an unfoliated fraction (12) is distinguished in every segment. (Figure from Grote and Reiter 2004).

- ### Grote and Pretzsch (2002)

The model BALANCE (Grote and Pretzsch 2002**,** partner project C3) divides the crown into disks with foliated and non-foliated fractions, which are distinguished in every segment (Figure 50, no. 11 & 12) and were parameterised with data from trees close to the experimental plot (Grote 2002). The geometrical shape of the foliated segment volume is similar to the shape of juvenile beech branches (Figure 47A), but at a larger scale, as the segments integrate several shoots and branches, as well as the space between them. To compare the foliated volume of the segments with the foliated volume of the branches, information about the incorporated gap fraction within the segment compared to within the ‘frustrum model’ are needed. This issue is covered in the next section 4.1.3 on page 108ff.

Generally, the results based on volume of the segments of the model BALANCE and on the volume of the ‘frustrum model’ are more similar in the upper sun crown and less similar lower crown regions. The gaps between the branches – these gaps are not included in the ‘frustrum model’ - are at a minimum in the upper sun crown. In the more shaded segments of the crown, the distance between the ‘leaf clouds’ of individual branches increases. Therefore, the volume of the segments of the BALANCE model are ‘diluted’ with non-foliated space in the shade crown, as the extension of the foliated volume is merely approximated on the basis of distal and proximal segment positions, without considering the sides or vertical dimensions. Hence, the direct comparison with results based on the ‘frustrum model’ is not possible, but see section 4.1.3.

- **Schulze et al. (1977)**

The foliated crown extension in the vertical profile of trees allows to calculate the foliated crown volume (e.g. Figure 51/ Schulze et al. 1977). As described in the previous paragraph (BALANCE model, Grote and Pretzsch 2002), the fraction of non-foliated gaps enclosed in the foliated crown volume is not known.

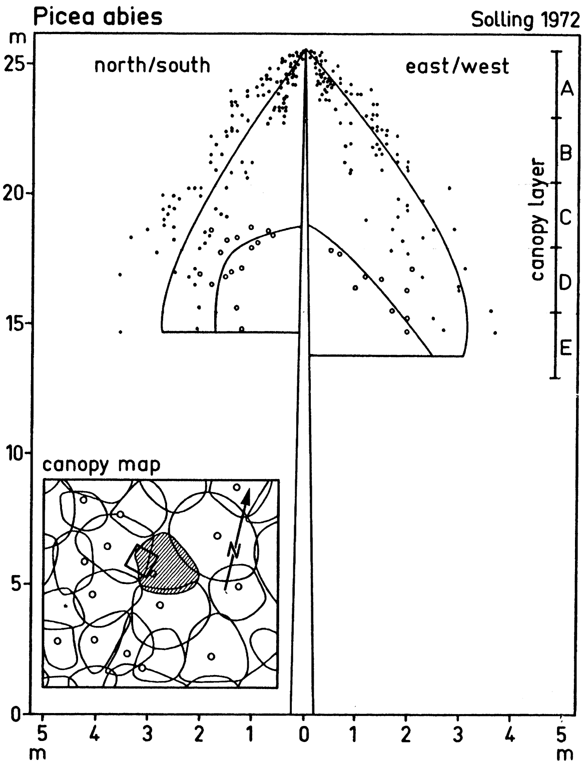


Figure 51: The cross section and crown projection of a mature *Picea abies* tree within a closed canopy. Small dots: end of branch, large dots: end of non-foliated branch area (figure from Schulze et al. 1977).

Figure 52: Two growth types of spruce which differ in growth pattern and in the gap fraction of the crown. To the left: ‘comb spruce’ and to the right: ‘brush spruce’ on the Campus Weihenstephan/ Freising / Germany (see section 1.8.1, figure from Seifert 2003).

Space-related results on the crown or crown layer level, can not be compared directly with results on the branch level, unless the proportion of non-foliated gaps within the foliated branch volumes and the fraction within the volume in the crown is known. This proportion is variable, which is apparent, when different growth patterns occur, that differ in the gap fraction between the foliated branch volumes within the crown, as observed for spruce (cf. Figure 52, e.g. Pöykkö and Pulkkinen 1990, Pulkkinen 1991, Ellenberg 1996) and beech (e.g. Rust and Hüttl 1999) or poplar (Ceulemans et al. 1990). Hence, in the same species, crown layers of same height can have different proportions of non-foliated volume. It is highly likely that that a change in growth form bears changes in e.g. in light transmittance through the capability to form a closed crown rather than a crown with gaps (Figure 52), in capacity of the crown volume increment, in the space-related C gain of branches or in the space-related 'running' respiratory investments of the branch. Thus, it appears to be important to quantify and compare competitiveness at the branch level. Else different competitiveness due to different growth form of branches may be masked. Providing that the quantification of space is essential to describe competitiveness, a geometrical model is necessary that can account for changes in growth form. The 'frustrum model' that was developed for the branch level in this study meets all the important requirements in volume quantification to be applicable in a wide range of growth forms.

4.1.3 Integration of measured and modelled space-related datasets

Space-related results, which are based on volumes that differ in their proportion of gap fraction due to different geometrical models, can be compared, if the results are scaled to a mutual volumetric unit and related to each other (relative volume in Figure 53). In this case, results based on segments of the model BALANCE and results based on volume derived with the 'frustrum model' were scaled to the foliated layer of the canopy (phyllosphere). This was achieved through measurement and calculation of the foliated fraction of the canopy volume ("foliated canopy (phyllosphere)" in Figure 53): (1) Volume occupied by branches: In the vertical profile of the crown ($rheight$), the foliated fraction was calculated (Eq. 39) as the leaf area density of the canopy, $LADcan$, divided by the leaf area density of the study branches, $LADbranch$ (Figure 54). $LADcan$ was assessed through vertical profiles of optical leaf area index measurements (LAI-2000, see Annex C for methods and leaf area density).

$$Sequestered\ crown\ space = \int_{rheight=0}^{1} \frac{LADcan_{rheight}}{LADbranch_{rheight}} \qquad \text{Eq. 39}$$

The mean foliated fraction is given species-specifically in Figure 53 ("Foliated branch, leaf cloud").

(2) Volume occupied by segments: The foliated canopy volume was calculated by relating the foliated and the total crown volume generated by the BALANCE model to stand scale (Figure 55) of the experimental plot (Figure 53).

For comparison, Figure 53 also includes published data on *Pinus sylvestris* (Cermak et al. 1997). The volume of the foliated crown segment of the model BALANCE was about 2.5 times larger in both species per unit of foliage area than the volume of the study branches. This is an average value for the whole profile. An example for the efficiency of space sequestration (occupied crown volume per invested C mass): A mean efficiency of spruce sun and shade branches is 15 m^3 $kmol^{-1}$ C (see Table 7). This is equivalent to an efficiency of 38 m^3 $kmol^{-1}$ C based on segments in BALANCE. Therefore it is possible to directly compare measured and modelled efficiencies. This allows validation of modelled datasets or configuration of such segments with the space-related characteristics of branches. In a second step, this can support understanding of aboveground competitiveness at the tree level, through examining the interaction of the individual competitive abilities of branches.

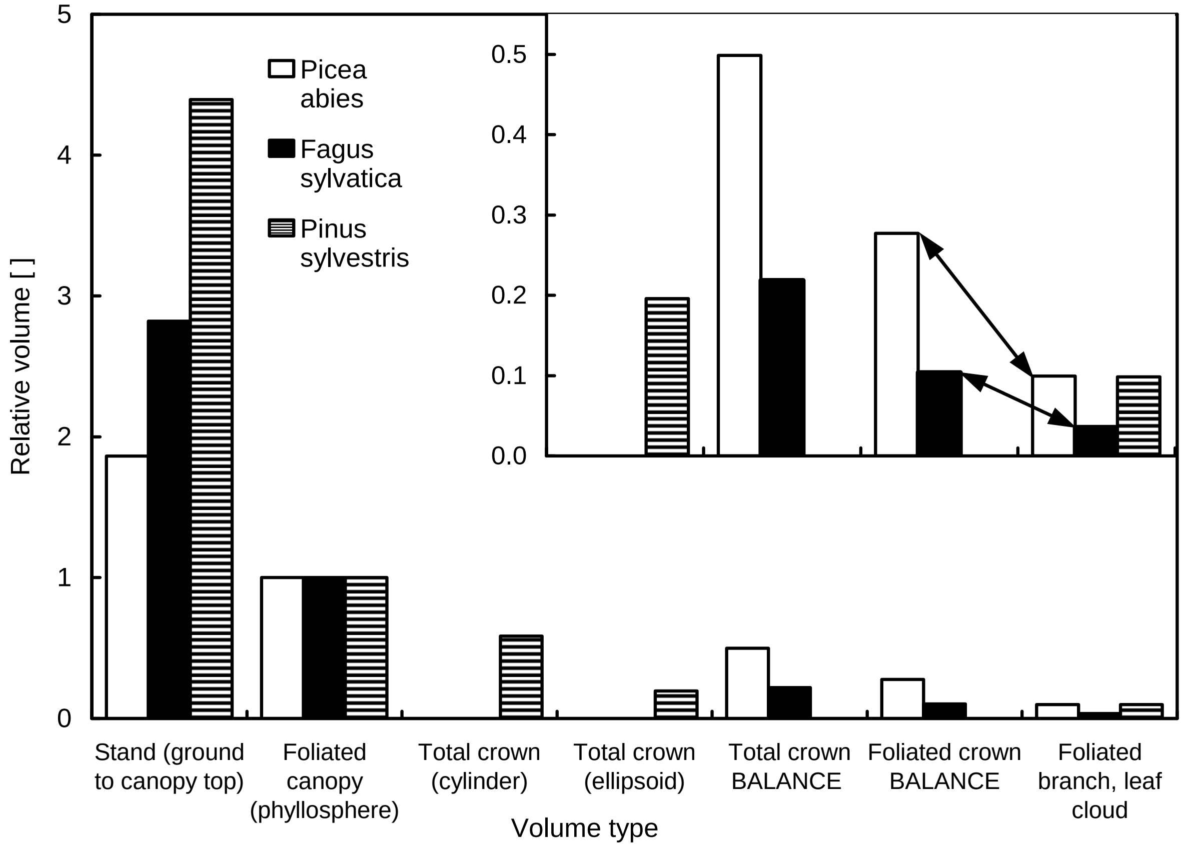


Figure 53: The relative foliated fraction of the stand. Fraction depends on volumetric unit of interest, stand to branch scale (=from left to right) in relation to the foliated canopy volume (=100%). Data at the stand and crown scale for spruce (open bars) and beech (solid bars) of this study was calculated in cooperation with Rüdiger Grote, project C3 (cf. Figure 50, Grote and Reiter 2004). Data on *Pinus* (hatched bars) was taken from Cermak et al. (1997). The inserted figure presents the fraction on crown and branch level at a higher resolution (see ordinate). The arrows point out the relationship between the modelled foliated crown fraction and the crown fraction occupied by the measured foliated branch volume.

The comparison of relative volumes of this study with published data of *Pinus sylvestris* (Cermak et al. 1997) shows good agreement (Figure 53). The volume of the 'leaf cloud', approximated with an ellipsoid, comprised a higher fraction of the crown volume than compared to the results based on the 'frustrum model' of this study. This is due to the fact that the ellipsoid encloses a higher fraction of non-foliated volume than the 'frustrum model'. Nevertheless, these relationships show that space-related findings on the branch level can be transferred to the stand scale to support analyses of whole-tree competitiveness.

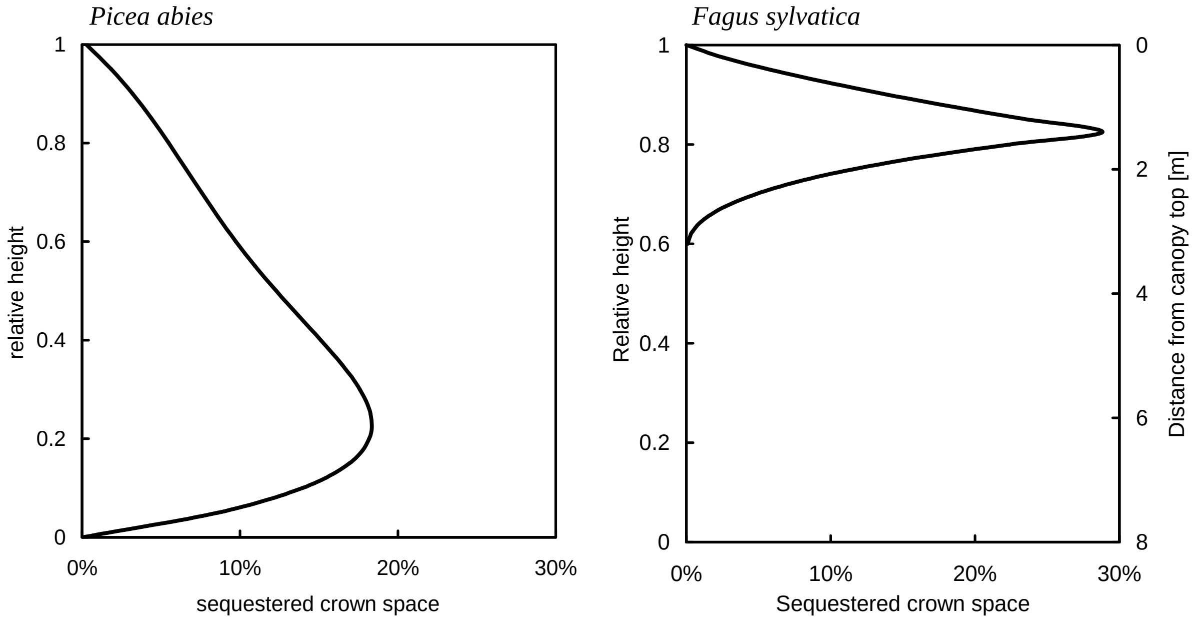


Figure 54: Vertical profiles of the sequestered canopy space of spruce (left) and beech (right), calculated as the ratio of the leaf area density within the canopy layers through the leaf area density of the leaf cloud.

Figure 55: Three-dimensional view of the mixed forest at plot 1 generated with simulation model BALANCE and visualized with TreeView, (Chair of Forest Yield Science, TU-München, Germany). Note that trees are presented as asymmetric disc structures (figure from partner project C3).

4.1.4 Comparison of space-related results through allometric relationships

This section focuses on the comparability of space-related data, as many current experimental approaches to quantifying competitive interactions introduce size bias, which may significantly impact the quantitative and qualitative conclusions (Connolly et al. 2001).

A branch (cf. Figure 47) has a certain space-related characteristic at one instant of time. However, characteristics of a branch can change during growth, as was shown for the branch shape of this study (Figure 45, page 101) and in *Fagus sylvatica* & *Quercus petraea* branches (Fleck 2001). In beech shaded axes are self-pruned (section 3.1), in spruce second-order branches may become more pendulous or new shoots have planar growth, old spruce shoots shed some of their needles. i.e. the larger the foliated volume that is being analysed, the more ontogenetic and morphological changes may be integrated. Thus, space-related branch characteristics can be related to size. This is in analogy to a series of studies by Weiner and colleagues (Weiner 1988, Weiner and Thomas 1992, Weiner and Fishman 1994, Weiner 1996, Weiner et al. 1997, Müller et al. 2000, Weiner et al. 2001, Stoll et al. 2002) who analysed allometry in several species in relation to the size of plant parts or individuals. As the findings are based on allometric relationships, these non-linear relationships can be converted into a linear relationship through logarithmic transformation:

$$y = a \cdot x^{b} \iff \ln y = a + b \cdot \ln x \qquad \text{Eq. 40}$$

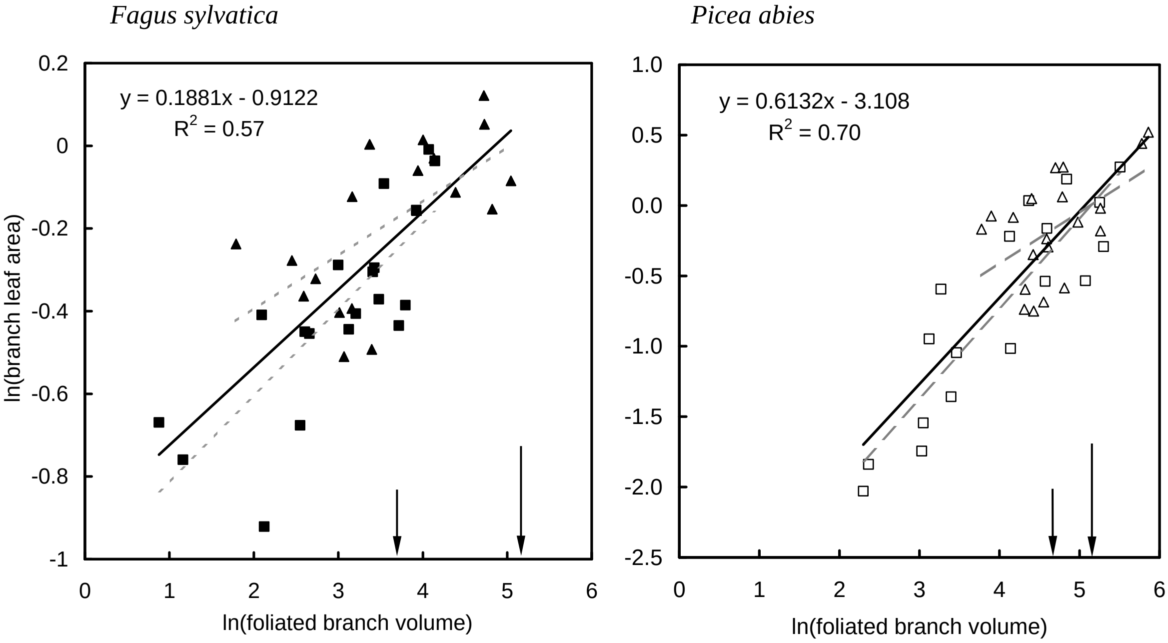


Figure 56: Logarithmically transformed data of the leaf area of a branch and its foliated volume, of beech (left) and spruce (right) for the years 1999 and 2000. The solid line denotes linear regression for all branches (n=20, p<0.001), hatched lines denote linear regressions for sun and shade foliage (n=10), the short arrows indicate the mean volume of the study branches, the long arrows indicates the volume where the regressions of spruce and beech intercept. Note difference in scaling of the ordinate.

Such a transformation was performed for the foliage area and volume of the study branches, which revealed strong linear relationships (Figure 56). Between 57 % in beech and 70 % in spruce of the variance of the measured foliage area in relation to the foliated volume can be explained by the size of the foliated volume. The allometric relationship to space was not different between sun and shade branches. The analyses also show that results can be similar for spruce and beech for a certain branch size where the regressions of the allometric relationships intercept (indicated with the long arrows in Figure 56), but are different based on the mean species-specific size of their branch volumes (see Table 18 and short arrows in Figure 56). It must be considered that the ontogeny of a branch attributes to the size. Branches in the lower crown had more time to develop than branches of the upper crown, so that the lower shade crown generally had larger foliated volumes in spruce branches and smaller foliated volumes in beech branches.

To compare differences within these datasets a transformation to a mutual size of foliated crown volume through a shift parallel to the regression line must be performed. This calculation was performed for the relationship of foliated volume and leaf area found in beech and spruce (Figure 56). The original data as measured in the study branches is expressed as leaf area density and given in Figure 57. The scaling of the data to the mean species specific volume (bold values, Table 18) resulted in lower variance, particularly in beech (Figure 57A). The changes of the efficiency of space sequestration in the vertical profile of the stand was therefore a function of specific leaf area. Apparently, the leaf area and foliated volume share a strong allometric relationship, which indicates conservative branching and leafing pattern. For young shaded and open grown trees of *Fraxinus americana* no difference in the bifurcation ratio – the number of axes of a given order to the number of axes of the next higher order - was found (Whitney 1976). The slope of the numbers of axes to the order of the axis is similar for various deciduous and coniferous species (Leopold 1971, Whitney 1976). Nevertheless allometric relationships can be changed through competition (Kozovits 2003), which was analysed as a change in slope of an allometric relationship. The allometric relationship of space-related results can also be the basis (1) to compare studies at the branch level within different environments, e.g. results from beech at the ‘Kranzberger Forst’ and from *Fagus sylvatica* in the ‘Fichtelgebirge’ (Fleck 2001), (2) to identify bias depending on the person conducting the measurement of the foliated volume, and (3) to empirically compare results of different geometrical models applied to approximate the same foliated space.

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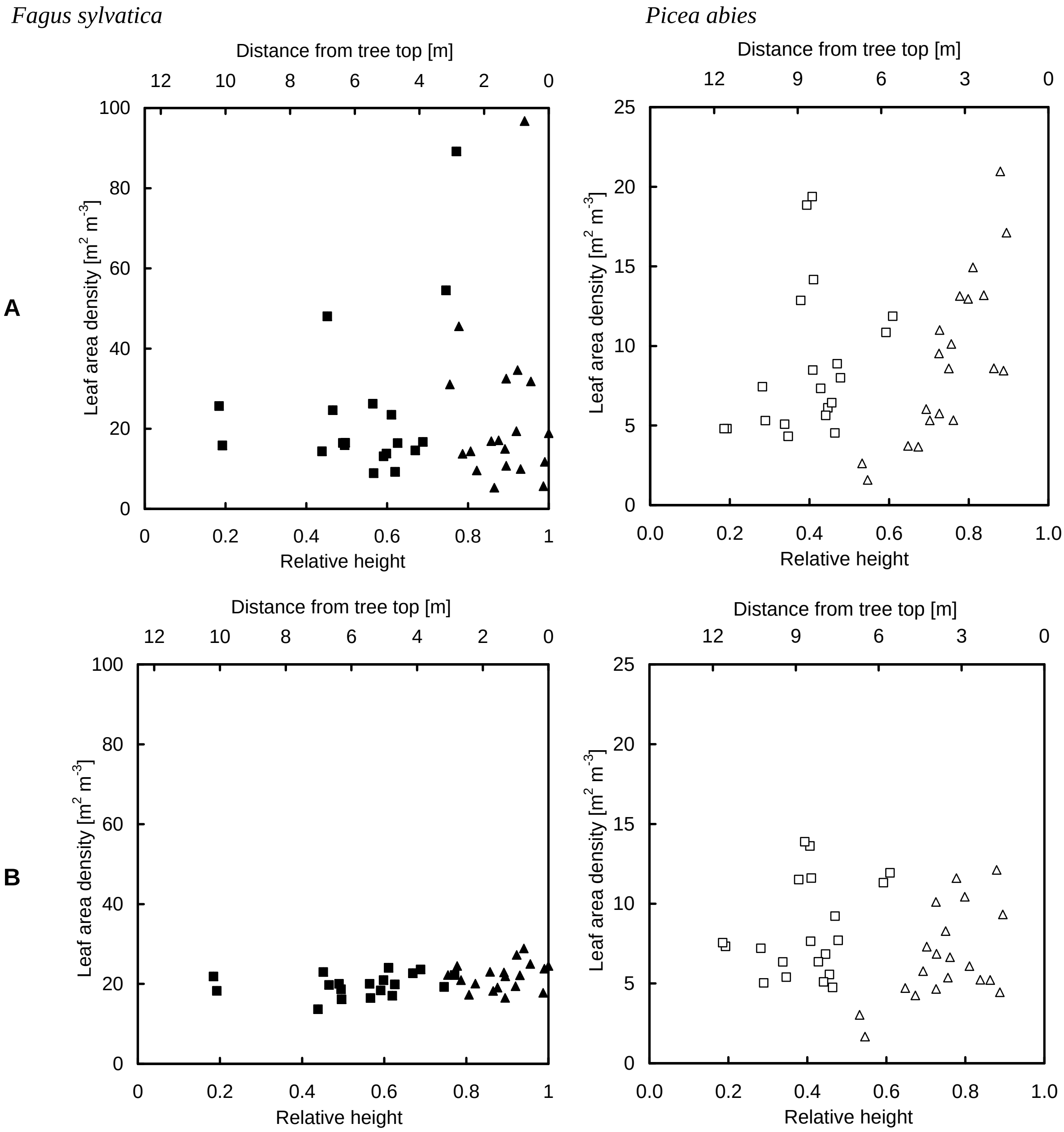

Figure 57: Leaf area densities within the foliated branch volume, in the vertical profile of the foliated crown (1= tree top, 0= crown base) in beech (left) and spruce (right), for the years 1999 and 2000. In (A) originally measured leaf area densities are presented, in (B) leaf area densities of study branches were scaled to their mean species-specific crown volume (cf. Figure 56, Table 18).

Table 18: Mean and standard deviation of the foliated volume [dm³] of spruce and beech branches during year 1999 and 2000, in the shade and sun crown. Bold numbers were used as base to scale allometric relationships (cf. Figure 57).

		spruce			*beech*		
		1999	*2000*	*1999 & 2000*	*1999*	*2000*	*1999 & 2000*
shade branch	***mean***	122	133	128	24	30	27
	sd	87	86	84	18	20	19
sun branch	***mean***	77	100	89	56	49	53
	sd	64	81	72	54	33	44
sun & shade branch mean		99	117	**108**	41	39	**40**
sun & shade branch sd		77	83	80	43	28	36

4.1.5 Space sequestration and social status of the crown

The variance of efficiencies of individual branches, as exemplified by the arrows in Figure 19, were argued to be dependent on the social status of the tree. A good indicator for the social status is the size of the tree (Kramer et al. 1988, Pretzsch 2001). The tree height is not as appropriate, as processes determined by the social status promote height equality among individuals in a canopy. However, diameter at breast height, whole crown biomass, projected crown area or crown volume are alternative measures of tree size.

The efficiency of space sequestration by the branch axes was divided by the relative height in the crown to account for the morphological variance that is explained by the height in the canopy (see hypothesis 5 and discussion 2.2.4.1, page 55). It is valid to divide by relative height as the tree heights were rather similar.

The results show that tree size does matter in beech (Figure 58). The larger the tree was the more extreme were the efficiencies of space sequestration of sun and shade branches, which were corrected for the trend of the efficiency with relative height in the crown. This was true, regardless whether stem diameter, whole tree biomass, projected crown area or whole crown volume were chosen as measures of tree size. In general about 30-40 % of the remaining variance was explained, when separate relationships for sun and shade branches were applied. No such relationship was found in spruce.

The results suggest that the length of the crown might be the cause, as a similar light regime in similar crown heights might be the answer to the converging of efficiencies in sun and shade branches in smaller trees. However, no relationship existed between the length of the crown and the efficiencies of space sequestration of sun and shade branches, which was corrected for the trend of the efficiency with relative height in the crown (Figure 59, $R^2<0.03$).

These findings are of relevance for the competitiveness of trees as they explain a change of whole plant branching pattern. Fleck (2003) reported that the branch angles of a suppressed *Fagus sylvatica* were steeper at the same height in the shade crown than branches of the dominant individual and had about the same angles in the upper crown layer. On the basis of average seasonal light availability branches of suppressed beech were consistently steeper inclined. This reflects a change in the search behaviour of suppressed and dominant trees, when foraging for light. Changes of the crown shape in response to competition have been stated. The predictions of crown dimensions of *Fraxinus excelsior* were satisfying, except for some trees that were suppressed for a long period (Cluzeau et al. 1994). These findings show how trees can respond to a generally lower resource availability with a change in whole tree branching pattern and inherently in competition for space.

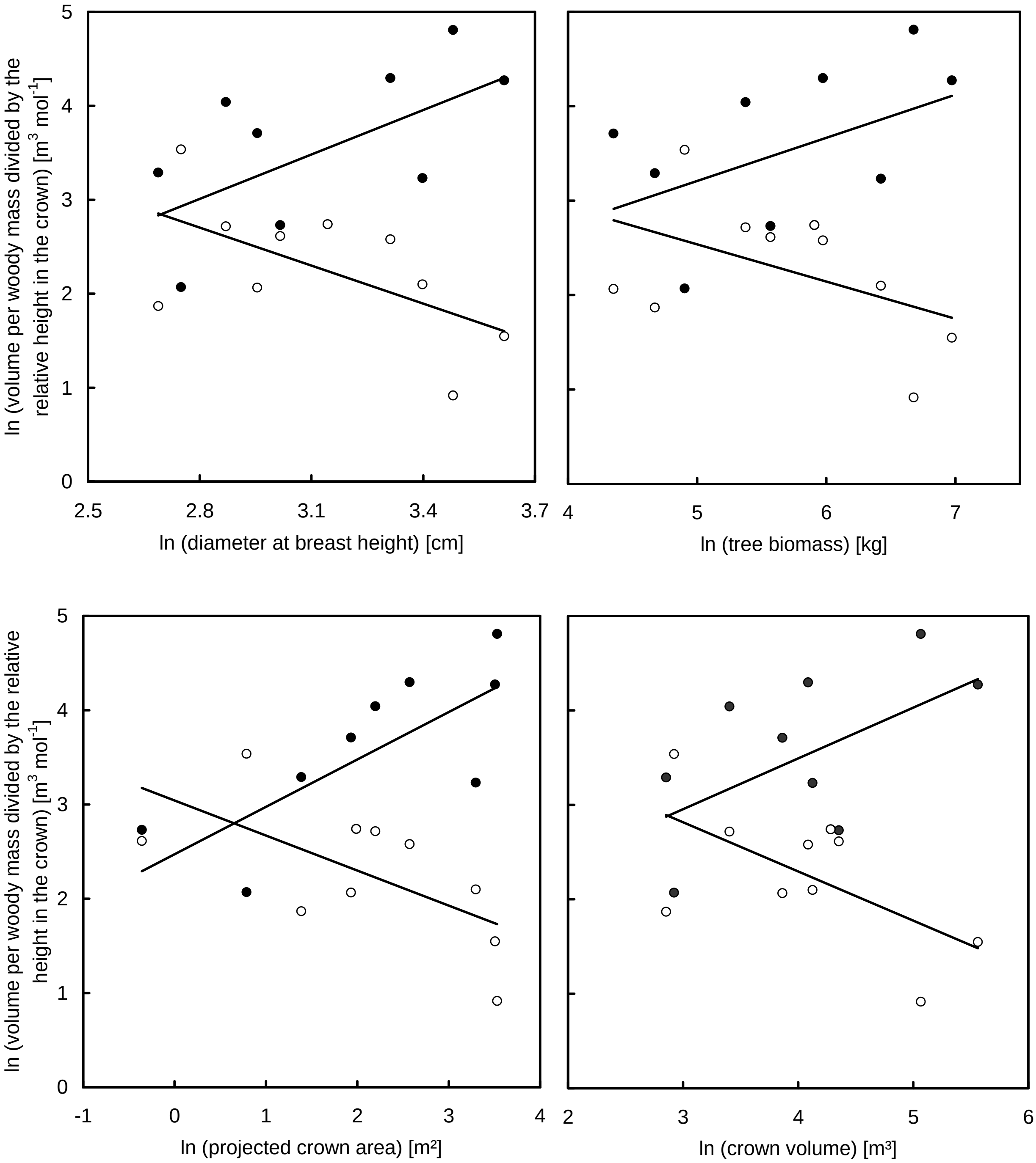

Figure 58: Allometric relationships in beech of the efficiency of space sequestration of branch axes (which was corrected for the trend of the efficiency with relative height in the crown; see Figure 13A, page 30) and measures of tree size: (A) Diameter at breast height, (B) whole tree biomass, (C) projected crown area, (D) crown volume. Open circles and closed circles denote sun and shade branches of beech respectively. Data for measures of tree size were elaborated by Dr. Rüdiger Grote of partner project C3.

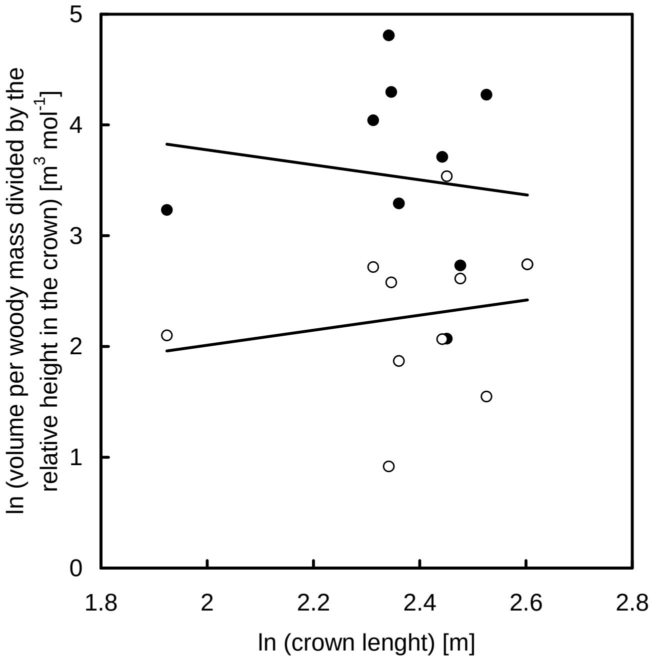

Figure 59: Allometric relationships in beech of the efficiency of space sequestration of branch axes (which was corrected for the trend with relative height in the crown; see Figure 13A, page 30) and the vertical crown length. Open circles and closed circles denote sun and shade branches of beech respectively. Data of the height of the crown base, were elaborated by Dr. Rüdiger Grote of partner project C3.

5 General discussion

“… for I know by experience, that a short and spreading tree, having ample room, will increase twice or three times as much, as a tall small headed tree.” (Marsham 1777)

5.1 *To what extent can space-related resource investments* versus *gains provide conclusions about tree competitiveness ?*

The presented study extends the analysis of resource-based efficiencies in the sequestration and exploitation of aboveground space from early-successional, light-demanding shrub and shrub-like tree species in a hedgerow (Küppers 1985, Schulze et al. 1986, Küppers 1994) and a chamber study with 2-3 year old trees (Kozovits 2003) to adult late-successional and shade-tolerant deciduous broadleaved and evergreen coniferous trees under closed forest canopy conditions. Spruce and beech represent the contrasting extremes of forest tree species in Central Europe in terms of growth pattern and foliage type with respect to the longevity and carbon, water and nutrient characteristics at the leaf level (Schulze 1982, Matyssek 1986, Stitt and Schulze 1994). Apparently, such leaf level characteristics (as well as differences in ontogenetic stage, Kozovits, 2003), can vanish when relating physiological performance to space, as space appears to become a resource itself and object of competition (Grabherr 1997). Hence, competition for resources intrinsically is competition for space, and by relating these two aspects of competitive acquisition to each other *via* the introduced resource cost/benefit-orientated efficiencies, a measure of competitiveness is provided.

One needs to caution that the presented analysis is a case study that is valid primarily for the status of competition at the time of observation, but incapable to extrapolate competitiveness across future decades (Connolly et al. 2001). The growth of trees in aggregated groups however is natural (Condit et al. 2000).

5.1.1 Perspectives at the foliage level

Mature beech and spruce predominantly appear to pursue contrasting strategies in space sequestration (Figure 13A-C, page 30). Given this finding, how may standing foliage mass *versus* annual investments in foliage or branch volume increment (cf. Figure 13A-C) be viewed in affecting competitiveness (Weldon and Slauson 1986)? Pretzsch (2003) demonstrated a productivity gradient as reflected in height growth of spruce and beech in mixed stands across Germany. This is consistent with the observation at the “Kranzberger Forst” in that spruce is presently overtopping beech. Nevertheless, beech can profit from disturbance relative to spruce as a consequence of a rapidly responding increment in crown volume, which is in line with our findings at the branch level (cf. Figure 13C). Compared to spruce, the sun branches of beech sequestered more canopy space per unit of occupied foliage mass, which is the prerequisite for initiating rapid crown volume increment next to gap formation (Pedersen and Howard 2004). On the one hand, rapid access to gaps between trees or space above the crown is decisive for competitive light interception (Monsi and Saeki

1953, Tappeiner and Cernusca 1998). Less investments are needed by beech for a standing foliage mass to achieve the same space-related carbon gain as spruce, which appears to support the ability to access space rapidly (Figure 13A & Figure 14, page 30f). On the other hand, the subsistence of beech foliage under deep shade allows immediate proficiency from an ameliorated light regime, as no carbon investments for growth is needed to gain access to more light in the gap. This can overcompensate the negative carbon balance of this foliage. Beech shade branches are in advantage to spruce shade branches as their light compensation point of the foliar carbon balance is at lower light intensity (Figure 27A, page 68). The efficiency of space-related investment into standing foliage mass, in combination with a rapid responsiveness in the annual increment of crown volume, can therefore determine competitiveness.

5.1.2 Perspectives including foliage and axes

Through integration of the space-related traits of the axes *and* of the foliage in the scope of this investigation it was revealed that the main difference between species remained to be the efficiency of space sequestration. Conclusions about the space sequestration based on foliage biomass only, need to re-viewed (cf. 5.1.1, page 118f). Instead of having lower carbon investments for space sequestration as based on the foliage C mass, sun branches of beech afforded a higher space-related C investment compared to spruce when the C mass of the axes was included. Beech compared to spruce allocated 1.5 (and 2.4) times more C into growth of foliage and axes (in sun and shade branches respectively). Spruce compared to beech had ‘saved’ a great proportion of C investments for the axes, through reduced construction cost due to a lower wood density (Figure 60A-C).

The assessment of space-related C mass of foliage *and* axes is in many cases redundant as the allometric relationship between the C mass of foliage and axes is rather conservative (see Figure 44, page 97, $R^2>0.58$). A comparison of species based solely on the foliage may only be performed if the species are rather similar in their allometric relationship of foliage and axes, which is not the case in spruce and beech. Possibly it may be sufficient to compare space-related traits of the foliage, if the species’ foliage type is similar (e.g. winter deciduous and broadleaved) and the growth form is similar (Küppers 1989), but this is an assumption that must be investigated thoroughly beforehand, else foliage *and* axes need to be included in the analysis of space sequestration.

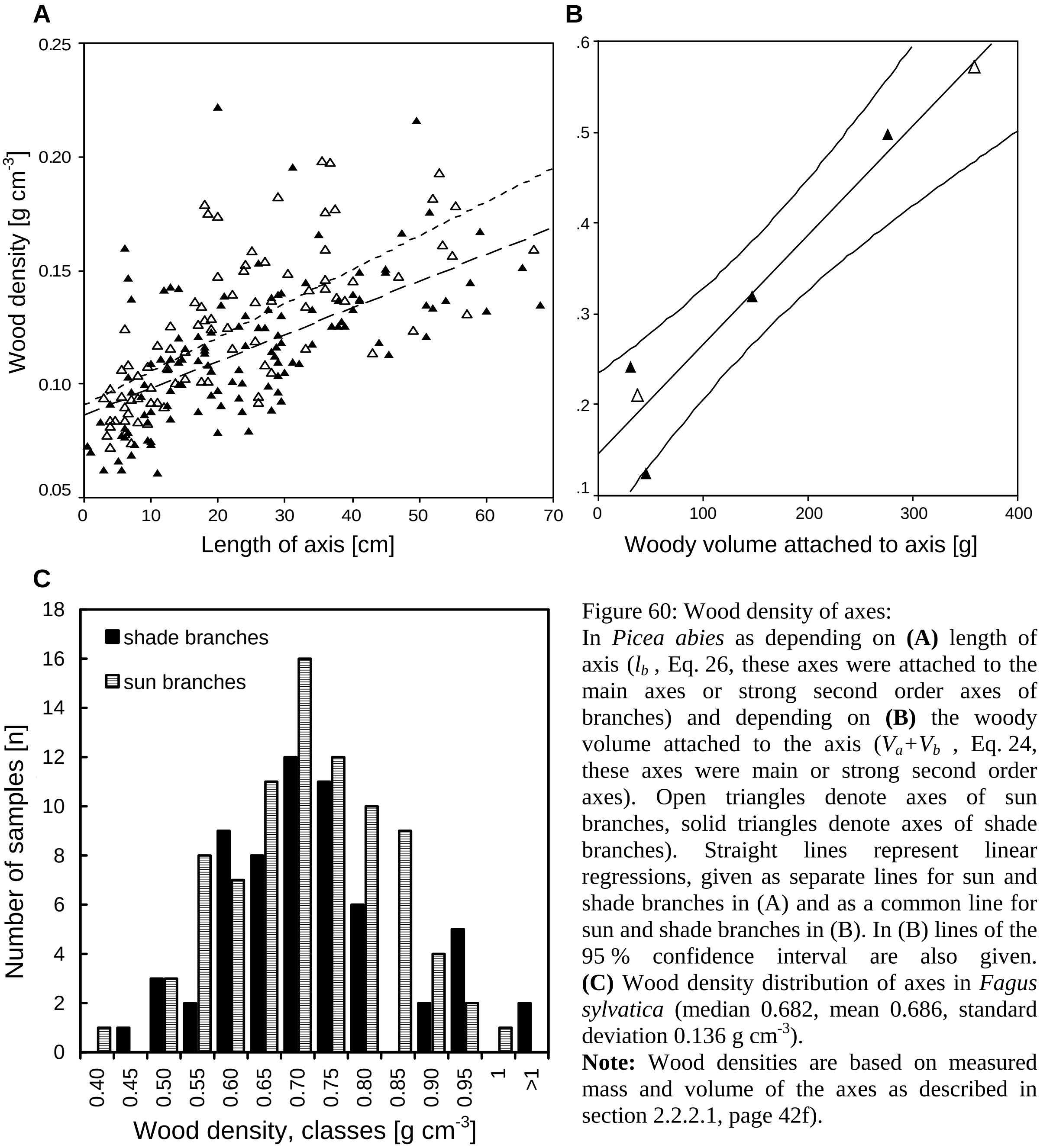

Figure 60: Wood density of axes:
In *Picea abies* as depending on **(A)** length of axis (l_b, Eq. 26, these axes were attached to the main axes or strong second order axes of branches) and depending on **(B)** the woody volume attached to the axis (V_a+V_b , Eq. 24, these axes were main or strong second order axes). Open triangles denote axes of sun branches, solid triangles denote axes of shade branches). Straight lines represent linear regressions, given as separate lines for sun and shade branches in (A) and as a common line for sun and shade branches in (B). In (B) lines of the 95 % confidence interval are also given. **(C)** Wood density distribution of axes in *Fagus sylvatica* (median 0.682, mean 0.686, standard deviation 0.136 g cm^{-3}).
Note: Wood densities are based on measured mass and volume of the axes as described in section 2.2.2.1, page 42f).

Shade branches seemed to be similar in terms of space-related C investment (Figure 23, page 62). However, spruce compared to beech presumably saved carbon investments in shade branches by developing a longer crown than beech, i.e. lower crown base at similar tree height (cf. Figure 12A, page 29). Having branches at low stem height is an economic aspect as thereby C investments are saved for shade branches of spruce: A greater height of the branch insertion into the stem inherently increases constructional and respiratory costs of branches, as more stabilizing stem and root tissue is needed to support the branch (Sibly and Vincent 1997), to stabilize the stem and root system (see calculations by Witowski 1997) and to ensure sufficient transport capacity of water, nutrients and carbon metabolites

(Shinozaki et al. 1964). If the most of the foliage was situated at the top of the tree as in beech, then larger supportive costs had to be taken into account in spruce.

In contrast to the closed crown of beech, the ‘one-dimensional’ growth pattern of spruce branches provided gaps in the crown. This enhanced light transmittance down to the lower crown, which enabled shade branches of spruce to persist in a lower height than beech. As gaps in the crown are important to save C investments in spruce shade branches, it is necessary that these gaps remain unoccupied. Consequently, relative volume increment of sun branches had to be lower in spruce compared to beech, to avoid self-shading.

However, these low shade branches bear the risk of being shaded by neighbouring plants, which may deprive the economy of a low-investment growth strategy. This seems to be a minor problem in intraspecific competition as the surrounding spruce crowns also provide gaps for light to reach lower layers in sufficient quantity for the branches to survive. This may be different in a more structured stand for the subordinate individuals, as it is reported that the increased canopy transmittance in the upper part of the canopy of *Picea abies* is rather limited compared to deeper layers (Cescatti 1998). When spruce competes with trees that form a closed canopy, e.g. beech of this study (Figure 12A, page 29), then light transmittance can be more restricted as most of then light in the beech crown was intercepted within the first meters of the upper crown (Figure 12B). Additionally *Fagus sylvatica* can close gaps rapidly in the canopy (Pretzsch 2003) and is able to develop an extremely wide and spreading crown (Scott 2003). If the whole spruce tree is to remain competitive, then vertical growth as a shade avoidance strategy should be rather important (Weldon and Slauson 1986) to this species. This assumption is backed by low space-related investments of spruce compared to beech (Figure 19, page 50), which allow a high C allocation (fraction of C export in relation to C gain in Figure 26, page 66) to the C demanding processes of elongation and radial growth of the stem and the roots. But are the gaps within crowns of spruce endangered to become occupied or shaded by neighbours ? This may depend on tree size and wind exposition, which promote tree swaying. Losses of invested carbon through the physical interaction of swaying tree crowns showed that crowns did not mingle in this stand (lower right / Figure 35, page 86) and that spruce and beech lost about the same crown space through crown abrasion. An important advantage of the growth form of spruce is that a damage to branches will not have a direct impact on height growth of spruce, whereas the breaking of sun branches of beech is a direct reduction of gained height of a competing neighbour, which can decrease competition for favourable units of space in adjacent crowns in favour of spruce. In spite of the fact that beech can access and close gaps more rapidly than spruce, spruce seems to have an advantage in space sequestration within closed canopies of adult trees when competing with neighbours that rely on branch growth to gain height. However, large trees and a co-dominant or dominant position is necessary for this mechanism to apply. Subordinate individuals are more dependent on their C economy due to a more light-limited environment, where the low light compensation point of the carbon balance of beech branches gains importance and spruce is less competitive.

In summary, above examples of competitive interaction can be quantitatively described by the use of space-related cost-benefit analysis as an ecological tool that integrates structure and physiology. Apparently spruce compared to beech has developed a more economic growth form in terms of lower investments for branches, at similar C gain per unit of crown volume. This seems to allow greater height growth of spruce and may additionally be supported through crown abrasion. Benefit of beech through rapid increment of crown volume in competition with neighbours appears to depend on gap size. The strong competitiveness of spruce is contrary to the hypothesis that a response to a changed resource availability (cf. Figure 1) increases competitiveness (Goldberg 1996, Avalos and Mulkey 1999), as spruce was a weak responder compared to beech to a change in light environment and to changes in the social status of a tree.

5.2 Outlook and concluding remarks

In general, space-related efficiencies along with the associated resource turnover have the power to address competitiveness quantitatively and *do* offer the capacity of unravelling competitiveness in functional terms (cf. Grote and Reiter 2004), which allows comparison of contrasting species and promotes understanding of plant-plant interaction (Tilman 1988, Goldberg 1990, Cannell and Grace 1993, Schwinning 1996, Connolly et al. 2001). Efficiencies support the interpretation of how environmental condition can bring benefit to a species in competitive interaction. It is encouraged to include space-related resource gains and investments in competition studies as space is object of competitive interactions and appears to be a resource itself. Many other approaches that quantify competition or competitiveness have used one- or two-dimensional, either vertical or horizontal measures of competitive performance (e.g. Anten and Hirose 2001, Falster and Westoby 2003, Weigelt and Jolliffe 2003), although the three-dimensional integration of both measures to a volume suggests itself.

Here, the focus was on the aboveground use of the resource space by woody plants. Approaches have been proposed in this study that allow comparison among space-related investigations. The transfer and the expansion of space-related analysis to studies of e.g. responses in different interactions between herbaceous and woody plants, belowground interactions or invading neophytes, is very promising, as new insights and understanding of the processes can be expected that determine competitiveness of species and individual plants.

Annex

The interdisciplinary research program (Sonderforschungsbereich 607) has established a database, that may be accessed from the world wide web via the link:

http://ibb.gsf.de/~sfb607/

All relevant data of this thesis is provided at that address. Unpublished data may not have public access, but can be transferred through consultation of the authors.
Please consider ‘terms of use’ and ‘agreements’ of the database.

A Distribution of Specific Leaf Area & Specific Needle Length

A.1 Introduction

Specific leaf area (SLA) scales with light conditions in evergreen and deciduous, broadleaved and coniferous tree species in boreal, temperate, Mediterranean and tropical climates. SLA is therefore well suited to characterize and scale the physiological and morphological properties of the foliage within branches, which experience gradually changing light conditions from distal to proximal positions (cf. Figure 9, page 11, scheme of study branch). Light, and therefore also SLA, scales with height in the canopy, which allows scaling of SLA with height (Monsi and Saeki 1953, Matyssek 1986, Oren et al. 1986, Niinemets and Kull 1995, Morales et al. 1996, Yokozawa et al. 1996, Cermak 1998, Niinemets et al. 1999, Carswell et al. 2000, Kazda et al. 2000, Landhäusser and Lieffers 2001, Meir et al. 2002). The relation of SLA to height was shown in harvested trees just outside the intensive investigation plot (in collaboration with partner project C3, Grote and Reiter 2004).

A.2 Material and Methods

SLA is expressed as the projected foliage area per foliar dry mass [m^2 kg^{-1}]. The foliage area was scanned at (300 dpi, black and white drawing, "S/W 4x geschärft", brightness 125, Scanjet 3c, Hewlett Packard, Camas, Wash., USA) and the projected leaf area calculated (DT-Scan, Delta-T devices, Burwell, Cambridge, UK).

A.3 Results and Discussion

A.3.1 *Fagus sylvatica*

The width to length ratio of the lamina in the beech study trees was the same for the foliage of sun and shade crown, as was the size of the leaves (Figure 63). However, there was a tendency for small leaves to be narrow and for large leaves to be wide (Figure 63). Although distinct sun and shade branches had been chosen, the ratio of leaf area to biomass (=SLA) of sun branches had a broad range (Figure 61). The SLA of the sun branches can even be close to that of shade branches, as SLA scales linearly within the light gradient of branches (Figure 62, Eq. 9, page 22) due to the gradually shading of the proximal foliage. In two harvested trees, the greatest difference in mean SLA between proximal and distal branch position was found in sun branches (Figure 64A), but the difference in SLA declined in lower branch positions.

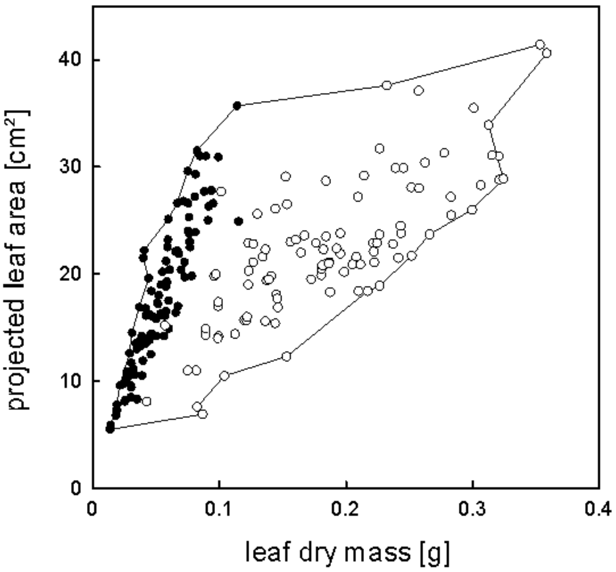

Figure 61: Relationship between the projected leaf area and leaf mass of beech leaves. Open symbols and solid symbols represent sun leaves (n=100) and shade leaves (n=100) respectively. Lines envelop datasets.

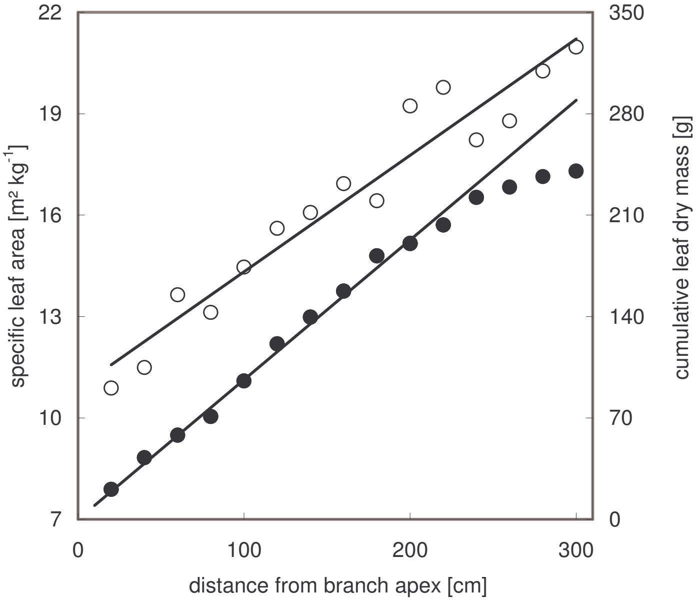

Figure 62: Development of specific leaf area (open circles) and cumulative leaf mass (solid circles) in dependence of the distance from the branch apex. Solid lines represent linear regression (distance from apex < 2 m, $R^2>0.93$, harvested beech tree 1000, branch 3/1, sun crown, year 1999 cooperation with partner project C3).

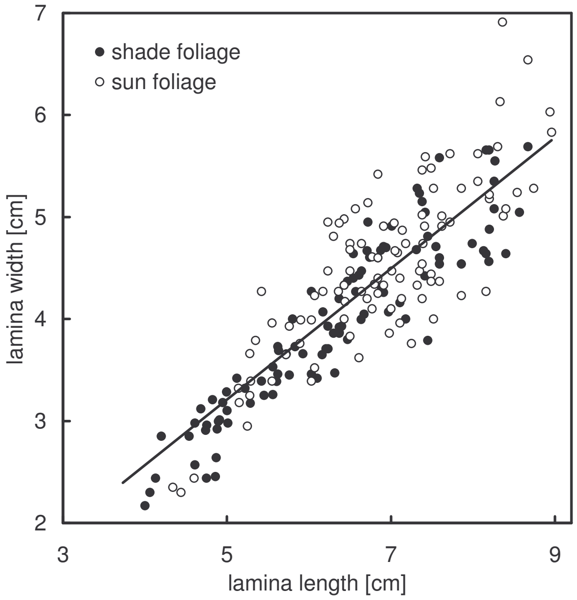

Figure 63: Relation of lamina width to lamina length in sun and shade leaves of beech in August 1999 (width=0.642*length, n=200, R^2=78, p<0.001)

The slope of the increase of specific leaf area of a branch with distance from the branch apex (Figure 64B) and height (Figure 64C) from distal to proximal positions, depended on the crown position of the branch and was highest in the sun branches, but was never zero or negative in the shade branches. As no similar trend from distal to proximal positions was found for light in shade branches (data not shown), there seems to be an ontogenetic effect.

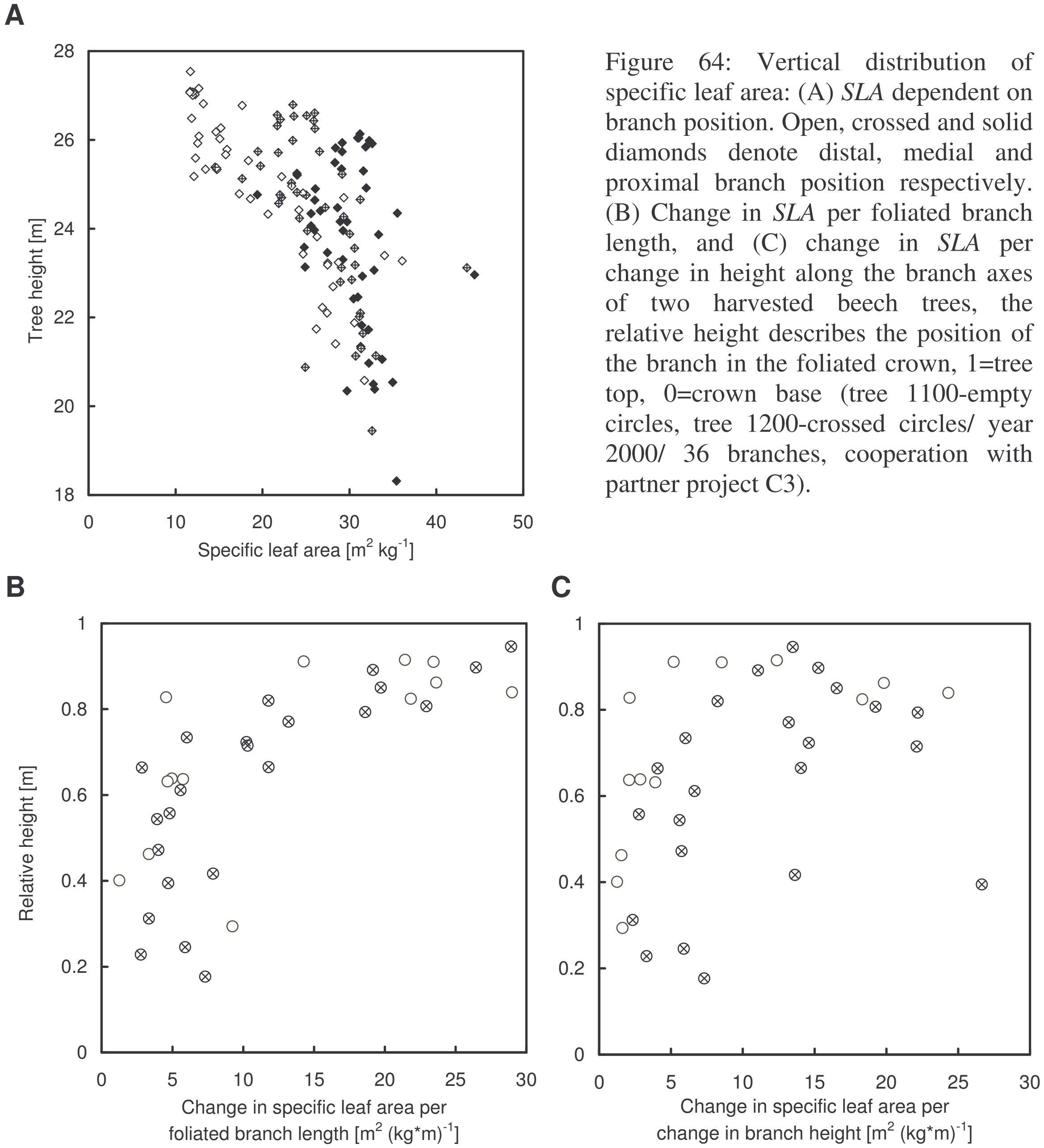

Figure 64: Vertical distribution of specific leaf area: (A) *SLA* dependent on branch position. Open, crossed and solid diamonds denote distal, medial and proximal branch position respectively. (B) Change in *SLA* per foliated branch length, and (C) change in *SLA* per change in height along the branch axes of two harvested beech trees, the relative height describes the position of the branch in the foliated crown, 1=tree top, 0=crown base (tree 1100-empty circles, tree 1200-crossed circles/ year 2000/ 36 branches, cooperation with partner project C3).

The range and absolute values of *SLA* found in the canopy of harvested and study trees in the ‘Kranzberger Forst’ was similar compared to results of other investigations: similar absolute range, 3-4-fold between the canopy top and base, in *Fagus sylvatica* (Fleck 2001, Fleck 2003), in *Fagus japonica* (Kimura et al. 1998), in *Fagus orientalis* (Fleck 2003) and in

Fagus crenata (Yasumura et al. 2002). Therefore *SLA* is a rather conservative and predictable measure. *SLA* of exceptionally shaded foliage close to the stem base in beech was 5.5-fold higher than minimum, which is similar to reports on *Fagus sylvatica* by Gansert and Sprick (1998).

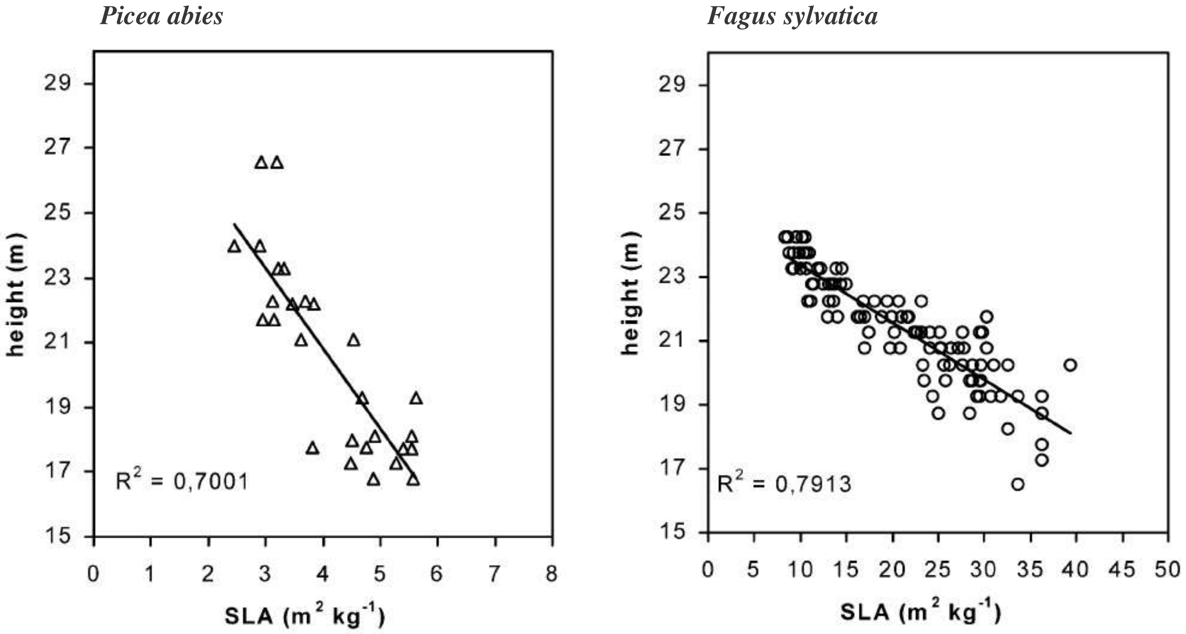

Figure 65: Measured vertical distribution of the specific leaf area (*SLA*) of previous year shoots of 7 spruces (triangles) and 11 beeches (circles) within the experimental plot on the study site, published in Grote and Reiter (2004).

In *Quercus robur* (Cermak 1998), the range of *SLA* was 3-fold; the sigmoidal trend in the vertical profile indicates that morphological extremes of *SLA* were reached in the uppermost sun crown and the lowermost shade crown. In this study the vertical distribution of *SLA* of beech was also slightly sigmoidal (Figure 65). Nevertheless, high water stress is expected to decrease *SLA* in deciduous species (*Fagus sylvatica, Populus tremula Fraxinus excelsior Tilia cordata Corylus avellana*) through increasing lignification (Niinemets 1999). In *Fagus sylvatica*, the tannins content increases in the epidermal cells (vacuoles and walls) in xeric conditions and *SLA* is decreased (Grossoni et al. 1998). However, only in the evergreen *Quercus coccifera* and *Quercus ilex* an decrease in *SLA* along a rainfall gradient was found, but not in the deciduous *Quercus faginea* (Castro-Diez et al. 1997). The minimum *SLA* of from *Quercus robur* growing in the dry climate of South Africa (van Rensburg et al. 1997) was about the same as in *Quercus robur* from the floodplain forest in the Czech Republic (Cermak 1998). Therefore, *SLA* of adult beech is an outstanding scaling tool to compare measurements within the study site, that were not performed on the identical foliage (e.g. nutrient analysis by partner project B10, pigments by A4, phenolics by A1, gas exchange this study). In addition *SLA* is a tool to compare and link measured with modelled data (Grote and Reiter 2004, partner project C3).

A.3.2 Picea abies

The same dependencies of *SLA,* and also of specific needle length (*SNL*), as in beech were found for spruce. However, more than the vertical height in the crown and the branch position, needle age was important. The decrease of *SLA* and *SNL* with needle age is shown for current and previous year needle samples on study trees close to study branches (Figure 66), and for destructive sampling from study tree 374 (Figure 67 & Figure 68).

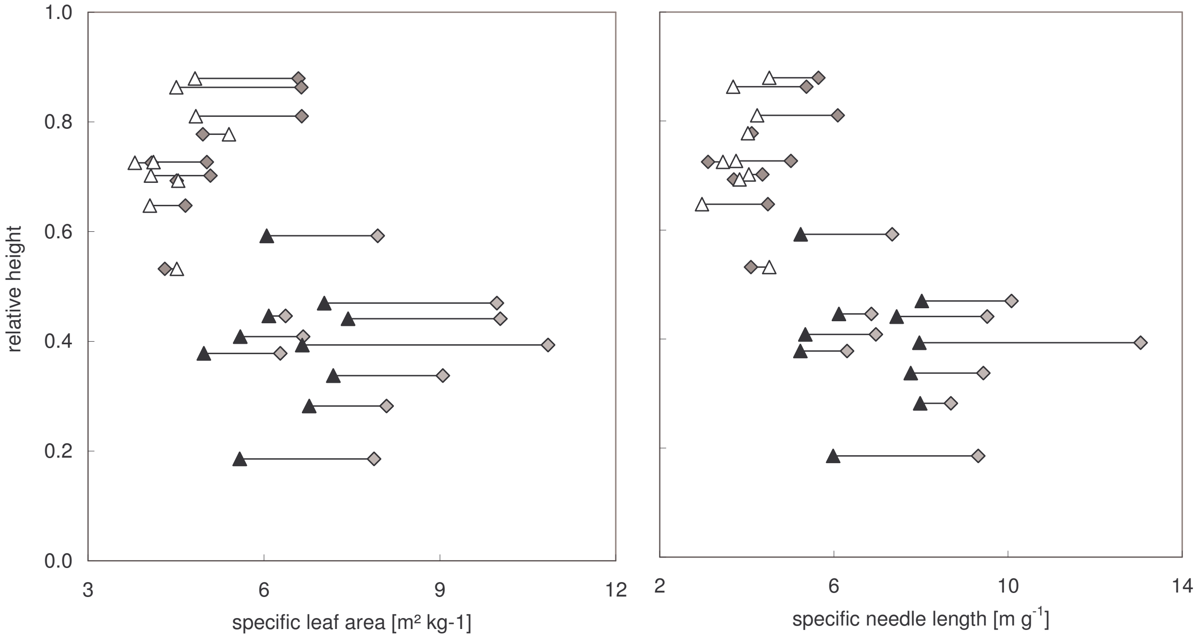

Figure 66: Specific projected leaf area (left figure) and specific needle length (right figure) of spruce (August 2000) in the vertical profile of the foliated crown (40 shoots from 20 branches and 10 trees). Diamonds denote current year shoots (grown 2000) and triangles denote previous year shoots (grown 1999). Open triangles represent samples from sun and solid triangles from shade branches. Shoots from the same branch are connected with lines.

The age dependence was non-linear and approximated logarithmically (see Eq. 5 & Eq. 6, page 21). Measured agreed with modelled data of *SLA* and *SNL* parameterised for a shade and sun branch. However, if the branch position was not an available input, then a underestimation occurred for half of the samples (Figure 69). The results of the model is exemplified for distal and proximal branch positions in the vertical profile of the stand (*SLA* / Figure 70*, SNL* / Figure 71). *SLA* and *SNL* of all needle age classes increase with age. *SLA* and *SNL* increase less rapidly with increasing age, and are limited to a minimum value (2.8 m^2 kg^{-1} and 2.8 m g^{-1}, cf. Figure 68). The foliage in the lower canopy and closer to the stem, was developed from higher *SLA* and *SNL* than in the upper crown and did not reach the minimum value. This is a steady and linear shade adaptation to linearly decreasing light availability (cf. Figure 12, page 29) and is also reflected in the conversion factor from projected to total leaf surface area (see Annex B, Figure 78, Eq. 47).

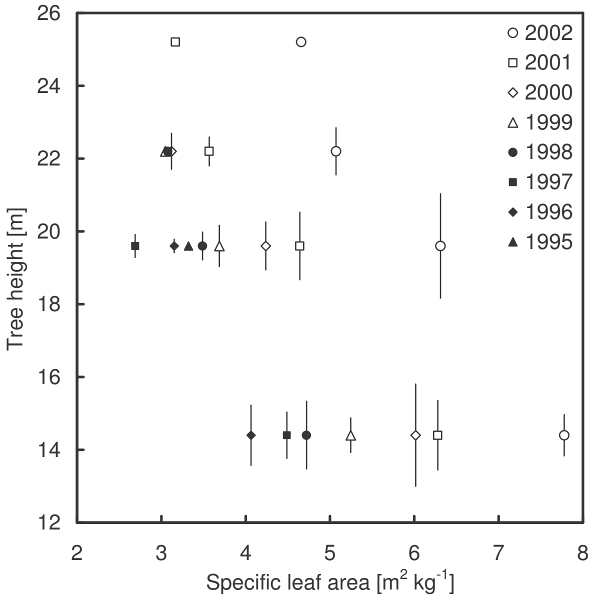

Figure 67: Measured specific leaf area of current year needle age class (=1) to age class 8 (see legend) in the vertical profile of spruce tree 374 (4 branches, 56 shoots on 2° order axes, July 2002). NOTE: Error bars, although in parallel to tree height, denote standard deviation of the specific leaf area of each age class. If no error bar is present, then only one sample was processed.

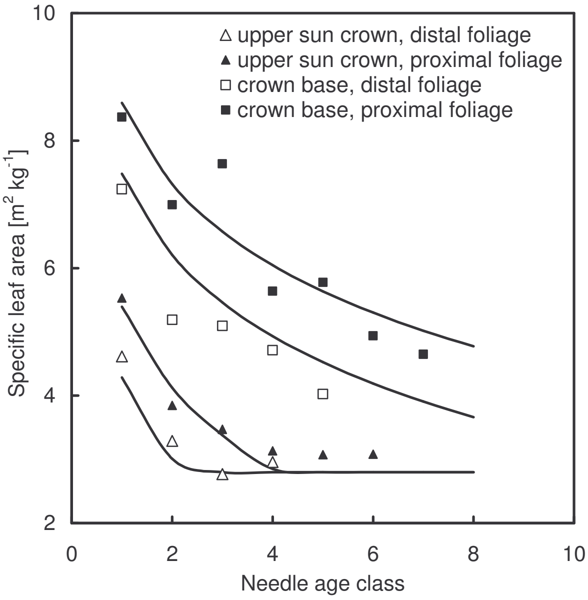

Figure 68: Measured and modelled specific leaf area of the current year needle age class (=1) to age class 8 of spruce tree 374. An example for four distal and proximal branch positions in branches from the upper sun crown and from the crown base (see legend). Lines represent a common function dependent on needle age class, vertical position in the crown, horizontal position on the branch and a constant derived from non linear regression (Eq. 6, page 21).

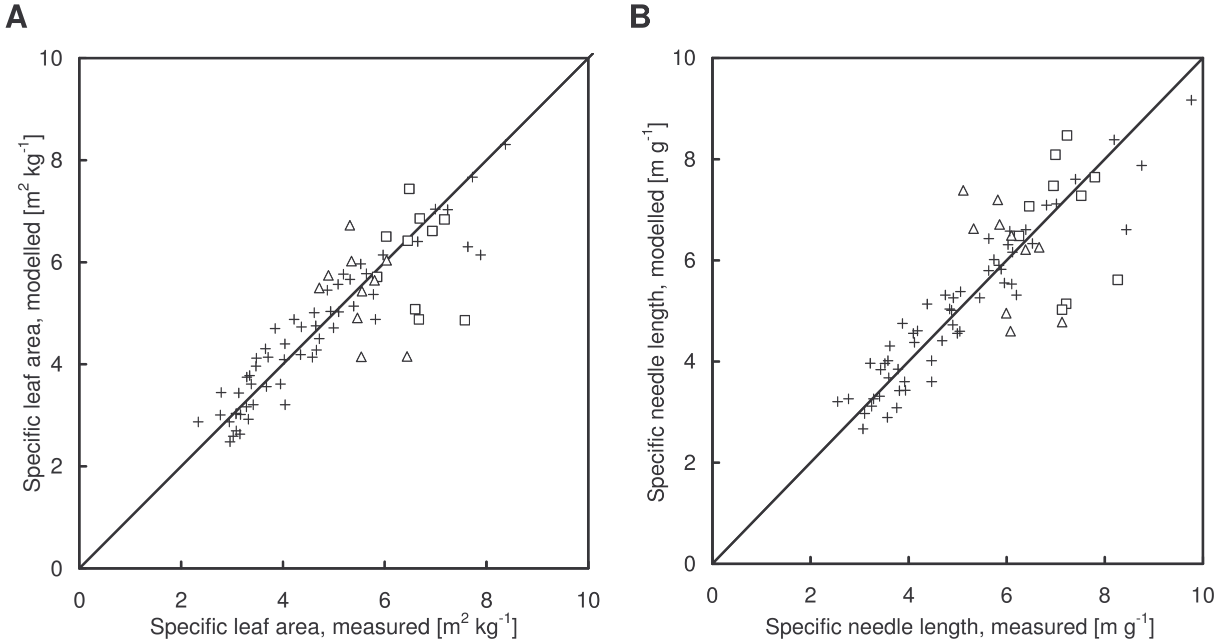

Figure 69: Measured and modelled (A) specific leaf area and (B) specific needle length of all needle age classes along branches of different heights in spruce tree 374 (+). Vertical position of the branch in the crown, horizontal position of the sample on the main axis, needle age class and a constant were included in the model (Eq. 5 & 6, page 21). For nutrient analysis samples from sun (triangles) and shade branches (squares) modelled without respect to the horizontal position of the sample on the branch.

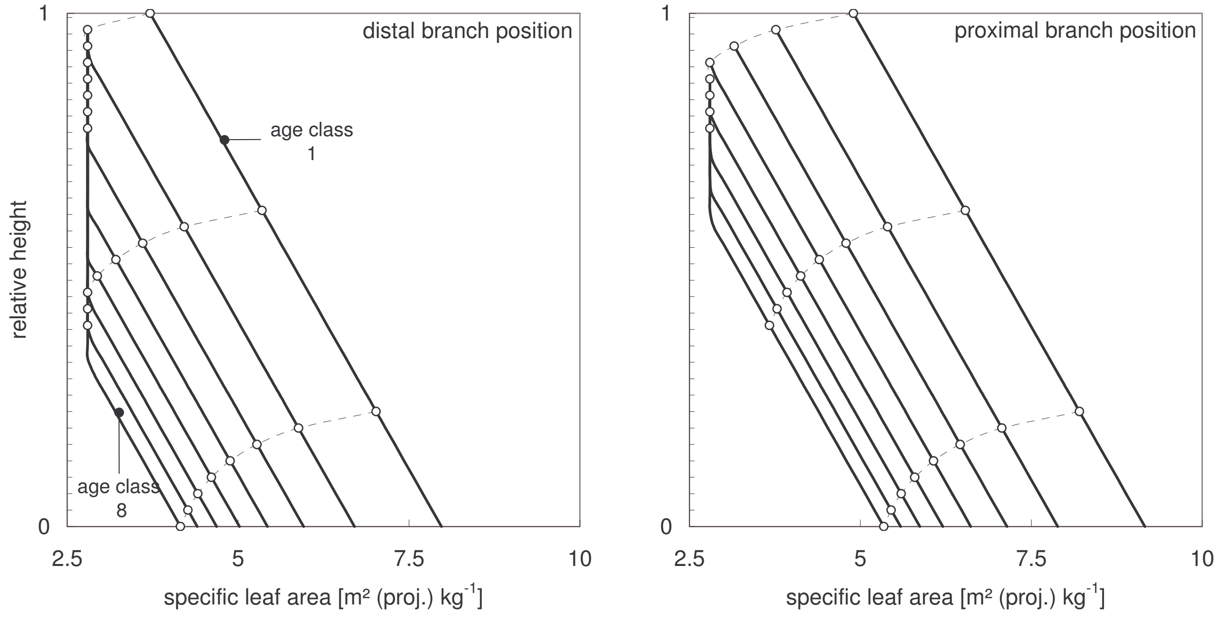

Figure 70: Simulated specific leaf area ($m^2\ kg^{-1}$, solid lines, Eq. 6) in the vertical profile of spruce (tree apex=1, crown base=0), tick marks of the height axis denote the mean annual height increment of the study trees (0.45 m). Eight age classes are shown, starting with the current year needle age class (age class 1) up to needle age class 8 in time steps of one year. The left figure represents a shoot in a distal position of the foliated branch axis, in the right figure, a shoot in a proximal branch position presented. In three different heights of the crown examples of the development of the specific leaf area of a individual shoots in time are presented (dotted line with open circles), based on the simplification that the foliated stem length remains constant.

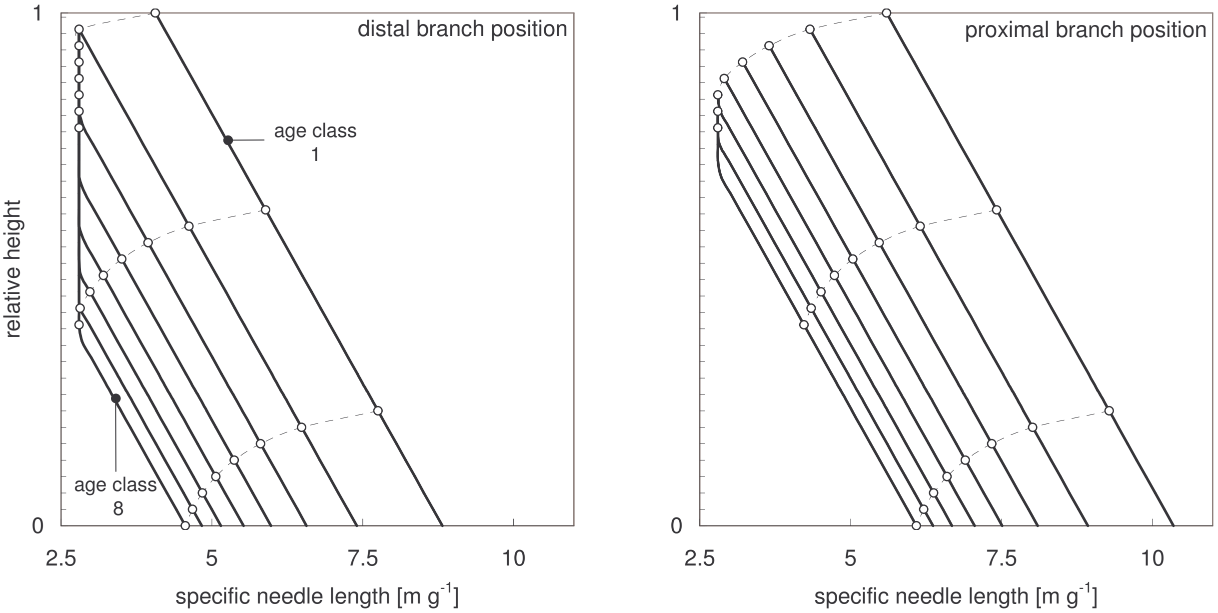

Figure 71: Simulated specific needle length (m g^{-1}, solid lines, Eq. 5) in the vertical profile of spruce (tree apex=1, crown base=1), tick marks of the height axis denote the mean annual height increment of the study trees (0.45 m). Eight age classes are shown, starting with the current year needle age class (age class 1) up to needle age class 8 in time steps of one year. The left figure represents a shoot in a distal position of the foliated branch axis, in the right figure, a shoot in a proximal branch position presented. In three different heights of the crown examples of the development of the specific needle length of a individual shoots in time are presented (dotted line with open circles), based on the simplification that the foliated stem length remains constant.

The same results on SLA as in spruce of this study are reflected in other detailed studies on *Picea abies* (Hager and Sterba 1984, Pokorný and Marek 2000, see Figure 72). The largest deviation from the mean was found in the rapidly developing current year shoots. Foliage from lower crown layers has higher SLA, and does not reach the minimum SLA of the sun foliage. Whereas the minimum SLA was the same as in this study, the highest SLA values were higher than in this study, which indicates that their stands might be more closed and having lower light availability at the crown base.

The regression model for SLA of this study was parameterised through destructive sampling of two study branches during the growing season. The nutrient samples have been taken at the end of the growing season. SLA of current year shoots of conifers, rapidly decreases in the annual course (cf. *Pinus contorta*, started with SLA of 6 m^2 kg^{-1} in July and reached 3.5 m^2 kg^{-1} in November, Gower et al. 1989). Therefore the agreement of the measured and modelled SLA of the nutrient samples (see Figure 69), should be better than depicted.

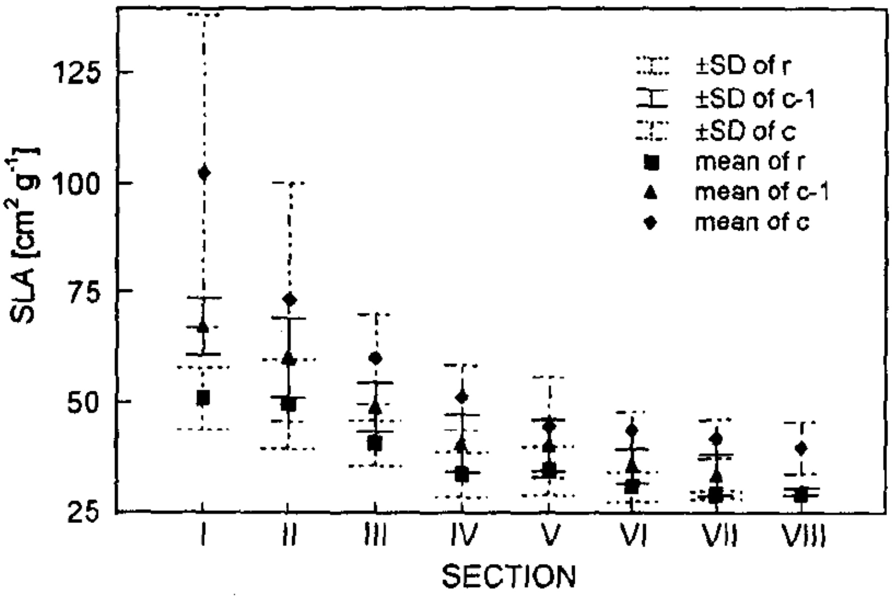

Figure 72: Specific leaf area of current year (c), previous year (c-1) and older needles (r) in 20 year old spruce, in the vertical profile of the stand. Sections represent 1 m height increments from the base (I) to the apex (VIII) of 11 trees (From Pokorny and Marek 2000).

B Conversion factor of projected to total leaf area in Picea abies

B.1 Introduction

In contrast to most broad leaves, the thickness and efficient absorption of photosynthetically active radiation by conifer needles cause them to act functionally as three dimensional, optical ‘black’ surfaces with respect to photosynthesis (Stenberg et al. 1995). Further, Stenberg et al. argue, needles should be treated as unifacial and the assimilating leaf area should be defined based on total surface area rather than on the basis of a one-sided area, because the photon flux density incident on one side of the needle is negligibly transmitted to the other side. This may hold for diffuse radiation, during overcast skies or in the lower canopy, where direct sunlight usually is scarce, whereas in direct radiation the one-sided needle area also is justified (cf. Küppers 1993, Küppers et al. 1997, Pearcy et al. 1997, Tognetti et al. 1997, Watling et al. 1997, Kirschbaum et al. 1998). The transmission of photon flux densities by broad leaves in the shade crown is also rather low under ambient light conditions (Hagemeier 2002), but a total surface area for these leaves was not proposed. The discussion, which basis to use (projected, one sided, two-sided surface area or the surface area with stomata only) for gas exchange rates continues, and currently different inconsistent units in ecological studies are being used, e.g. basis for stomatal conductance of *Fagus sylvatica* and *Picea abies*: two-sided leaf & needle area by Emberson et al. (2000a), and Emberson et al. (2000b), but projected leaf & needle area by Karlsson et al. (2004).

The dorsiventral leaves of beech are hypostomatous, whereas the stomata of the ‘equifacial’ needles of spruce (Figure 79, page 141) are aligned in the convex (Figure 74 & Figure 75) part of the needle , which approximately make up a maximum of one third of the surface area. This gives reason to choose a separate basis of needle area in terms of gas exchange and light interception, but a definite base for the carbon relation is then no longer given.

Nevertheless information on the conversion factor is needed, in order to correctly scale leaf area of spruce in the vertical profile of the stand (see C.2). In beech projected leaf area was used in this study, though the surface of the lamina is not even (cf. Hendrich 2000, Fleck 2003).

B.2 Material and Methods

Whole needle area for the PSN6 model (see chapter PSN6 model) was the product of the projected needle area with a factor of 2.6 (Oren et al. 1986).

Further investigations on total surface area of needles were conducted sensu Perterer and Körner 1990. We cut three cross sections of 81 needles of 14 shoots from spruce 374 in three different heights (Figure 73, 18.5 m, 21.5 m and 24 m) accordingly. Samples were taken of needles of previous year shoots in proximal and distal positions on a branch. We sampled a radial profile within the sun crown, and a vertical profile north of the stem, where we expected great variance in the light climate due to a strong shift from in proportion of direct and diffuse radiation.

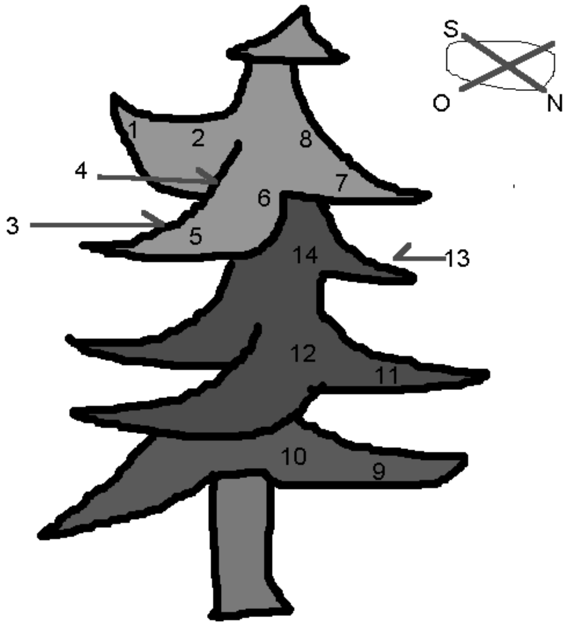

Figure 73: Sampling positions in tree 374 for the analysis of the conversion factor from projected to total needle surface area. Positions 1 to 8 represent circular profile at proximal and distal positions on the branch, positions 7 to 14 represent a vertical profile north of the stem at proximal and distal positions on the branch, even numbers represent proximal and uneven numbers distal positions on a branch (Figure by Alexander König).

Applying the same model for the needle body (Figure 74), we improved the calculation of the cross sectional area, as beginning an end of the lengths b_x and d_x for the original calculations (Eq. 41, Eq. 42, Eq. 43, Eq. 44) were difficult to define and therefore difficult to be measured precisely. First we measured the needle cross section like Perterer and Körner 1990 with a microscope (Dialux 788727, Ernst Leitz Gmbh, Wetzlar, Germany; 10 x 40 (Periplan NF x 170/ 0.17 40/0.65) and a scale. We drew the exact outline of the cross section, the lengths b_x and d_x, and a scale of 1 mm on paper (~1:70) with help of a projection. Lengths b_x and d_x were measured with help of the scale. The outline of the cross section was scanned in analogy to the specific leaf area samples (see A.2) and the interior filled black (Microsoft ® Paint, Windows 98, Microsoft Corporation, Redmond, WA, USA). This image was processed (DT-Scan, Delta-T-Devices, Cambridge, UK) to retrieve the outline and the area of the cross section and the length of the scale. Exact values in metric units were calculated proportional conversion of scale values.

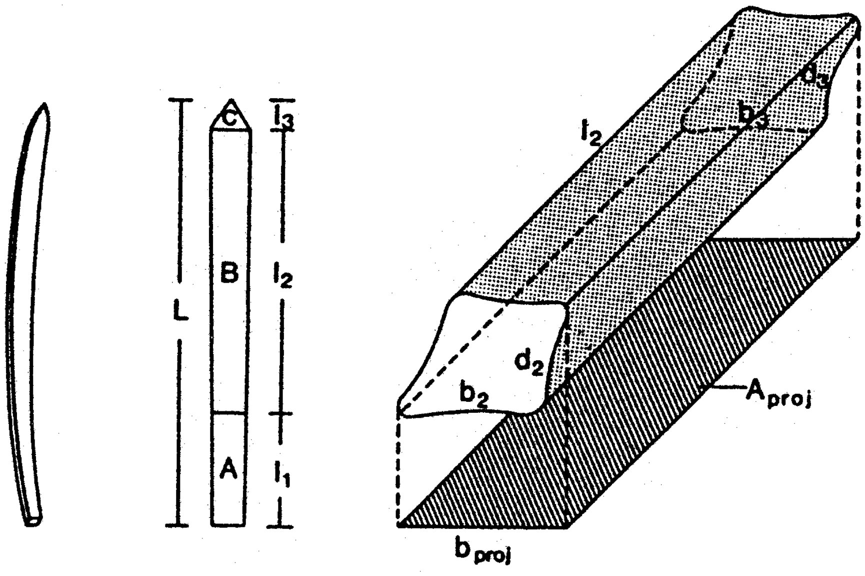

Figure 74: Model of a spruce (Picea abies) needle for the geometrical determination of total leaf area. For symbols see Eq. 41 to Eq. 44 and Figure 75. (From Perterer and Körner 1990.)

$$A = A_A + A_B + A_C$$ Eq. 41

$$A_A = (b_1 + b_2) \cdot l_1 + (d_1 + d_2) \cdot l_1$$ Eq. 42

$$A_B = (b_2 + b_3) \cdot l_2 + (d_2 + d_3) \cdot l_2$$ Eq. 43

$$A_C = b_3 \cdot \sqrt{\frac{d_3^{\ 2}}{4} + l_3^{\ 2}} + d_3 \cdot \sqrt{\frac{b_3^{\ 2}}{4} + l_3^{\ 2}}$$ Eq. 44

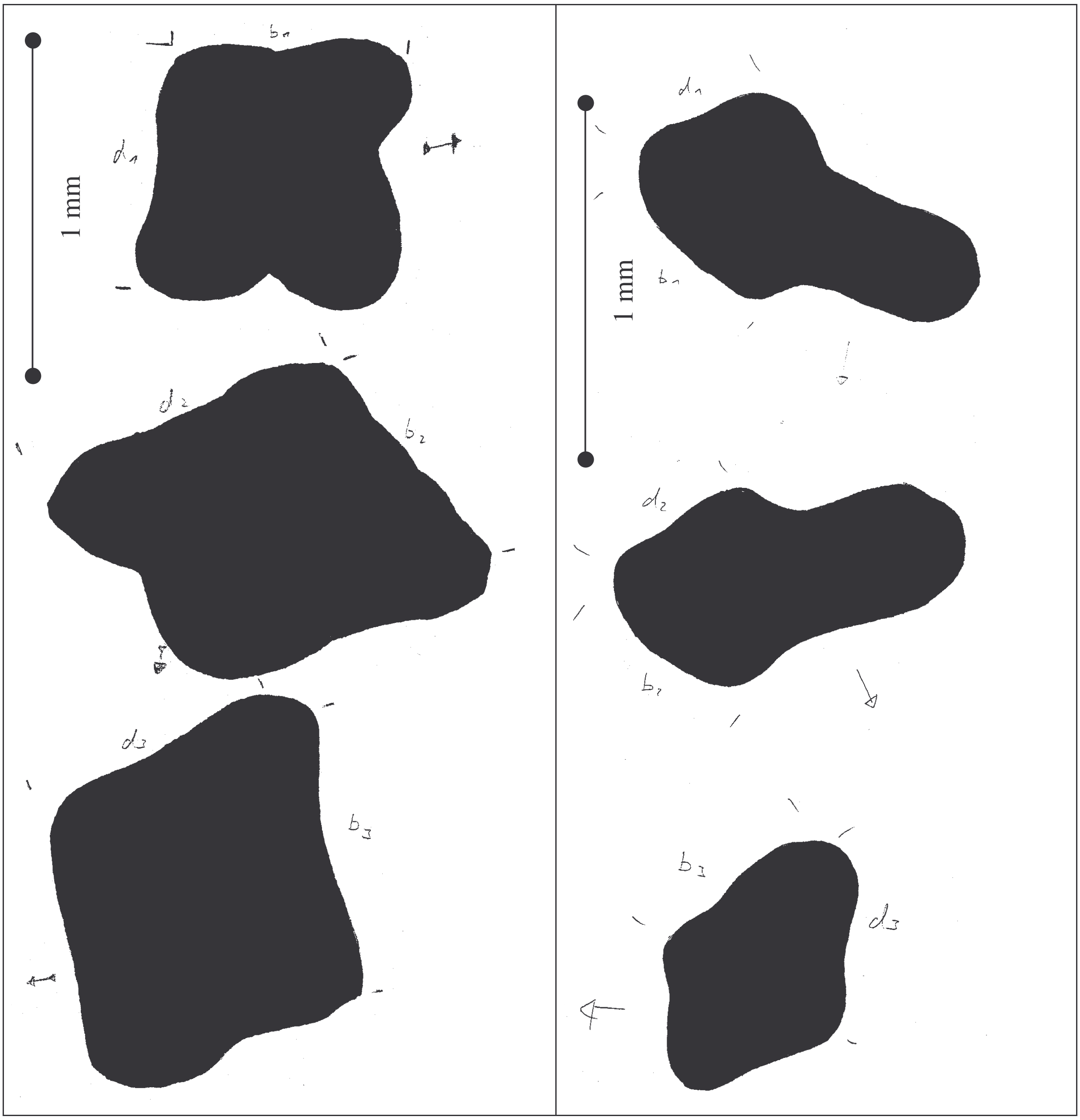

Figure 75: Examples of original drawings of the cross section of needles of current year shoots from a spruce tree (no. 374). They were taken from positions in terms of light climate, left column was from the distal shoot in the sun crown (uppermost sampling position), exposed southeast, whereas the right column is from a proximal position in the shade crown (lowermost sampling position), exposed north. The upper cross sections were from the base of the needle (section A, Figure 74), the cross sections in the middle were cut 5 mm from the base (section A/B, Figure 74), and the lower cross sections were cut 1 mm from the tip of the needle (section C, Figure 74). Letters $b_{1,2,3}$ and $d_{1,2,3}$ between the ticks correspond with the lengths of the geometric needle model (Figure 74, Eq. 41-Eq. 44). Arrows indicate the upper side or the most light exposed side of the needle on the intact shoot.

B.3 Results

The correlation of the needle surface area calculated according to Perterer and Körner 1990 and calculated according to this study were biased by an offset of about 16 mm^2, whereas the slope of the correlation remained very close to 1 (Figure 76A). The comparison of the conversion factor (*ko*) from projected to total leaf area between the two methods (Figure 76B) showed a lower slope, as the number of samples was reduced from 81 needles to 14, because the projected surface areas were treated on a whole shoot basis.

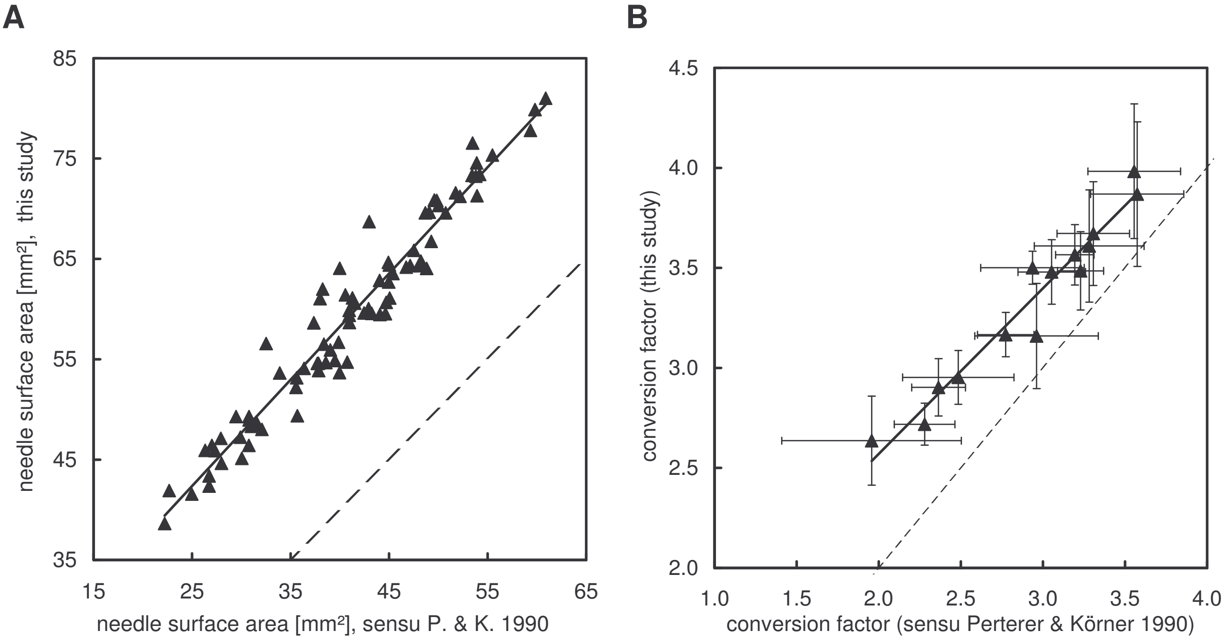

Figure 76: (A) Comparison of the needle surface area calculated according to Perterer and Körner 1990 and according to this study (linear regression: $y= 1.0592*x + 15.886$, n=81 needles from 14 shoots of spruce tree 374). the dashed line represents the 1:1 ratio.: (B) Comparison of the conversion factor (*ko*) from projected to total needle surface area measured according to this study and to Perterer and Körner 1990. The dashed line represents the 1:1 ratio, linear regression $y= 0.8269*x +0.9171$, n=14 shoots of tree 374, $p>0.001$, $R^2=0.95$, triangles with error bars represent means of 6 needles per shoot, 3 needles were sampled in proximal and 3 in distal positions on the shoot and in medial and two lateral positions (left and right of the medial position, error bars are standard deviations.

A logarithmic regression (**Eq. 45**, $R^2=0.63$) based on specific leaf area (*SLA*, **Figure 77**) to was chosen to calculate *ko*. The relationship of *ko* and *SLA* was base on data from this study and published data. An logarithmic regression was preferred as it was inbetween a power ($R^2=0.61$) and a exponential ($R=0.59$) regression. Inspite of the fact that data points were of different weight (higher weight due to mean values of *several* analysis in Oren et al. 1986, Götz 1996) the regression was satisfactory.

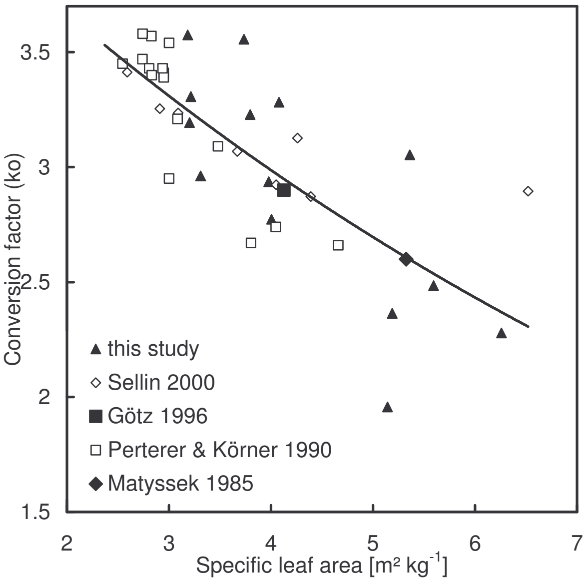

Figure 77: The conversion factor from projected to total leaf area (*ko*) in dependence of specific leaf area (based on the projected needle area) of spruce needles. Data from this study, 'Hohe Warte' / Germany (Matyssek 1985, also in Oren et al. 1986), Grafrath / Germany (Götz 1996), Austria (Perterer and Körner 1990), Estonia (Sellin 2000). The line represents logarithmic regression (Eq. 45, n=42, R^2=0.63, $p<0.001$).

With the application of Eq. 45, the conversion factor *ko* was determined as a mean value of all shoots and age classes at the branch level (Eq. 46) and could be scaled in the vertical profile (*rheight)* of the foliated tree crowns (**Eq. 47**, Figure 78A). An extrapolation of how the conversion factor on the branch level increases within two years, is presented in Figure 78B.

$$ko = -1.23 * \ln(SLA) + 4.67 \qquad \text{Eq. 45}$$

$$ko_{branch} = \sum_{axes} \frac{\sum_{age=1}^{8} total\ surface\ area}{\sum_{age=1}^{8} projected\ surface\ area} \qquad \text{Eq. 46}$$

$$ko_{branch} = 0.85 * (rheight) + 2.3 \qquad \text{Eq. 47}$$

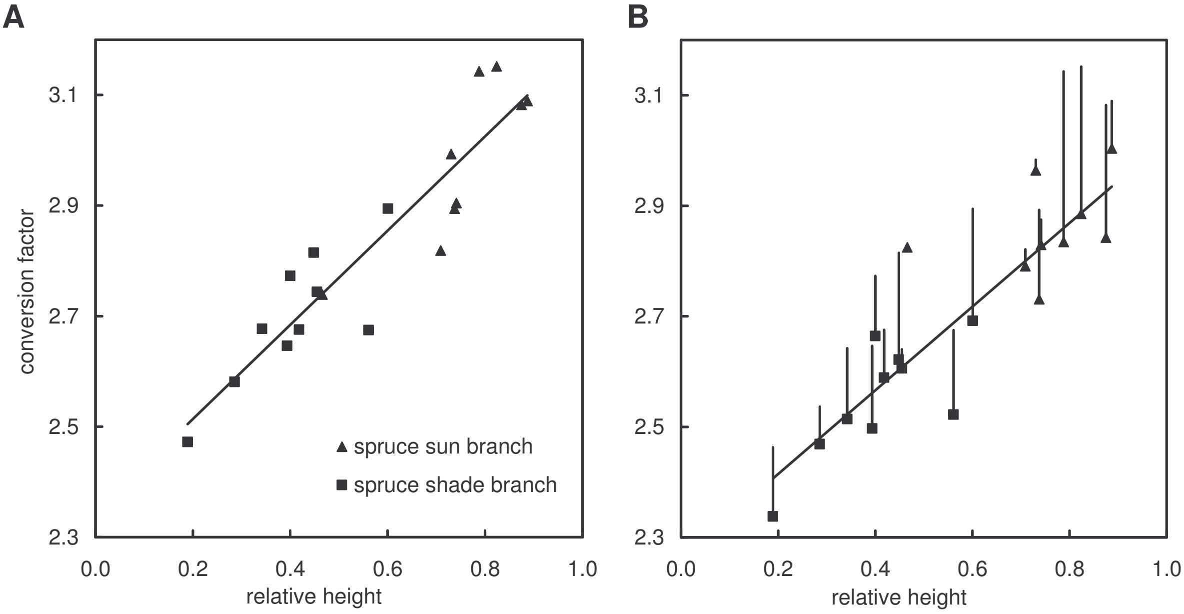

Figure 78: The conversion factor of projected to total leaf area of spruce (ko_{branch}, Eq. 46) at the branch level. **(A)** The line denotes linear regression (Eq. 47, 19 branches of 10 trees, $R^2=0.83$, $p<0.001$) with the relative height in the spruce crowns. Presented are measured datasets of year 2000 and 2001. **(B)** Extrapolated data, symbols denote ko_{branch} values from 1998, error bars represent the increase within two years. The line denotes linear regression ($y = 0.7568x + 2.2635$, 19 branches of 10 trees, $R^2=0.78$, $p<0.001$) .

B.4 Discussion

This study integrates information on ko from the shoot to the level of *entire* first order branches (ko_{branch}) in the vertical profile of the stand. Still, there is good agreement with the range of ko_{branch} in the vertical profile in this study and in *current year shoots* in Estonia (ko=2.5 to 3.5 /Niinements 1995, Niinemets and Kull 1995). According to published data at the stand scale a ko_{stand} of ~2.76 (Table 19) can be expected. If ko is generally underestimated by 16 % as shown in Figure 76AB, then our study has a corrected ko_{stand} of 3.11, which is very close to the detailed study by Sellin (2000, see Table 19). Perterer and Körner (1990) also reported that their method in the comparison to the glass bead method underestimation needle surface area by about 5 % to 15 %. In the study, besides going one step further in scale (foliage to branch level), the dimension (area to volume) is increased. Thereby, problems have been overcome, that occur when trying to compare foliage with very different morphology as in conifers and broadleaved species in terms of e.g. gas exchange rates. Nevertheless, implications for optical estimates of the vertical leaf area distribution need to be taken into account, as the ratio of total leaf area to projected leaf area is 30 % higher in the upper sun compared to the lower shade crown (see C, *LAI & LAD*).

Table 19: Conversion factors, ko_{stand}, of Picea abies on the stand level

ko_{stand}	*site*	*source*
2.69	'Kranzberger Forst' / Germany	this study, as Perterer and Körner 1990
3.11	'Kranzberger Forst' / Germany	this study, corrected see Figure 76A
3.09	‚Vooremaa' /Estonia	Sellin 2000, mean of 2.84, 3.06, 3.38
2.57	'Bílí Kríz' / Czech Republic	Pokorný and Marek 2000
2.6	‚Fichtelgebirge' / Germany	Zimmermann 1990
2.3 to 3.5	Tyrol / Austria	Perterer and Körner 1990
2.66 to 2.83	‚Fichtelgebirge' / Germany	Riederer et al. 1988
2.61	Denmark	Münster-Swendsen 1987
2.6	‚Fichtelgebirge' / Germany	Oren et al. 1986
mean **2.75**	(except this study, one common value for all 'Fichtelgebirge' studies)	

B.5 Comments on the needle shape of spruce

Though the needle shape and the needle morphology in relation to light interception has been discussed in many studies (e.g. Kerner et al. 1977, Riederer et al. 1988, Perterer and Körner 1990, Niinemets 1995, Niinemets and Kull 1995, Stenberg 1995, Niinemets 1997), not much has been stated about the ecological implications of the needle shape in relation to the position of the stomata. What advantage does this complex shape have (Figure 74 & Figure 75) ? If a light beam hits the lateral side of a needle (viewed as the cross section), which is round e.g. *Pinus* (Perterer and Körner 1990), then *one* point, gets the maximum amount of light intensity and to either side of this point the light intensity decreases, as the angle of the needle surface to the direction of the light beam gets steeper. If a needle is built like a rounded cuboid with concave sides as in *Picea abies,* then two or three points receive higher light intensities than directly neighbouring spots. Possibly, this allows e.g. a more homogeneous distribution of light intensity inside the needle or a advantageous light reflection. As the stomata are in the concave part of the needle, they are more protected from wind (lower boundary layer conductance, von Willert et al., 1995) and from radiation (lower temperature of the concave part of needle above the stomata reduces the water vapour deficit, von Willert et al., 1995). The surface is coated with a complex structure of epicuticular wax and the position of stomates is in cavities (Brehmer 1981, Trimbacher et al. 1995). Possibly explanations for this shape and surface structure are:

- Saving of water through higher boundary layer resistance and lower VPD, compared to a non-cavitated structure
- A higher boundary layer resistance also increases the resistance to CO_2. In hypostomatous leaves a contrary gradient of light compared to CO_2 exists (Smith et al. 1997) and CO_2 has to travel a ‘long’ way inside the leaf to the light or more precisely until it can be fixed through photosynthesis. In *Picea* this distance is shorter as stomata are more evenly distributed across the whole surface, which could compensate the higher boundary layer resistance.
- The complex wax structure may be an effective filter for O_3, which dissociates on the large surface of the wax crystals (e.g. Fruekilde et al. 1998). Also in the ‘calm’, porous cavity, volatile organic compounds of *Picea* abies (e.g. Kempf et al. 1996) may persist in higher concentration. More volatile organic compounds are emitted in ozone treated plants *Pinus sylvestris* and *Nicotiana tabacum* (Heiden et al. 1999) and are thought to react with and dissociate ozone. The special wax structure should allow a more economic production (see Kesselmeier and Staudt 1999) of volatile organic compounds for the same number of interactions of ozone and volatile compound molecules - which may make this system efficient against O_3 uptake and ozone injury less likely (see section 3.2.3).

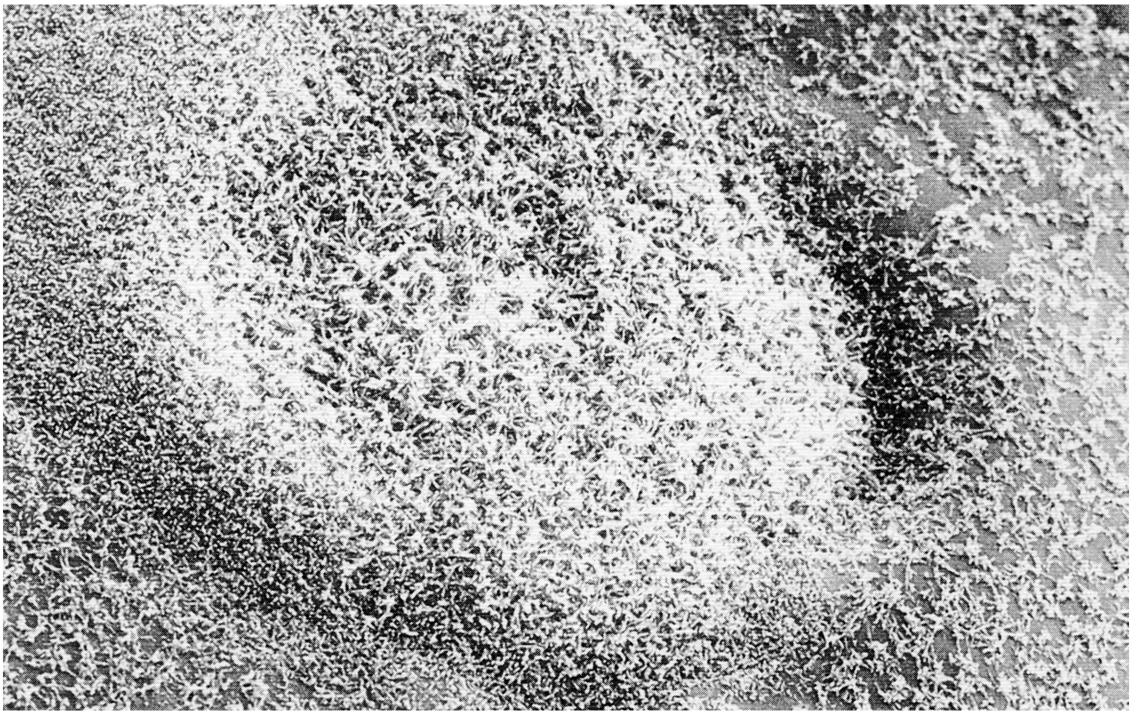

Figure 79: Stomatal cavity of *Picea abies*. Note the porous wax structure. Electron microscopy 1500x (from Trimbacher et al. 1995).

C Leaf Area Index and Leaf area density

C.1 Introduction

Tree species can differ dramatically in crown structure and in their strategy to exploit canopy volume (Monsi and Saeki 1953, Küppers 1985, Schulze et al. 1986, Küppers 1994, Küppers 2001a, Küppers 2001b).

A certain fraction of a stand can be sequestered by a crown, but the crown itself consists of branches that again occupy only a fraction of the crown (Cermak et al. 1997). Thus, although a canopy can appear to be closed, there are always regions, which are unfoliated. The unfoliated fraction of the canopy increases with a decrease in scale from crown to branches or voxels (Hendrich 2000, Reiter et al. 2004). To determine the unfoliated fraction in the vertical profile of a stand at the scale of branches, foliage area densities of the stand must be divided by the foliage area density of the branch in the corresponding height. An optical system to determine foliage area index (LAI) of the stand was used (LAI-2000, LI-COR Inc., Nebraska, USA). Foliar morphology (particularly of conifers / Chen and Black 1992, Chen 1996, but also broadleaved foliage / Fleck 2003) and stand structure (e.g. Pokorny and Marek 2000) is known to bias these measurements, and they need to be corrected. It is advised to use the one-sided needle area (Chen and Black 1992).

Besides giving information on crown structure and the gap fraction, the measured leaf area density of the stand can serve as an interface to a modelled crown volume (cooperation with project C3), if the relationship between foliated stand volume and the foliated crown volume simulated by the model is known.

C.2 Methods

Vertical profiles, which characterize beech and spruce study trees, were assessed during the growing season of 1999 and 2002 respectively (in cooperation with Michael Leuchner / partner project B10, and Bettina Baumeister) . We measured in 50 cm intervals from 16.5 m up to the top of each tree with a leaf area canopy meter (LAI-2000, LI-COR Inc., Nebraska, USA). The system consists of two units. One being the reference, which was placed above the canopy on one of the towers (see Figure 6 & 7, page 10). Half of the lens was covered with a azimuthal masking view cap to avoid influence of the operator and the scaffolding on the readings. The sensor is a ‚fish-eye‘ lens, which is divided into 5 concentric segments. Leaves are ‘seen’ as black objects, which is achieved by means of red light filter (wavelengths < 490 nm). The program C-2000 (LI-COR Inc., Nebraska, USA) derives the leaf area index above the measured position from the readings of both units (see product brochure). Only the inner four rings of the lens were used for calculations (Pokorny and Marek 2000).

> Optical LAI measurements are biased by the clumping of foliage and rather represent projected shoot area than projected needle area Gower and Norman 1991, Fassnacht et al. 1994, Stenberg 1996, Pokorny and Marek 2000, but see Stenberg 1996). Besides the problems with the interpretation of measured LAI values due to clumping, shoot structure and leaf morphology (especially in conifers) another bias for optical LAI-measurements must be considered - the interception of light by the hemisurface of branches and stems (e.g. Küßner and Mosandl 2000, 37 % and 82 % underestimation in spruce, 'Erzgerbirge', Germany). Foliage masked branches by 95 % in Boreal aspen (*Populus tremula*). In jack pine and black spruce 80-90 % of the branches are masked by the foliage. Therefore (Kucharik et al. 1998) suggest that the fraction of indirect LAI that consists of (the hemisurface area of) branches intercepting light is less than 10 %. This is quite an acceptable and predictable error in vertical profiles of LAI within the life crown. But stems that can comprise up to 30-50% of the total woody area are not preferentially shaded by foliage and can not be overlooked. This is especially a problem when measuring from the forest floor. The bias increases with increasing crown base height Pokorny and Marek 2000.

The LAI measurements were submitted to the following methods of correction procedures - subtraction of the LAI value above the canopy from all readings (Figure 80A, B), absolute heights were transformed into relative heights (0=base of foliated canopy, 1=apex), and the datasets were linearly mapped (Diadem 8.0, NI) to the vertical profile with the most readings.

Two further methods were applied for spruce to correct the readings of the optical LAI measurements:

1. LAIs of spruce were converted into projected surface needle area by multiplication with a correction factor of 1.52 (Fassnacht et al. 1994). The projected leaf area was transformed to hemi surface leaf area by multiplying leaf area densities in the vertical profile with the corresponding conversion factor $0.5* ko$ (Eq. 47, page 138, see B.3). Leaf area densities were calculated by derivation (stepwise subtraction of cumulative LAI) and the corrected cumulative leaf area index calculated as the sum of the corrected leaf area densities (Figure 81A).
2. As method 1, but application of the correction factor of 1.825 (cf. Table 2/1M-0 in Pokorny and Marek 2000) instead of 1.52, and a conversion factor of 2.59 instead of π was applied (Figure 81B).

Above corrections can be expected to be more precise than the simple multiplication of the raw data with 1.6 as proposed by (Gower and Norman 1991). Scattering effects of blue light were not corrected as measurements were performed under overcast skies, dusk or dawn (Leblanc and Chen 2001).

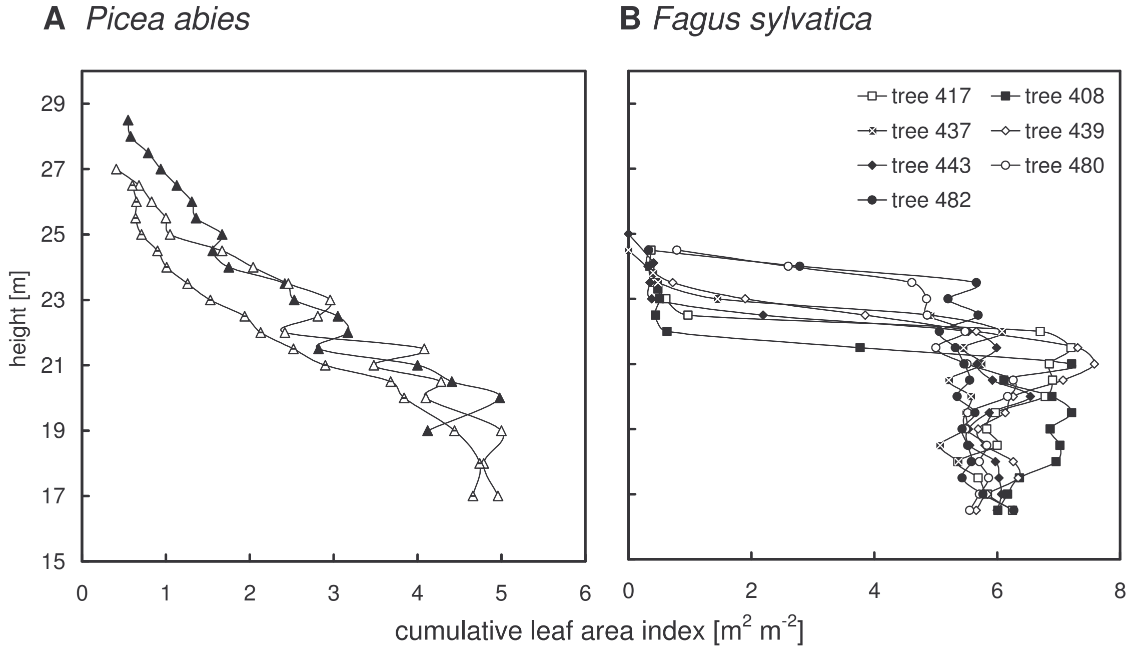

Figure 80: Cumulative leaf area index as measured with the plant canopy analyser LAI-2000 (A) 3 vertical profiles the spruce canopy (solid triangle, mainly tree 535, north of tower/ open triangle, mainly tree 537, east of tower / hatched triangle, several crowns in southern direction of the tower. (B) 7 vertical profiles of the beech canopy, each symbols denotes a profile taken in front of a specific tree, see legend..

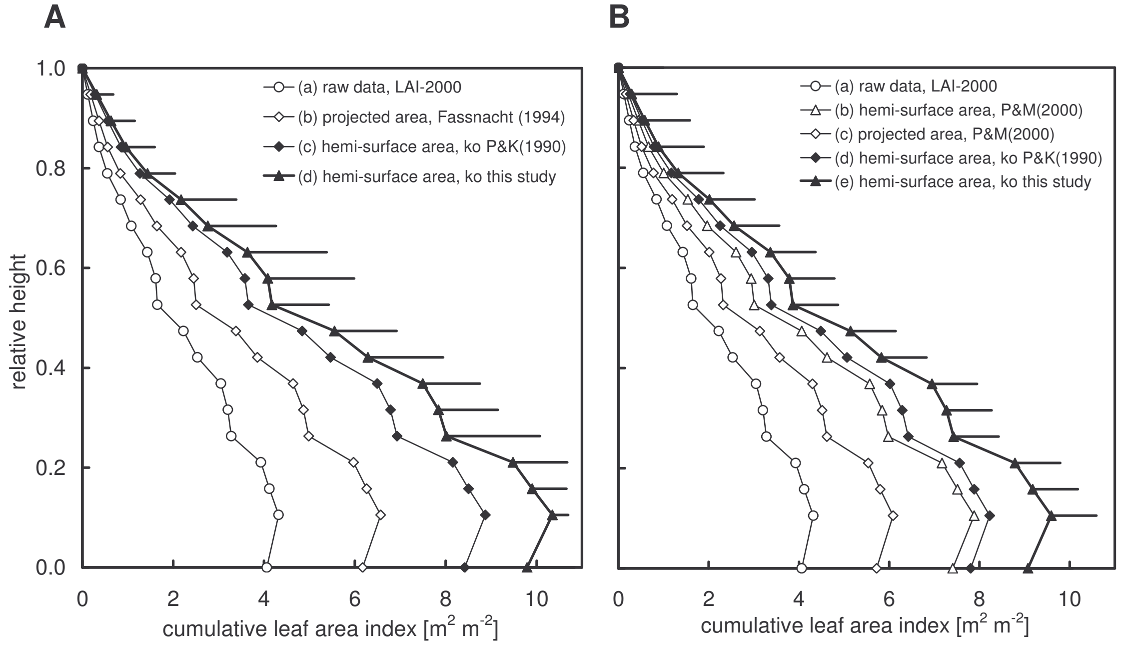

Figure 81: Cumulative leaf area index in the vertical profile of the canopy (0=base, 1=apex). Letters in brackets denote subsequent steps of correction: (A) method 1, and (B) method 2.

C.3 Results and discussion

C.3.1 Leaf area index

The corrected cumulative leaf area index of spruce increased linearly from the apex to the crown base (Figure 82A), which agrees with the linear decrease of light in the spruce canopy (Figure 12B, page 29). In beech (Figure 82B), the corrected cumulative leaf area increased rapidly within the first two meters from the apex, and irregularly decreased and increased 3 m below canopy top, which was a relative height in the foliated canopy of about 0.7, and a height of 21 m above ground level. In beech leaf area index (*LAI*) had decreased below the maximum value in 5 of 7 profiles. I expect this to be the effect when the sensor's field of view exceeds the single crown extension and gaps between the trees have a pronounced effect on the average *LAI* calculations (Figure 83 & section 3.1, cf. Küßner and Mosandl 2000). So that the readings taken in the direction of the stem of a tree, map a leaf area index on the crown scale in the upper canopy, which gradually turns into a canopy leaf area index when measured at lower stem height.

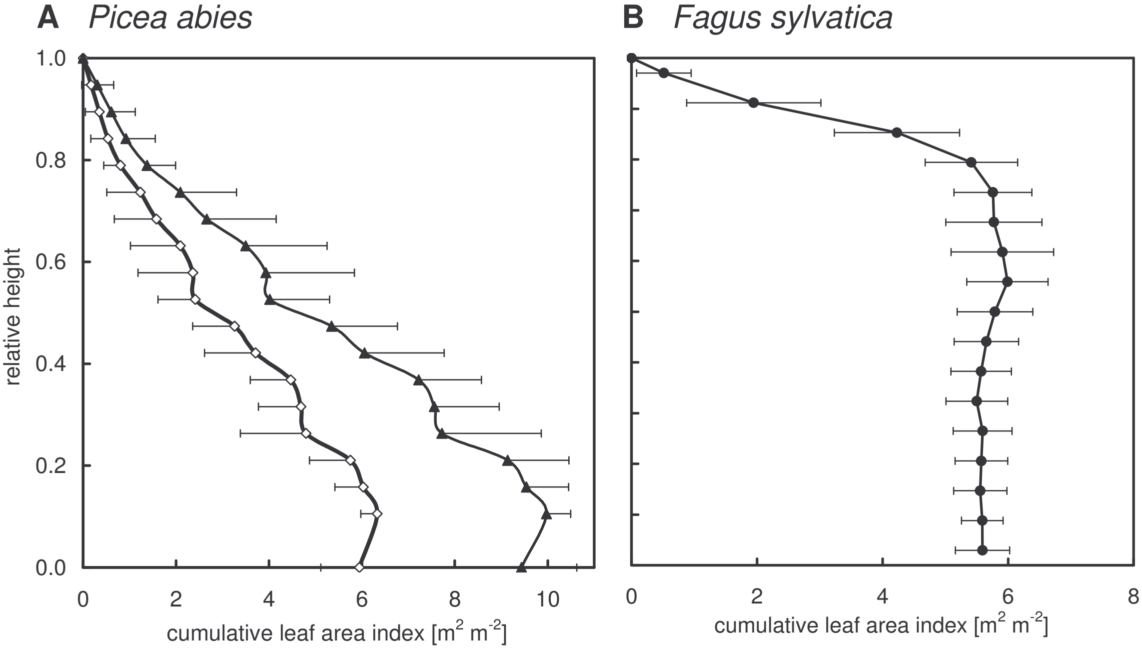

Figure 82: Mean cumulative leaf area index in the normalized vertical profile of the foliated crown, error bars denote standard deviation. (A) Cumulative projected (open diamonds) and hemi surface (solid triangles) leaf area of spruce 3 profiles, which had been corrected according to Pokorny and Marek 2000 and Fassnacht et al. 1994. (B) Mean cumulative projected leaf area index of 7 profiles in beech.

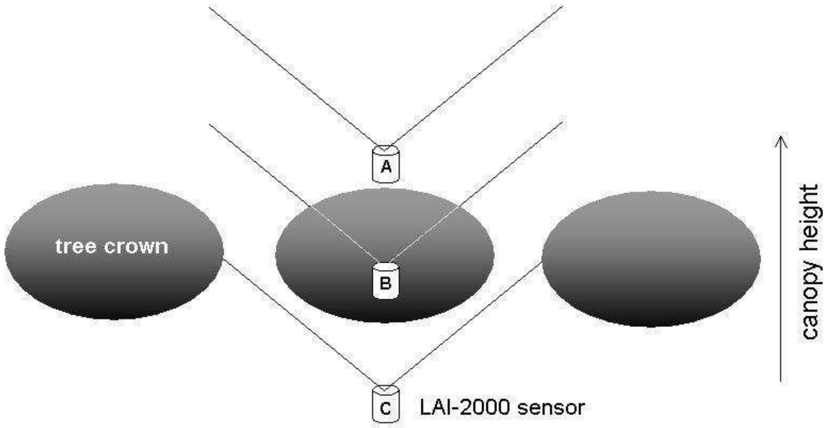

Figure 83: View of the sensor of the plant canopy analyser (LAI-2000, v-shaped lines) in the vertical profile of the canopy: (A) above the canopy, (B) inside a crown, and (C) lower the canopy. No gaps between the crowns are within the direct view of the sensor in position B, but at lower position C gaps are within the view of the sensor.

The profiles taken close to spruce trees 535 and 537 are more irregular (open and solid symbols, Figure 80A) than the profile taken more distant (~3 times further) from the trees. This is probably due to the stronger direct shading effect of clumps of foliage close to the sensor, as the penumbral effect is greater at greater distance from the individual foliage ‘clumps’ (Oker-Blom 1984).

At the canopy level, beech (5.6 m^2 m^{-2}, Figure 82A) had developed only one half of the one sided leaf area index of spruce (10 m^2 m^{-2}, Figure 82B), but almost the same projected leaf area index (6.2 m^2 m^{-2}) as compared to spruce. The profiles on spruce and beech in this study, qualitatively agreed with simulated *LAI* data of the study site generated by the model BALANCE. In absolute terms, *LAI* of spruce was over- and *LAI* of beech underestimated by the model (Grote and Reiter 2004).

Although optical *LAI* determination with LAI-2000 seem generally to underestimate high *LAI*, reaching a saturation level at about *LAI* of 5 (Jonckheere et al. 2004, the likely cause is a gap fraction saturation as *LAI* approaches 5-6, Gower et al. 1999), the results of the canopy *LAI* correspond with the mean of findings in other studies (Table 20A,B). Particularly when taking into account that *LAI* of beech can vary considerably from year to year (12 % - 19 % at Grossebene & 3 % - 9 % at Steinkreuz /Fleck and Schmidt 2001).

Table 20: Hemi-surface leaf area index of spruce (A) and beech (B) as determined through litter collection, biomass harvest, optical assessment, and allometric relationships

site	***tree age [years]***	***tree height [m]***	***LAI*** $[m^2 m^{-2}]$	***method***	***source***
A ***Picea abies***					
Helsinki, Finland	80	20- 28	7.49	allometry harvest	Cescatti 1997a
Coulee, Wisconsin, USA	27		14 –16.3	harvest	Bolstad and Gower 1990
Fichtelgebirge, Germany	40	24	7.9 - 8.2	harvest	Falge 2001
Coulee, Wisconsin, USA	23		10.2	harvest	Gower et al. 1993
Erzgebirge, Germany	105	28	9.6	harvest	Küßner and Mosandl 2000
Germany	55		6	harvest	Möller 1945
Germany	60		8.4	harvest	Möller 1945
Switzerland	35		9.6	harvest	Möller 1945
Denmark	15-40		6-7.5	harvest	Möller 1945
Bily Kriz, Czech Republic	20	7	8.6	harvest	Pokorny and Marek 2000
mean			**10 ± 4.5**	**harvest**	
B ***Fagus sylvatica***					
Fichtelgebirge, Steinkreuz & Grossebene , Germany	120 -130	30 - 39	6.3 - 6.4	litter, LAI-2000, allometric	Fleck and Schmidt 2001
Hesse, France	30	13	5.6	litter	Granier et al. 2000
Alice Holt, England	65	20-25	6	---	Meir and Grace 2002
Germany	22-66		7.5	litter	Möller 1945
Switzerland	80		7.8	litter	Möller 1945
Denmark	8 - 200	2-30	4 - 7.5	litter	Möller 1945
Germany			6.3	---	Schenk et al. 1989
Italy	90	25	4.7	---	Valentini et al. 1996
mean			**6.25 ± 1**		

C.3.2 Leaf area density

The vertical distribution of leaf area density (*LAD)* of spruce was very irregular but increased towards a maximum of 2.6 m^2 m^{-3} in the lower half of the foliated canopy (Figure 84A), which is about one third lower compared to beech (Figure 84B). The irregularities in *LAD* of spruce depict the crown structure, where the growth pattern of branches left gaps, that allowed more light than in beech canopy to penetrate to lower canopy strata (cf. Figure 12B, page 29). About the same *LAD* along with a large variation (2.62 1.94 m^2 m^{-3}) was found by Falge et al. (1997) for *Picea abies* in Germany. Beech had a pronounced maximum of its LAD between 4 and 6 m^2 m^{-3} in the upper third of the canopy (data published in Häberle et al. 2003).
Measured leaf area densities were approximated with polynomial functions (Figure 84C,D; parameters see Table 21). In the case of spruce, the approximation does not account for the heterogeneity of the canopy layers, but the maximum was similar to the maximum leaf area density of 1.3 m^2 m^{-3} found for *Picea abies* in Helsinki/ Finland (Cescatti 1997b). This is also in agreement with results on *Picea sitchensis*, where the maximum *LAD* was between 2 m^2 m^{-3} in unthinned and 1 m^2 m^{-3} in thinned stands (Milne 1995). Whereas the vertical distribution of leaf area was similar in this study and findings by Pokorny and Marek (2000), the observed needle area distribution of an average *Picea abies* tree (Fig. 1e/ Moren et al. 2000) is different from our study in that the maximum leaf area density is in the 10 % of the crown. *Pinus sylvestris* had a similar distribution compared to beech in this study. However, when the needle area was modelled on the stand scale, the maximum leaf area density was between the mid and the upper third of the crown height. Like the maximum *LADs* of beech and spruce in this study, the maximum *LADs* of *Picea* and *Pinus* also were at about the same height (Fig. 6 in Moren et al. 2000). Maximum leaf area densities in layers of two *Fagus sylvatica* trees was between 5 and 6 m^2 m^{-3}, but the vertical distribution was different, in that one individual had a second maximum in the lower half of the foliated crown. Both individuals have higher leaf area densities in the shade crown compared to beech in this study (Fleck 2001).

The leaf area (and biomass densities) may have similar maxima, but the distribution is apparently species (cf. Monsi and Saeki 1953) and stand-specific (cf. Figure 85). Management practice, species mixture play an important role, and also age is reported to have an decisive effect on *LAD* and its distribution (e.g. *Larix kaempferi*, Osawa 1990). The differences in distribution imply differences in structure (cf. Yokozawa et al. 1996, Figure 85) and shape (Grote and Reiter 2004), which will change the efficiency of branches (Reiter et al. 2004) and can thus affect the trees' competitiveness.

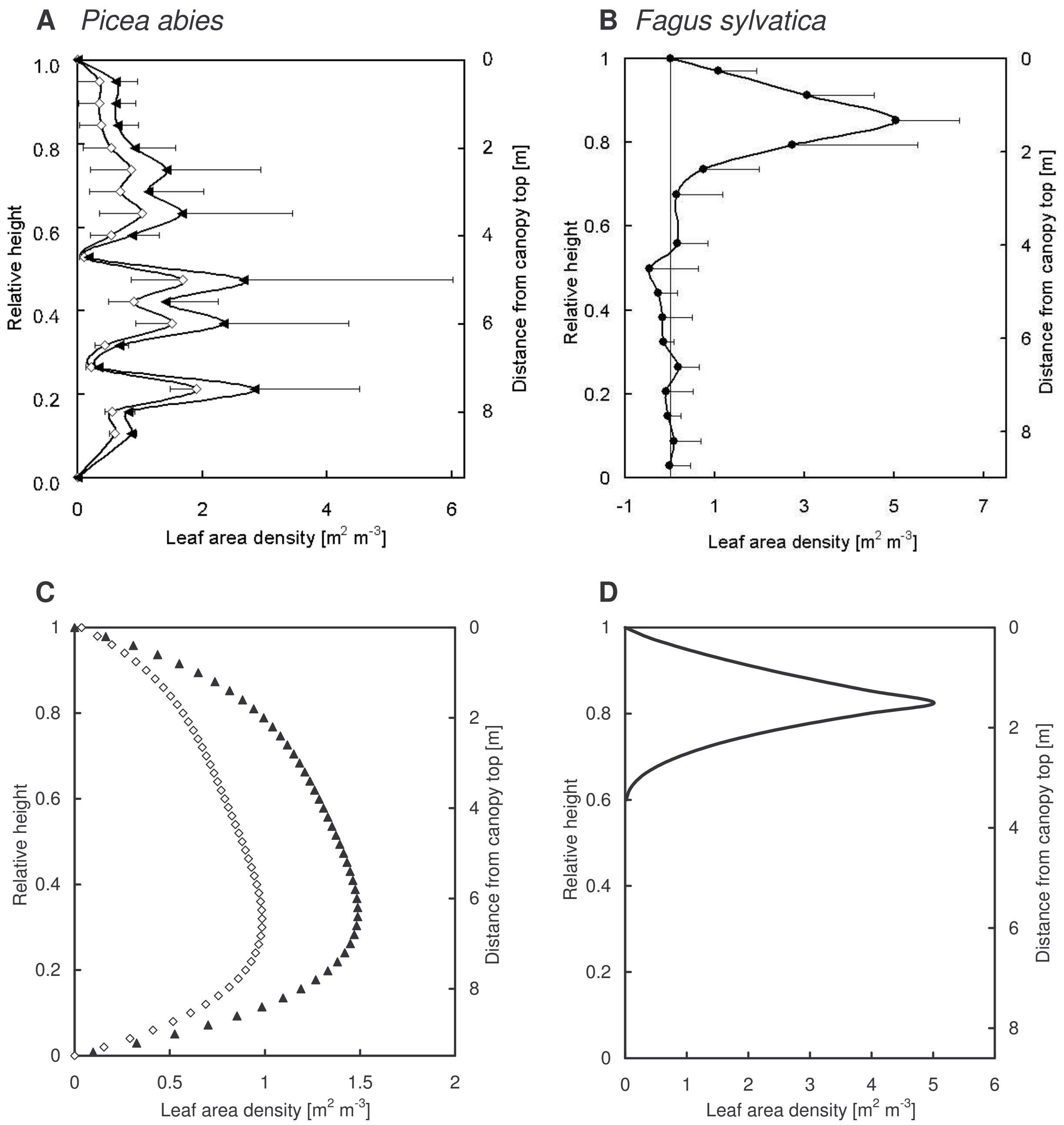

Figure 84: Mean measured (A&B) and modelled (C&D) leaf area densities of spruce and beech in the vertical profile of the foliated crown. Open diamonds denote projected and closed triangles denote hemi-surface leaf area densities of spruce, for beech projected leaf area densities are shown. Error bars denote standard deviation. See Table 21 for parameters of polynomial approximations (C&D).

Table 21: Parameters for spruce and beech to approximate leaf area density in the vertical profile of the foliated canopy (*rheight*) and with distance from the canopy top (*distance*) on the stand level , model: LAD = $ax^4+bx^3+cx^2+dx^1+e$

species	***x:=base***	***a***	***b***	***c***	***d***	***e***	***condition***
projected leaf area density							
Fagus sylvatica	*rheight*	0	109.2	-234.2	125.0	0	1 ≥ x≥ 0.824
		0	172.8	-252.4	117.1	-16.73	0.824 > x≥ 0.6
Fagus sylvatica	*distance*	0	-1.549	4.244	0.7325	0	0 ≤ x≤ 1.38
		0	-0.3602	4.342	-16.71	20.84	1.38 < x≤ 3.14
Picea abies	*rheight*	-11.40	26.44	-23.16	8.157	0	1 ≥ x≥ 0
Picea abies	*distance*	$-1.504*10^{-3}$	$2.455*10^{-2}$	-0.1514	0.5111	0	0 ≤ x< 9.48
hemi-surface leaf area density							
Picea abies	*rheight*	-16.66	37.63	-32.73	11.83	0	1 ≥ x≥ 0
Picea abies	*distance*	$-2.265*10^{-3}$	$3.844*10^{-2}$	0.2522	0.8658	0	0 ≤ x< 9.48

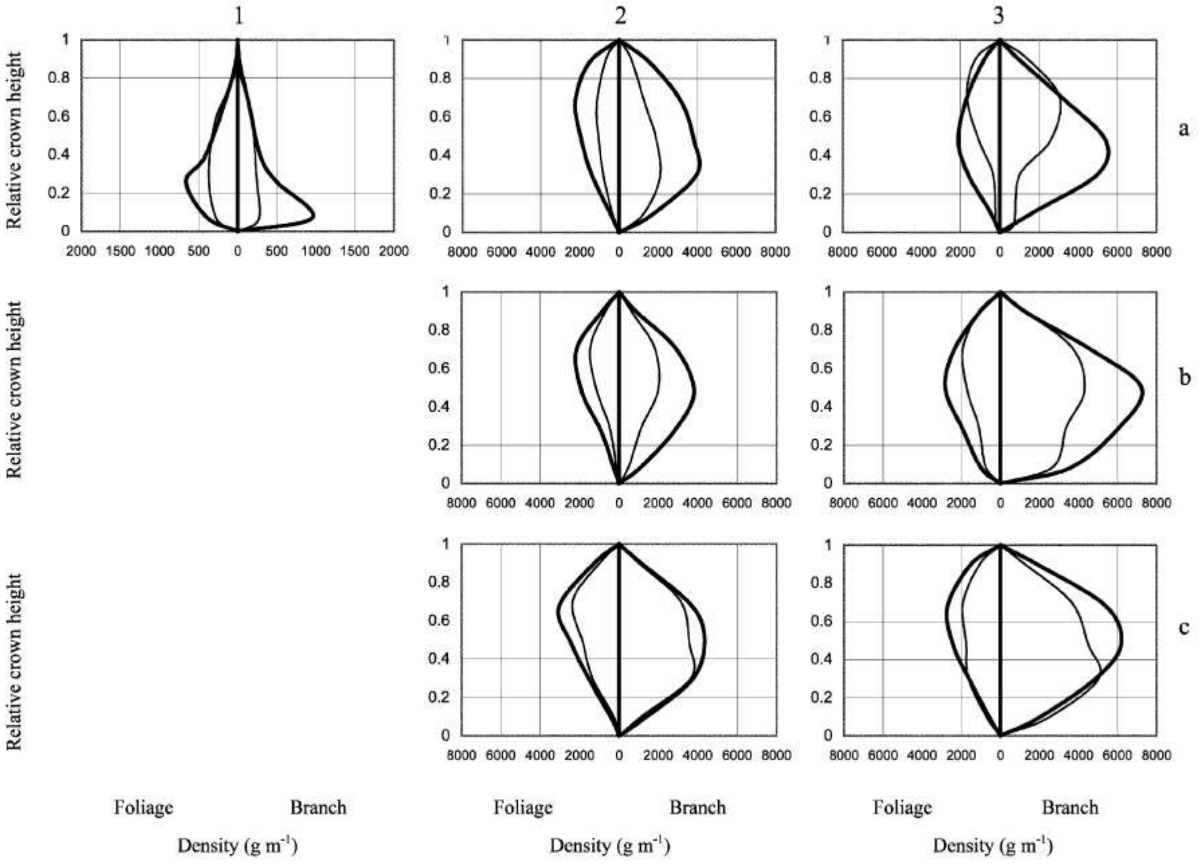

Figure 85: From Kantola and Mäkelä (2004): Vertical density distributions of foliage and living branch wood in selected sample trees as a function of relative height. Stands are: 1 young, 2 middle-aged, and 3 mature stand. Thinning intensity is: a unthinned, b normal thinning, and c intensive thinning. Thick line is most dominated and thin line is most suppressed tree in a plot.

D Geometric model

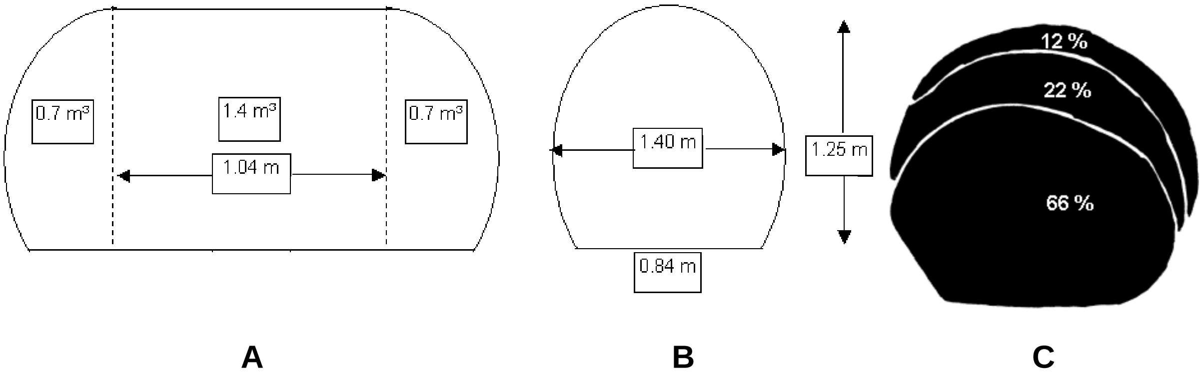

Figure 86: Geometric model for a *Corylus avellana* shrub system, derived from Lilienfein et al. (1991): (A) Projected frontal view of the horizontal and vertical dimensions of the model [m]. The volume [m^3] was constructed of a cylinder between two hemi-shells (B) Vertical cross section of shell and cylinder (C) The crown was divided into three compartments. Their proportion is given in per cent, from top to bottom: sun layer, intermediate layer, shade layer.

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