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SPATIAL VARIATION OF PHOTOSYNTHETIC CAPACITY OF EARLY-, MID-, OR LATE-SUCCESSIONAL BROAD-LEAVED TREE SPECIES IN A TEMPERATE MIXED FOREST

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Nicole Legner

aus
Aalen

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Referentin/Referent: Prof. Dr. C. Leuschner

Korreferentin/Korreferent: Prof. Dr. F. Thomas

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Abbreviations

A_{max}	light-saturated net photosynthesis rate under ambient CO_2 concentration
Ap	*Acer pseudoplatanus*
Cb	*Carpinus betulus*
C_i	intercellular CO_2 concentration
DBH	diameter at breast height
Fe	*Fraxinus excelsior*
Fs	*Fagus sylvatica*
J_{max}	maximum electron transport rate
R_d	leaf day respiration rate calculated from the A/C_i curve
SLA	specific leaf area (area per leaf mass)
Tc	*Tilia cordata*
V_{cmax}	maximum carboxylation rate
Suffix ${}_{\text{‘a’}}$	scaled to leaf area
Suffix ${}_{\text{‘m’}}$	scaled to leaf mass
Suffix ${}_{\text{‘N’}}$	scaled to leaf N concentration
N_a	nitrogen per leaf area
N_m	nitrogen per leaf mass
RI	relative irradiance
VPD	atmospheric water vapour saturation deficit
$[CO_2]$	CO_2 concentration

CHAPTER 1

General introduction

1.1 Introduction

Forests are important not only as habitat for many plant and animal species, but also for storing large amounts of carbon, timber production, protection of soil (erosion control) and local recreation area and forests also provide air purification and adequate water supply. In Germany, 11.1 million hectare of forests are currently existing, which relates almost to one third of Germany's total area (BMVEL 2008). Thereof, 40.1 % are deciduous and 57.6 % are coniferous forests. Coniferous forests are built up of 28.2 % of spruce (mostly *Picea abies*) and 23.3 % of pine trees (mostly *Pinus sylvestris*). Deciduous forests consist of 14.8 % beech (*Fagus sylvatica*) and 9.6 % of oak (*Quercus* sp.). The forest economy contributes with about 2 % to the gross economic product of Germany and therefore plays an important role on the decision how to manage forests (BMVEL 2008).

Managed forests and in particular monocultures have been threatened by massive pest attacks. Especially in coniferous forests, the bark-beetle (and other pest insects) has caused financial losses (Sampedro et al. 2009). Therefore, large scale forest conversion to broad-leaved forests attempts to improve the ecosystem services provided as outlines above. From an economic point of view, a mixture can have the advantage of minimisation the risk of losing the complete area due to storm or pest insects. Additionally, coniferous forests mixed with deciduous tree species (e.g. beech) also can have increased yield (Knoke et al. 2005). The portion of deciduous trees is therefore increasing in Germany with the result that in the years 2001-2002, nearly three quarters of the forests were mixed-species stands (BMVEL 2008). 15.3 % of the beech forests are monocultures and 21.8 % are mixtures with coniferous trees. The greatest portion of monocultures belongs to pine trees with 44.5 %, 55.5 % are mixed-species stands (BMVEL 2008).

The productivity of a forest can be derived from biomass production measurements or assessed through canopy assimilation rate. Photosynthetic capacity can be measured with gas-exchange instruments or down-scaled from eddy covariance measurements. For the selection of tree species which are suitable for mixed forests, it is important to get a better understanding of tree species' characterisation. The economically less used tree species are not well analysed. Additionally, the possible advantages are not made clear to the forest management (Hein et al. 2009). Studies about two-species mixtures exist, but if the mixtures seem to have a positive or a negative influence on the productivity depend e.g. on soil or climate conditions (Pretzsch et al. 1998, Pretzsch 2005). Some studies show a positive influence of the species mixture on the abundance of pest insects, for example, a mixture of *F. sylvatica* and *Picea abies* reduced the abundance of mono- and polyphageous pest insects (Heiermann & Schuetz 2008). The increasing knowledge of the function of mixed-tree species is therefore of increasing interest (Kelty 2006).

Forest tree diversity can be accessed in different ways, for example by comparing the successional status, the sun and shade leaf photosynthetic capacity or the shade tolerance of the species. Early- and late-successional tree species show characteristic differences in their physiology (e.g. Lambers et al. 2008) and wood production is predicted to be generally higher in early- than in late-successional species (Vilà et al. 2005). Most of the early-successional species are fast growing and they colonize areas with stressful environmental conditions (e.g. temporarily flooded areas). Mid- to late-successional species often prefer somewhat more fertile and less drought-affected soils (e.g. hornbeam; Roloff & Schütt 2006). How trees interact with the surrounding environment also play a crucial role. Soil nutrient status, water supply and the trees' competitive ability are also of great influence for the success of a tree species in forest dynamics. Therefore, forest research in mixed stands is needed to help to characterize the species and to build a scientific basis for forest management in the process of future forest conversion.

1.2 Objectives of the study

This study is part of the Research Training Group (Graduiertenkolleg) 1086 'The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests'. The project began in 2005 and consists of three phases of PhD students (2005 – 2008, 2008 – 2011 and 2011 – 2014). I have been member of the second phase of PhD students from 2008 onwards. Nine different working groups of the universities of Göttingen, Jena and München have participated in the second phase of the project. All projects have been split in three main parts: (A) Biodiversity analyses and biotic interactions, (B) biogeochemical cycles and (C) synthesis. The main goals of these interdisciplinary studies are to get a deeper knowledge of the impact of tree species diversity on the functioning of this mixed forest ecosystem. The focus lays especially on the biomass production, nutrient and water cycles, groundwater supply, and biotic interactions between key organisms. In the first part of the RTG 1086 (2005 – 2008), the investigations were mainly focussed on a plot-study design where plots of 50 x 50 m size with three different diversity levels were chosen. From 2008 onwards, the second phase concentrated more on smaller scaled diversity studies. We established 100 tree clusters which consisted of each three tree individuals. The clusters were composed either of one, two or three tree species. The focus was laid on the tree species *Fagus sylvatica*, *Tilia cordata*, *Fraxinus excelsior*, *Acer pseudoplatanus* and *Carpinus betulus*.

My project B1 had its focus in the comparison of the photosynthetic capacities of the five investigated tree species. The major hypotheses of this study are:

(1) The sun leaves have a rather uniform photosynthetic capacity among the species in response to the full light conditions in the canopy top. → Chapter 2

(2) The photosynthetic capacity of shade leaves is more variable among the species and reflects species-specific low light adaptations. → Chapters 2, 3

(3) The vertical light gradient is the major determinant of low light acclimation in the shade canopy. → Chapters 2, 3

(4) The photosynthetic parameters are all closely linked to relative irradiance (RI), specific leaf area (SLA) and nitrogen content per leaf area (N_a), but the relation is closer to N_a than to SLA. → Chapter 3

(5) The leaves of juvenile trees have a lower photosynthetic capacity then the sun leaves of mature trees. → Chapter 4

(6) The photosynthetic capacity decreases significantly from early- to late-successional tree species. → Chapter 4

1.3 Study site

The Hainich National Park is located in the middle of Germany, in the Federal State of Thuringia (Fig. 1.1). The Hainich forest consists of an area of 160 km² and is part of the largest undivided deciduous forest area of Germany. Being exposed to different selective cutting regimes in the past with low forestry impact, the utilization ended with the declaration of the Hainich National Park in 1997 which consists of an area of 75 km² (Schmidt et al. 2009). In June 2011, part of the national park was declared as World Heritage Site.

Figure 1.1: Overview map of Germany and the location of the Hainich National Park where the studies of the RTG 1086 took place. Source: http://upload.wikimedia.org/wikipedia/ commons/ 5/55/ Karte_Nationalpark_Hainich.png, 20.02.2012, Wikimedia Commons, Creative Commons licence, description= Karte des Nationalparks Hainich in Deutschland, author= Lencer. Modified by the author. The red square in the right detail map illustrates the part of the national park where this study was conducted.

The forest is located on the south-eastern side of the Hainich mountain range and the soil type is a Luvisol developed from loess over Triassic limestone. The topsoil is free of carbonates and has a pH (H_2O) in the range of 4.5 to 6.8 (Christina Langenbruch, personal communication). Noteworthy is the large abundance of tree species with up to ten and more tree species per hectare. The most abundant tree species is European beech (*Fagus sylvatica*), but also species like European ash (*Fraxinus excelsior*), European hornbeam (*Carpinus betulus*), service tree (*Sorbus torminalis*) and species of the genera maple (*Acer*) and lime (*Tilia*) can be found. Also different communities are established in the national park such as Hordelymo-Fagetum community, Galio-Fagetum community or Stellario-Carpinetum community. Remarkable elements of the fauna are for example the Purple Emporer (*Apatura iris*), the wild cat (*Felis silvestris silvestris*), seven woodpecker species and 15 bat species.

The research site with an elevation of 350 m a.s.l. is close to the location Thiemsburg (51° 05’ 00’’ N, 10° 30’ 27’’ E) which lies in the south-eastern side of the national park. The weather during the study in the years 2008 and 2009 was similar in the average temperature (9.5 °C for 2008 and 8.9 °C for 2009 respectively) but differed in the sum of rainfall (500 mm in 2008, 774 mm in 2009, weather station Weberstedt/Hainich, meteomedia). The long-term means amount to 7.7 °C and 590 mm yr^{-1} precipitation.

For this study, a transect of 300 m length was established because of the disturbing impact that the mobile lifter would have had on the soil and vegetation. The transect was close to several tree clusters and three plots of the first phase of PhD students (Fig. 1.2). The mobile lifter (Fig. 1.3) had an operating height of up to 30 m and was replaced from one location to another by its own engine or with the help of a tractor.

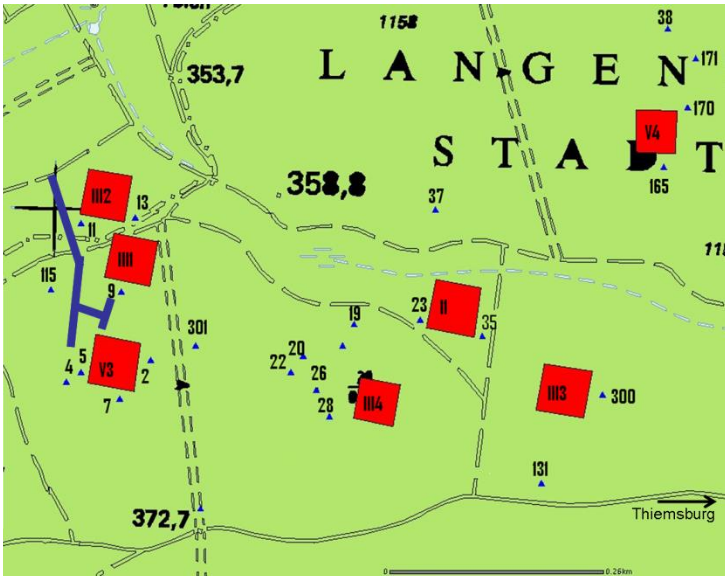

Figure 1.2: Map of the study area Thiemsburg. The red squares are research plots of the first PhD student phase; the small triangles are tree clusters of the second phase. The dark blue transect shows the mobile lift area where this research was conducted.

Figure 1.3: The mobile lifter from the ground (left) and from top view (right) at the measuring site in the Hainich National Park.

1.4 Studied tree species

This study was focused on the five tree species *Fraxinus excelsior* L. (European ash), *Acer pseudoplatanus* L. (sycamore maple), *Carpinus betulus* L. (European hornbeam), *Tilia cordata* Mill. (small-leaved lime) and *Fagus sylvatica* L. (European beech).

F. excelsior is a member of the family Oleaceae (Fig. 1.4). It is the only species with a ring-porous xylem anatomy and has arbuscular mycorrhiza. Ash is an early- to mid-successional species, which is fast growing and can tolerate a wide range of water availabilities. The species has a high flexibility to adapt to different environmental conditions. The light demand changes from moderate shade tolerance during infancy to high light demand as an adult. Ash trees are wind-pollinated (Roloff & Schütt 2006). In silviculture, it is one of the most frequent secondary tree species.

Figure 1.4: *Fraxinus excelsior* fully expanded leaves (left), flowers (middle) and developing leaves (right).

Acer pseudoplatanus is a member of the family Aceraceae (Fig 1.5). It also belongs to the secondary tree species in forest management. Like ash, maple trees have arbuscular mycorrhiza, but the xylem anatomy is diffuse-porous. *A. pseudoplatanus* is a mid- to late-successional tree species with a higher shade tolerance than ash trees. The species needs a good water supply but nutrient supply is tolerated from moderate up to good. Sycamore maple is insect-pollinated, in particular they are visited by bees and flies (Roloff & Schütt 2006).

Figure 1.5: *Acer pseudoplatanus* leaves (left), flowers (mid) and fruits (right).

Carpinus betulus belongs to the Betulaceae (Fig. 1.6) and *Tilia cordata* to the Tiliaceae (Fig. 1.7). Both are also mid- to late-successional species, have ecto-mycorrhiza, diffuse-porous xylem architecture and a higher shade tolerance than the earlier mentioned species. Hornbeam prefers areas with relatively base- and nutrient rich soils. Lime grows in a wide range of habitats and occurs in continental to oceanic regions. Hornbeam and lime are wind-pollinated (Roloff & Schütt 2006). Both species are economically rather unimportant.

Figure 1.6: *Carpinus betulus* leaves (left), flowers (middle) and fruits (right).

Figure 1.7: *Tilia cordata* fully-grown leaves (left), developing leaves (middle) and flowers (right).

Fagus sylvatica (Fig. 1.8) as a member of the family Fagaceae is a late-successional species and is known as important climax species in Central European forests. It is the main broad-leaved tree species in Germany’s forest management. From the five tree species beech has the highest shade tolerance. European beech is also wind-pollinated and has diffuse-porous xylem anatomy and ecto-mycorrhiza. The species needs adequate precipitation and can grow on nearly every type of soil. The juvenile trees are perfectly able to grow in deep shade and have therefore a high competitive ability.

Figure 1.8: *Fagus sylvatica* leaves (left), flowers (middle) and a fruit (right).

1.5 Study design

The study trees grew along the above-mentioned transect. All trees were mature, co-dominant and reached the upper sun canopy layer with their crown. The selection of the trees depended on the abundance of the tree species on that site and the accessibility by the mobile lifter. *F. excelsior* and *A. pseudoplatanus* were rather infrequent at this location. All trees were ≥ 10 m distant from each other (exception: two ash trees with 5 m distance). The heights of the five (six) trees per species was about 30 m and the DBH c. 36 cm to 50 cm.

Five tree individuals per species were selected; only for *F. excelsior* six trees were chosen. For each selected tree, three leaves were taken for the experiments. The sun leaves grew in the outer and uppermost part of the crowns. No leaf was located directly above them so that they were not shaded by other leaves. The leaves were more in the outer space of the crown because access by the mobile lifter was only possible there. The shade leaves grew in the lowermost part of the crown at the beginning of the crown basis. These leaves were closer to the trunk of the trees because the mobile lifter could reach them directly from below. The intermediate leaves taken into consideration were at the outer edge of the crown but in the middle part of it. The leaves were chosen directly between the position of the sun and shade leaves. The leaves were all fully developed and without any sign for diseases.

For each leaf, the following measuring program was processed:

- hemispherical photograph at leaf position
- height measurement, pictures of leaf and surrounding area
- A/C_i curves at 19, 25 and 29 °C at 2000 µmol m^{-2} s^{-1} with the CO_2 steps: 370, 30, 70, 100, 200, 370 (370, 370), 1200, 2000 ppm CO_2
- light response curve at 370 ppm CO_2 at 25 °C with the light steps: 2000, 1200, 500, 200, 100, 50, 20, 0, 0, 0 µmol m^{-2} s^{-1} (in 2008 in reverse order)
- sampling of the leaf and further processing in the laboratory (measuring of leaf size, leaf dry weight and C/N analysis)

The *in-situ* gas exchange measurements were carried out with a portable LI-6400XT (LI-COR Inc., Lincoln, Nebraska, USA) IRGA system equipped with a standard leaf chamber and a LED red/blue light source (type 6400-02B). The leaves were slowly adapted from the surrounding light environment to the maximum irradiance of 2000 µmol m^{-2} s^{-1} and exposed for at least 10 min. There was no strict sequential arrangement of the different measurements. When the weather was cooler I started with the 19 °C A/C_i curve, in case it was hotter, with the 29 °C A/C_i curve. The A/C_i curves were measured at three different temperatures, but for further calculation I only calculated the photosynthetic rate at 25 °C. The temperature dependence of the A/C_i curves is not included in the analysis. All measurements were accomplished from 9 a.m. to 5 p.m. on sunny or overcast days from June 22nd to August 22nd 2008 and May 29th to August 29th 2009.

The LI-6400xt (Fig. 1.9) is an open gas exchange system which measures the CO_2 concentration difference between measuring gas flow and reference gas flow. Temperature, wind speed, humidity, external light and CO_2 concentration could be controlled by the system. The leaves stayed undamaged and so repeated measurements were possible.

Figure 1.9: The measuring cuvette (left) and the control unit (right) of the Li6400xt. In the cuvette, a leaf of *C. betulus* is inserted. The IRGAs are located close to the cuvette. Left of the control unit, the gas mixing unit can be seen as well as the humidity adjuster.

The photosynthetic parameters ‘maximum carboxylation capacity’ (V_{cmax}), ‘maximum electron transport rate’ (J_{max}) and ‘maximum photosynthesis rate’ (A_{max}) as well as day time respiration rate (R_d) were calculated from the A/C_i and light response curves based on the equations of Farquhar et al. (1980), Harley & Tenhunen (1991) and Ball et al. (1987) (detailed description see Chapters 2 to 4). The photosynthesis parameters and R_d were expressed on basis of leaf area, leaf nitrogen content or leaf dry mass.

With the hemispheric photographs, canopy openness as well as relative irradiance were calculated. Both parameters give an estimate of light availability for the site where each measured leaf grew. This allowed relating photosynthetic activity to the local light climate.

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CHAPTER 2

Low-light acclimation in five temperate broad-leaved tree species of different successional status: the significance of a shade canopy

N. Legner, S. Fleck & C. Leuschner

Keywords*:* A_{max}, *Fagus sylvatica, Fraxinus excelsior,* J_{max}, mature trees, shade leaves, SLA, sun leaves, *Tilia cordata*, V_{cmax}.

2.1 Abstract

Context: Tree species differ largely in their capability to produce characteristic shade leaves with effective morphological and physiological acclimation or adaptation to low light.

Aims: By examining the sun/shade leaf differentiation in leaf morphology, foliar nitrogen and photosynthetic capacity in five temperate tree species of different successional status, we aimed at identifying those leaf traits that determine the development of a typical shade crown with low light-adapted leaves.

Methods: Leaf morphology, foliar N content, photosynthetic capacity (V_{cmax}, J_{max} and A_{max}) and leaf dark respiration (R_d) were measured in the canopies of 26 adult trees of *Fraxinus*, *Acer*, *Carpinus*, *Tilia* and *Fagus* species.

Results: Six traits (the sun/shade leaf differentiation in specific leaf area, leaf size, A_{max} per leaf area or per mass, photosynthetic N use efficiency, and R_d) were found to characterise best the degree of low-light acclimation in shade leaves. All five species exhibited certain modifications in leaf morphology and/or physiology in response to low light; *Fagus sylvatica* showed highest, *Fraxinus excelsior* lowest shade leaf acclimation.

Conclusions: Our results indicate that the five early/mid- to late-successional species have developed species-specific low-light acclimation strategies in their shade crowns which differ in terms of the relative importance of leaf morphological and physiological adaptations.

2.2 Introduction

Mixed forests are composed of tree species with often largely different size, structure, phenology and functioning of their canopies. These features control the growth rate and competitive success of the species in the stand. The degree of morphological and functional dissimilarity in the canopies of mixed forest species also determines whether complementarity in light use does occur or not. However, the study of functional differences among co-occurring tree species in mixed forests is still at its infancy, mostly because canopy access is inherently difficult.

A number of partly competing functional classification systems for temperate and tropical trees have been proposed. A widely used approach focuses on the light requirement for regeneration and distinguishes between shade-tolerant species, that can not only germinate and successfully survive in the shade but also grow there to maturity, and light-demanding species, that can survive in the canopy shade as seedlings and saplings but need gaps to grow to full size (e.g. Turner 2001). Alternatively, tree species could be grouped according to the functional properties of adult instead of juvenile trees; relevant traits could be the within-canopy light gradient and the degree of morphological and functional differentiation between a tree's sun and shade canopy. The existence of a distinct shade canopy may be decisive in competitive interactions, because it determines light transmissivity to the ground, and trees with a distinct shade canopy may be more productive than trees lacking typical shade leaves (Sims et al. 1994) as the former typically produce larger stand leaf areas (Ellenberg & Leuschner 2010). We argue that the capability of a tree to form a typical shade canopy does represent a key functional trait determining the life cycle, productivity, stress tolerance and successional status of a species.

The sun leaves in the uppermost crown and the shade leaves at the crown base represent extremes of a continuum of intra-canopy modification in leaf morphology and physiology along the vertical light gradient. With decreasing light availability from canopy top to base, leaf thickness generally decreases and specific leaf area (SLA, leaf area per mass) increases. Since nitrogen content per leaf mass (N_m) typically changes only little with light availability in the canopy, N content per area (N_a) decreases in parallel with increasing SLA from the sun to the shade crown (Niinemets 2007). Due to the close link between photosynthetic capacity and N_a

(Niinemets 2007, Shipley et al. 2005), light-saturated net photosynthesis rate (A_{max}) and its partial determinants maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) typically decrease from the upper sun to the lower shade crown. Niinemets et al. (1998) concluded from analyses in four temperate deciduous woody species that the light-dependent acclimation of SLA, and not vertical gradients in N partitioning, is the key determinant of photosynthetic capacity within the crown of woody plants. However, it is not well studied how light-dependent within-crown gradients of leaf morphology and photosynthetic capacity are differing among co-existing tree species and what biological attributes are determining these patterns of functional intra-canopy differentiation. Nonetheless, the analysis of determinants and constraints of light-dependent plasticity in leaf morphology and physiology in coexisting tree species is of great importance for a mechanistic understanding of canopy interactions and complementary light use in mixed stands. Tree ecophysiology seeks a functional grouping of tree species which should include a categorisation of the light capture and light utilisation patterns of different trees. First steps in this direction are several comparative studies mostly in tropical trees (e.g. Gourlet-Fleury et al. 2005, Turner 2001).

Species-rich Central European broad-leaved forests of the Carpinion alliance (oak-hornbeam forests) may contain up to eight mid- to late-successional broad-leaved tree species of the genera *Carpinus, Quercus, Acer, Tilia, Fagus* and *Fraxinus* that are known to differ significantly in light demand, photosynthetic capacity, maximum growth rate, and shade tolerance (Bazzaz 1979, Ellenberg & Leuschner 2010). Thus, light capture and carbon assimilation and their spatial distribution in the canopy should differ significantly among these species or genera indicating that a certain degree of complementarity in light interception and canopy space occupation in these communities must exist.

We used a mobile 30 m-lifter in a species-rich old-growth Carpinion forest to gain access to the sun and shade canopies of 26 mature trees of five tree species (genera *Fagus, Fraxinus, Tilia, Acer* and *Carpinus*) in order to compile a comprehensive data set on leaf morphological and photosynthetic traits that would allow a functional comparison of the canopies of these species. The five tree species differ markedly in terms of shade tolerance in the regeneration stage (moderate to very high), successional status (early/mid- to late-successional), canopy architecture and physiological constitution.

We searched for traits suited to describe shade canopy properties in quantitative terms and to compare the species with respect to photosynthetic light use in their shade crown. The specific aims of the study were (i) to compare the five species with respect to the morphology and photosynthetic capacity of their sun and shade leaves, (ii) to identify morphological and physiological traits with a high indicative value of the functional differentiation between the sun and shade canopy, and (iii) to rank the species according to the degree of sun/shade canopy differentiation.

2.3 Materials and methods

Study site and tree species

The study was conducted in a temperate old-growth mixed deciduous forest composed of five to 14 tree species per hectare. The forest is located on the south-eastern side of the Hainich mountain range in western Thuringia, Germany, and consists of the largest un-fragmented deciduous forest area in Germany with a size of 160 km², of which a part is protected as Hainich National Park. The study plot is a transect of approximately 200 m length and 30 m width located in the south-east of the national park near the village Weberstedt close to the location Thiemsburg (51° 05’ 00’’ N, 10° 30’ 27’’ E) at 350 m a.s.l.. The soil type is a Luvisol developed from loess over Triassic limestone. The topsoil is free of carbonates and has a pH (H_2O) in the range of 4.5 to 6.8 (Christina Langenbruch, personal communication). The Hainich forest consists of limestone beech forests (Hordelymo-Fagetum community), beech forests on moderately acid soils (Galio-Fagetum community) and mixed oak-hornbeam forests (Stellario-Carpinetum community) with *Fagus sylvatica* L. (European beech) being the most widespread and abundant species. Locally, as at the Thiemsburg site, beech is only a subordinate member of the community with *Tilia cordata* Mill. (small-leaved lime), *Carpinus betulus* L. (European hornbeam), *Fraxinus excelsior* L. (European ash) and *Acer pseudoplatanus* L. (sycamore maple) being more abundant. Other tree taxa in this forest are additional *Tilia* and *Acer* species and members of the genera *Prunus*, *Ulmus*, *Quercus* and others. The forest has been subjected to a selective cutting regime in the past, but the impact of forestry was low during the last three decades and totally ceased in 1997 with the declaration of a national park (Schmidt et al. 2009).The age of the trees ranges between 80 and 120 years (Gebauer et al. 2008).

Photosynthesis measurements were conducted in the crowns of adult *Fagus sylvatica*, *Fraxinus excelsior*, *Tilia cordata*, *Acer pseudoplatanus* and *Carpinus betulus* trees using a mobile lifter (Denka Lifter model DL30, Rotlehner Arbeitsbühnen GmbH, Massing-Oberdietfurt, Germany). The five species occur at the study site with individuals of similar demographic status in direct neighbourhood to each other. We selected five trees per species (*F. excelsior*: six) that had representative diameter-at-breast height (DBH) and tree-height dimensions for the stand (Table 2.1). All 26 trees were adult co-dominant individuals that reached with their sun crown the upper sun-lit canopy layer of the stand. Tree height was measured with a Vertex inclinometer (Vertex IV, Haglöf Inc., Langsele, Sweden); DBH was recorded with D1 dendrometer bands (UMS, Munich, Germany).

Table 2.1: Characteristics of the 26 examined tree individuals of five species. DBH is diameter at breast height. Means ± SE.

Tree species	No. of tree individuals	Tree height [m]	DBH [cm]
Fraxinus excelsior	6	27.6 ± 0.9	36.2 ± 2.6
Acer pseudoplatanus	5	30.3 ± 0.9	58.3 ± 7.1
Carpinus betulus	5	26.7 ± 0.7	45.8 ± 4.7
Tilia cordata	5	27.0 ± 1.1	43.5 ± 5.8
Fagus sylvatica	5	29.5 ± 0.6	50.0 ± 3.2

The five species differ not only with respect to their systematic position (five families) but also in terms of light demand, shade tolerance, height growth, successional status and other traits (Table 2.2). Mainly based on the existing information about the species' capability to cast shade at maturity (i.e. crown transmissivity) and their successional status in natural forest dynamics (Ellenberg & Leuschner 2010), we arranged the five species in all figures and tables in the sequence *F. excelsior – A. pseudoplatanus – C. betulus – T. cordata - F. sylvatica*.

Table 2.2: Morphological and functional traits of the five species according to a relative categorisation of species traits in Hagemeier (2002), Hölscher (2004), Le Goff et al. (2004), Ellenberg & Leuschner (2010) and others. Extreme values of tree longevity in brackets.

	Fraxinus excelsior	*Acer pseudoplatanus*	*Carpinus betulus*	*Tilia cordata*	*Fagus sylvatica*
Family	Oleaceae	Aceraceae	Betulaceae	Tiliaceae	Fagaceae
Max. height [m]	< 40	< 40	< 35	45	50
Architectural model	Rauh	Scarrone	Troll	Troll	Troll
Longevity	250 - 300	150 - 600	150 - 300	400 (-1000)	350 (-900)
Shade intensity[1]	3	4	4	4	5
Leaf production[2]	Single flush	Single flush	Single flush	Single flush	Single flush
Leaf area index[3]	5.8	5.2	8.3	7.1	7.4
Xylem anatomy[4]	Ring	Diffuse	Diffuse	Diffuse	Diffuse
Type of mycorrhiza	Arbuscular	Arbuscular	Ekto	Ekto	Ekto
Successional status	Early / mid	Mid / late	Mid / late	Mid / late	Late

[1] Relative assessment of shade intensity below mature tress (3 – moderate, 4 – high, 5 – very high); [2] at maturity; [3] LAI values from 20 stands (beech) or 2 (1) stands in the other species; [4]Ring-porous, diffuse-porous

The weather conditions of the two study years were similar with respect to temperature but differed in rainfall. The mean air temperature in 2008 was 9.5 °C (14.6 °C in the growing season from April 1st to Sep 30th) and 8.9 °C (15.1 °C) in 2009 (weather station Weberstedt/Hainich, meteomedia). The vegetation period in 2008 was relatively dry (234 mm), that of 2009 relatively moist (469 mm); the annual rainfall totals were 500 mm and 774 mm.

Sampling design

The mobile lifter allowed reaching the upper sun canopies of all trees at 30 m. The lifter could be moved along the 200 m-long transect to access the sun and shade canopies of all 26 trees for *in situ*-gas exchange measurements. The five (six) trees per species were treated as true replicates because they were at least 10 m (in most cases >20 m) apart from each other except for two ash trees (5 m). Because we aimed at comparing the five species with respect to the magnitude of the sun – shade leaf difference in morphology and physiology, we examined in a first step the vertical gradient of leaf morphology and photosynthetic capacity in all 26 trees by measuring leaves in the sun canopy, the mid canopy and the lowermost canopy and related the data to canopy openness in the canopy. Thus, each one leaf per tree was investigated *in situ* for the light and CO_2 responses of photosynthesis in the fully sun-lit upper canopy, the partly shaded intermediate crown and in the fully shaded lower crown resulting in five replicates studied per tree species and canopy position (in *T. cordata*: six sun leaf replicates; in *F. sylvatica* and *A. pseudoplatanus*: the data of one sun and one shade leaf had to be omitted resulting in only four replicates). Thus, 15 leaves per species were investigated. All measurements were done on sunny or overcast days (8 am to 5 pm) in the summers 2008 (Jun 20th – Aug 22nd) and 2009 (May 29th – Aug 29th). Based on a plot of SLA against canopy openness (CO; Fig. 2.2), we defined typical sun leaves as leaves that were exposed to direct sun light for most of the day (i.e. they were not over-topped by other leaves) which referred to CO values of 40 to 70 %. From the SLA - CO plot, we defined typical shade leaves as leaves with CO values <15 %. In the subsequent com-parison of sun and shade leaves, we omitted all leaves from the middle crown.

Gas exchange measurements and hemispherical photography

Gas exchange measurements were conducted with a portable LI-6400XT (LI-COR Inc., Lincoln, Nebraska, USA) IRGA system equipped with a standard leaf chamber and a LED red/blue light source (type 6400-02B). We investigated non-detached, fully expanded and non-senescent leaves of most distal insertion on exposed peripheral twigs in the sun canopy sections, while the leaves of the shade crowns were positioned on branches in the interior of the lower canopy. In the case of the composed leaves of ash (*F. excelsior*), we measured gas exchange on fully expanded leaflets of the middle part of the leaf. On every leaf, the CO_2 response was investigated through three A/C_i curves established at leaf temperatures of 19, 25 and 29 °C (± 1°C) under a photosynthetic photon flux density (PPFD) of 2000 $\mu mol\ m^{-2}\ s^{-1}$. Before the establishment of an A/C_i or light response curve, incident PPFD was stepwise increased to the maximum flux density (2000 $\mu mol\ m^{-2}\ s^{-1}$) and the leaves in the chamber were allowed to adapt to these conditions for at least 10 min in order to avoid reductions in stomatal conductance. The IRGA channels were matched before every measuring point. For establishing the A/C_i curves, sample $[CO_2]$ was adjusted to the following 10 concentration steps in the given order:

370, 30, 70, 100, 200, 370, 1200, and 2000 ppm CO_2. The second 370 ppm measurement was repeated one or two times if the measured assimilation rate deviated from the first measurement at 370 ppm. On the same leaves, a light response curve at 25 °C and 370 ppm CO_2 was established in 10 steps: 2000, 1200, 500, 200, 100, 50, 20, 0, 0, and 0 µmol m^{-2} s^{-1} PPFD (in 2008 in reverse order). The vapour pressure deficit was held constant at ambient conditions during a measuring campaign on a leaf (mean ± SE for the 15 data sets per species: *F. excelsior* 1.53 ± 0.02 kPa, *A. pseudoplatanus* 1.78 ± 0.02 kPa, *C. betulus* 1.60 ±0.02 kPa, *T. cordata* 1.64 ±0.02 kPa, *F. sylvatica* 1.53 ±0.02 kPa).

For every leaf, a hemispherical photograph (Nikon Coolpix 8400 camera with Nikon Fisheye Converter FC-E9) was taken with the lens positioned exactly at the location where the sampled leaf grew in order to determine canopy openness above a leaf as a proxy of seasonal integrated PPFD during summer at the leaf position.

The measured leaves were brought to the laboratory and scanned to determine leaf area. Thereafter, they were dried (70°C, 48 h) and weighed for determining specific leaf area (SLA) and analysed for the C and N concentrations (element analyzer NA 2500, CE-Instruments, Rodano, Milano, Italy) and the signature of $\delta^{13}C$ (element analyzer NA 2500, CE-Instruments, Rodano, Milano, Italy; isotope mass spectrometer Delta plus, Finnigan MAT, Bremen, Germany).

Data analysis

The gas exchange data on the light and CO_2 dependence of photosynthesis were analysed using non-linear least-square regressions implemented in Mathematica (version 3.0, Wolfram Research, Champaign, Illinois, USA). For the fitting of the A/C_i curves, the program RACCIA (Fleck 2002) was used which is based on the equations of Farquhar et al. (1980) and Harley & Tenhunen (1991) and Ball et. al. (1987). J_{max} and V_{cmax} at the standard temperature of 25 °C were calculated with a model of the temperature dependence of the photosynthetic parameters that bases on the three A/C_i curves measured at different temperatures. Light response curves were fitted with a non-rectangular hyperbolic function (Ogren & Evans 1993; Thornley 2002) in the same software environment (equation 1). In cases where more than one leaf was measured for gas exchange because the first leaf broke away due to strong wind, we used the N content and leaf area data of the leaf that was analysed for the 25 °C A/C_i curve. To characterize the photosynthetic capacity of leaves, we chose the parameters light-saturated net photosynthesis rate under ambient CO_2 concentration (A_{max}), which was derived by non-linear regression with equation (1) from the light response curve, and maximum carboxylation rate (V_{cmax} from equation 2), maximum electron transport rate (J_{max} from equation 3) and 'dark respiration rate' (R_d), the latter three being calculated from the A/C_i curves according to the Farquhar model (von Caemmerer & Farquhar 1981) and the approach outlined in Brooks & Farquhar (1985). All parameters were expressed alternatively in relation to leaf area, leaf mass and foliar N content.

The expression for calculating A_{max} (on leaf area basis) is given by equation (1):

$$A_{\max} = -\left(\frac{A\ \alpha\ PAR - \xi\ A^2}{A - \alpha\ PAR} \right) \tag{1}$$

with A being the leaf photosynthetic rate at a given photosynthetically active radiation (PAR), ξ a factor which determines the sharpness in the knee of the non-rectangular hyperbolic curve (set to 0.9; Thornley 2002), and α the initial slope of the light response curve (quantum efficiency of photosynthesis).

V_{cmax} and J_{max} (on leaf area basis) were calculated by the equations (2) and (3):

$$V_{c\max} = \frac{(A+R_d)\left(C_i + K_c\left(\frac{1+O}{K_c}\right)\right)}{\left(1-\frac{\Gamma_*}{C_i}\right)C_i} \tag{2}$$

$$J_{\max} = \frac{(A+R_d)(4C_i + 8\Gamma_* C_i)}{4(C_i - \Gamma_*)} \tag{3}$$

with A being assimilation rate, R_d leaf dark respiration rate, C_i the intercellular CO_2 concentration, K_c the Michaelis-Menten constant for carboxylation, O the oxygen concentration at the site of fixation and Γ_* the CO_2 compensation point without consideration of mitochondrial respiration.

The hemispherical photographs were analyzed with the program GLA (version 2.0, SFU, Burnaby, Canada) to calculate canopy openness in %. The following supplementary information was incorporated in the analysis: (1) The growing season lasted from May 1st to September 15th in both years, (2) the beam fraction (fraction of direct radiation, 0.38) and the spectral fraction (0.34) were derived from the cloudiness index (0.46) which was calculated from the measured data, and (3) the clear-sky transmission coefficient for direct radiation through the atmosphere was set to 0.6 (Frazer et al. 1999).

As we aimed at comparing the five species with respect to sun – shade leaf differences in foliar morphology and physiology, we pooled in the analysis all sun or shade leaves of a species that met the mentioned criteria. All photosynthetic parameters were analysed for a dependence on time (day of the year); none of the parameters showed such a dependency (data not shown). We then compared the data from 2008 with those from 2009 but found no significant inter-annual difference; thus, both years were pooled. The lower summer precipitation in 2008 than in 2009 and a possible reduction in photosynthetic capacity were not visible in our data. Phenotypic plasticity was calculated as an index (ranging from 0 to 1) for each variable and species as the difference between the maximum and minimum value in the canopy divided by the maximum value (Valladares et al. 2002).

The statistical analyses were carried out with the software R, version 2.0.8 (R Development Core Team 2008) and SAS 9.2 (SAS Institute, Cary, NC, USA). As the assumption of ANOVA and ANCOVA were not met by all data sets, we analysed differences between the five species with a permutation test at a significance level of $p \leq 0.05$ by applying the routine perm in R (using the tests permKS and permTS, exact enumeration) (Fay & Shaw 2010). The Wilcoxon test with a significance level of $p \leq 0.05$ was used for detecting differences between the sun and shade leaves of a species. Differences between means with a significance of $0.05 < p \leq 0.1$ were treated as ‘marginally significant’.

2.4 Results

Within-canopy gradients of irradiance and leaf traits

In the canopies of all five species, canopy openness decreased rapidly from the tree top to a relative canopy height of ~0.7 (lower sun canopy), where about 10 % of incident radiation was available (Fig. 2.1a). SLA increased and foliar nitrogen content per area (N_a) decreased from the canopy top to the base at markedly different slopes in the five species (Figs 2.1b and 2.1c, Table 2.3). Steeper SLA increases were found for *F. excelsior* and *A. pseudoplatanus* than for the other three species, while the N_a decrease from top to base was particularly large in *C. betulus* and *T. cordata* and less steep in the other three species. Plotting SLA against canopy openness as a proxy of integrated PPFD during leaf development and exposure gave tight relationships that were described in all five species with functions of the form $y = 1 * (ax + b)^{-1}$ (Fig. 2.2). Accordingly, the downward decrease in canopy openness was linked to a continuum of leaf morphological types from the typical sun to the typical shade leaves in all species. However, distinct shade leaves with a very high SLA (>200 up to 400 $cm^2\ g^{-1}$) were only found in *C. betulus, T. cordata* and *F. sylvatica*. With SLA values in the range of 130-200 $cm^2\ g^{-1}$, the shade leaves of *F. excelsior* and *A. pseudoplatanus* differed less from the respective sun leaves (difference approx. 100 $cm^2\ g^{-1}$), while the sun-shade leaf difference was much more pronounced in the first three species (approx. 200 $cm^2\ g^{-1}$). In its average over the canopy, leaf size was largest in *F. excelsior* (difference significant to the other species for sun and shade leaves). Significantly larger shade than sun leaves were found only in two species, *T. cordata* and *F. sylvatica* (Table 2.3). All five species were characterised by significantly higher N_a and $\delta^{13}C$ values and lower SLA values in their sun than shade leaves (N_a differences only marginally significant in *F. excelsior*; Table 2.3).

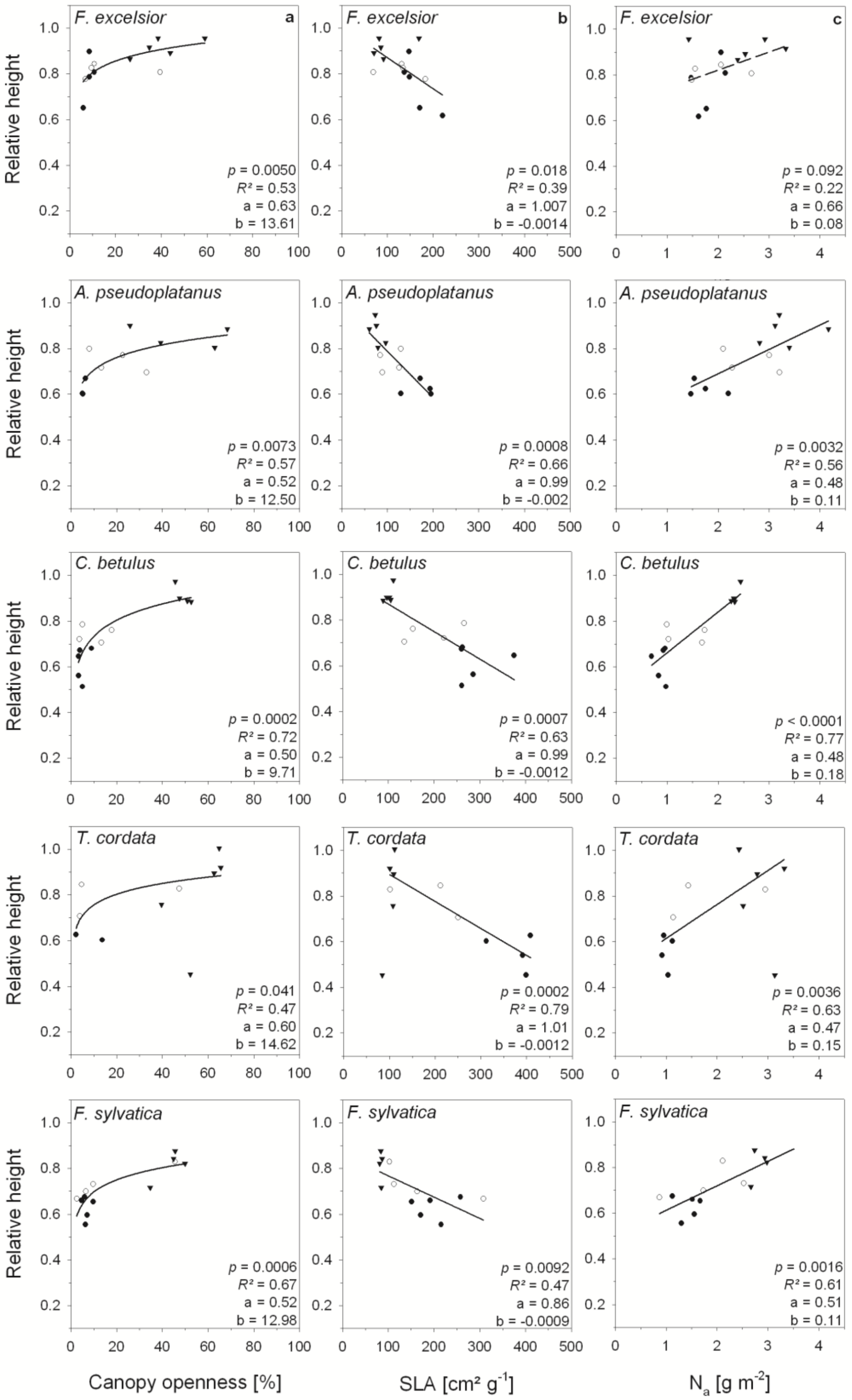

Figure 2.1: Relationship between relative height in the canopy and relative irradiance (a), SLA (b) or N_a (c) for leaves in the sun (filled triangles), the intermediate (open circles) and the shade crown (filled circles) of the five tree species. Given are *p*, *R²* and the coefficients a and b for the regression equations (canopy openness: y = a + ln x / b; SLA and N_a: y = a + bx).

Table 2.3: Leaf area, SLA, N_a and $\delta^{13}C$ signature of typical sun and typical shade leaves of the five species according to the definition based on canopy openness given in the Methods section (means ± SE). PI – plasticity index after Valladares et al. (2002). Different lower case letters indicate significant ($p < 0.05$) differences between the sun and shade leaves of a species (Wilcoxon test); different capital letters significant differences between the shade leaves of the species and different Greek letters significant differences between the sun leaves of the species (both tested by permutation test).

Species	n	Leaf size [cm²]	SLA [cm² g^{-1}]	N_a [g m^{-2}]	$\delta^{13}C$ [‰]
F. excelsior sun	5	289.5 ± 63.9 $^{a\,\Gamma}$	99.9 ± 17.7 $^{a\,\Gamma}$	2.5 ± 0.3 $^{a\,\Gamma}$	-25.7 ± 0.3 $^{a\,\Gamma}$
F. excelsior shade	5	202.0 ± 54.0 $^{a\,A}$	164.9 ± 15.0 $^{b\,B}$	1.5 ± 0.1 $^{a\,A}$	-27.8 ± 0.4 $^{b\,B}$
PI		0.965	0.680	0.573	
A. pseudopl. sun	5	79.6 ± 7.9 $^{a\,\Delta}$	77.2 ± 5.8 $^{a\,\Gamma}$	3.3 ± 0.2 $^{a\,\Delta}$	-26.4 ± 0.5 $^{a\,\Gamma}$
A. pseudopl. shade	4	79.9 ± 11.1 $^{a\,B}$	172.7 ± 15.2 $^{b\,B}$	1.7 ± 0.2 $^{b\,A}$	-30.2 ± 0.3 $^{b\,A}$
PI		0.475	0.691	0.648	
C. betulus sun	5	26.5 ± 3.4 $^{a\,\Delta}$	100.7 ± 3.8 $^{a\,\Gamma}$	2.3 ± 0.03 $^{a\,\Gamma}$	-26.0 ± 0.5 $^{a\,\Gamma}$
C. betulus shade	5	27.4 ± 2.2 $^{a\,B}$	288.6 ± 22.2 $^{b\,AC}$	0.9 ± 0.1 $^{b\,B}$	-29.3 ± 0.2 $^{b\,C}$
PI		0.537	0.764	0.717	
T. cordata sun	6	25.6 ± 3.5 $^{a\,\Delta}$	102.7 ± 4.1 $^{a\,\Gamma}$	2.9 ± 0.1 $^{a\,\Delta}$	-27.7 ± 0.2 $^{a\,\Delta}$
T. cordata shade	5	47.9 ± 2.8 $^{b\,B}$	349.6 ± 32.9 $^{b\,A}$	1.1 ± 0.1 $^{b\,C}$	-30.6 ± 0.3 $^{b\,A}$
PI		0.653	0.793	0.724	
F. sylvatica sun	4	18.6 ± 2.8 $^{a\,\Delta}$	83.5 ± 1.1 $^{a\,\Gamma}$	3.0 ± 0.2 $^{a\,\Delta}$	-26.4 ± 0.2 $^{a\,\Gamma}$
F. sylvatica shade	5	31.1 ± 2.5 $^{b\,B}$	197.3 ± 18.5 $^{b\,BC}$	1.4 ± 0.1 $^{b\,AC}$	-28.7 ± 0.3 $^{b\,BC}$
PI		0.682	0.686	0.680	

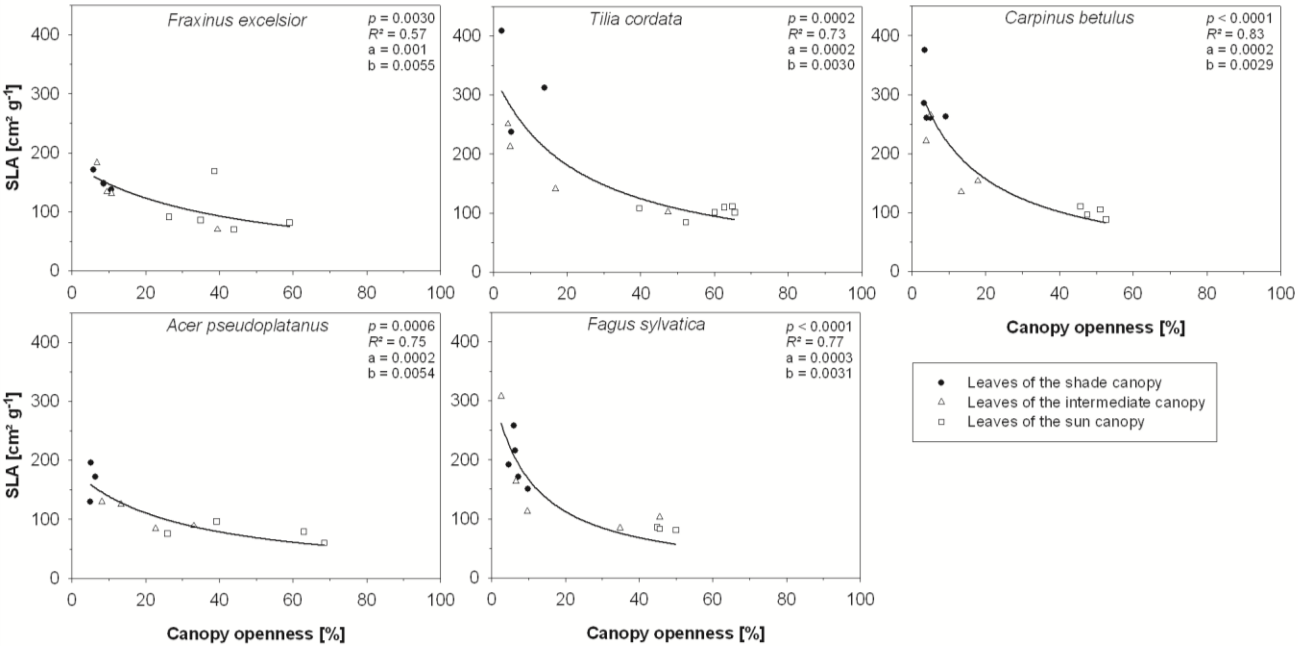

Figure 2.2: Dependence of specific leaf area (SLA) on canopy openness in the five tree species. Each point represents one leaf; the symbols indicate the three sun, intermediate and shade crown sections. The hyperbolic regression function has the form: $y = 1 * (ax + b)^{-1}$.

Photosynthetic and respiratory activity on a leaf area basis

Despite a considerable among-species variation in the three parameters used to characterise photosynthetic capacity ($V_{cmax,a}$ – maximum carboxylation rate, $J_{max,a}$ – maximum electron transport rate, $A_{max,a}$ – light-saturated net photosynthesis rate), significant species differences in sun leaf photosynthetic capacity were only detected for $V_{cmax,a}$ between *F. excelsior* and *C. betulus* but not between the other species. In our sample, a significant species differences was absent for sun leaf $A_{max,a}$. The range of species means for sun $V_{cmax,a}$ values was 56-81 µmol CO_2 m^{-2} s^{-1}, for $J_{max,a}$ 113-174 µmol e^{-} m^{-2} s^{-1} and for $A_{max,a}$ 7.6-15.8 µmol CO_2 m^{-2} s^{-1} (Fig. 2.3a–c). However, non-significant trends appeared pointing to somewhat lower $V_{cmax,a}$ and $A_{max,a}$ means in the sun leaves of *F. sylvatica* and *C. betulus* and to higher values in *F. excelsior*, *T. cordata* and *A. pseudoplatanus*. The among-species variation was larger in the shade leaves. A particularly low photosynthetic capacity (all three parameters) was observed in the shade leaves of *C. betulus* (significantly different from *F. excelsior*, *A. pseudoplatanus* or *F. sylvatica*, depending on the parameter), while *F. sylvatica* and *T. cordata* were intermediate and shade leaves of *F. excelsior* and *A. pseudoplatanus* reached highest values of $V_{cmax,a}$, $J_{max,a}$ and $A_{max,a}$.

The sun leaves had significantly higher photosynthetic capacities than the shade leaves of a species in *T. cordata* and *C. betulus* (all three parameters), *F. excelsior* ($V_{cmax,a}$ and $J_{max,a}$), *A. pseudoplatanus* ($J_{max,a}$), and *F. sylvatica* ($V_{cmax,a}$) (Fig. 2.3a-c).

Leaf dark respiration ($R_{d,a}$) as derived from the A/C_i curve varied between 1.1 and 2.5 µmol CO_2 m^{-2} s^{-1} in the sun leaves and between 0.7 and 1.5 µmol CO_2 m^{-2} s^{-1} in the shade leaves of the five species (species means, Fig. 2.3d).The sun-shade leaf difference was significant only in *F. excelsior* (Fig. 2.3d) and showed a non-significant tendency toward smaller $R_{d,a}$ values in the shade leaves for *F. sylvatica*.

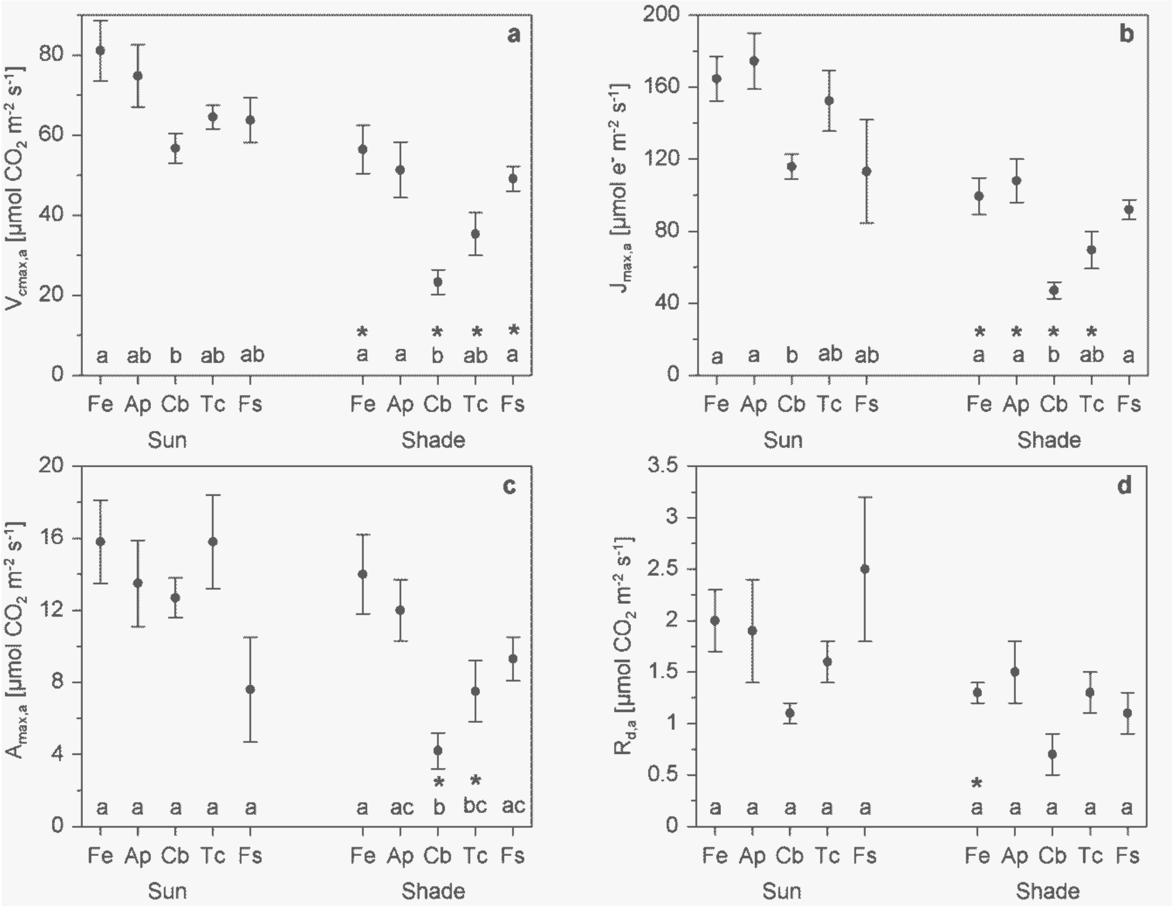

Figure 2.3: Parameters of leaf gas exchange for the sun and shade canopies of the five species expressed on a leaf area basis. Only data from typical sun and typical shade leaves according to the definition based on canopy openness given in the Methods section are considered. $V_{cmax,a}$ - maximum carboxylation rate (a), $J_{max,a}$ – maximum electron transport rate (b), $A_{max,a}$ – light saturated net photosynthesis rate (c) and $R_{d,a}$ – leaf dark respiration rate (d). Given are means ± SE. n = 4-6 (sun leaves) or 4-5 (shade leaves). Different letters indicate significant ($p < 0.05$) differences between the species in the sun or shade leaf category (permutation test), asterisks mark significant differences between sun and shade leaves of a species (Wilcoxon test). Species acronyms: Fe *Fraxinus excelsior*, Ap *Acer pseudoplatanus,* Cb *Carpinus betulus*, Tc *Tilia cordata* and Fs *Fagus sylvatica.*

Photosynthetic and respiratory activity on a leaf mass basis

The photosynthetic capacity per leaf mass of the sun leaves showed a tendency for a decrease in the sequence *F. excelsior* > *T. cordata* > *A. pseudoplatanus* > *C. betulus* > *F. sylvatica*, but none of the species differences in $V_{cmax,m}$, $J_{max,m}$ and $A_{max,m}$ were significant (Fig. 2.4a-c). In the shade leaves, *C. betulus* had the lowest and *T cordata* the highest mass-specific activities of all species (differences significant; Fig. 2.4a). With respect to shade leaf-$A_{max,m}$, *C. betulus* had a significantly lower activity than *F. excelsior*, *T. cordata* and *A. pseudoplatanus* (Fig. 2.4c). This species ranking differed from the sequence in area-related activity where highest shade leaf photosynthetic rates were found in *A. pseudoplatanus* and *F. excelsior*. The mass-related photosynthetic activity of the shade leaves was generally higher than that of the sun leaves, which contrasts with leaf area-related activity. This sun-shade leaf difference was significant for *T. cordata* and *F. sylvatica* (all parameters) and *A. pseudoplatanus* ($A_{max,m}$ only); further, at marginal significance only, shade leaves had a higher $A_{max,m}$ in *T. cordata*, and a higher $J_{max,m}$ in *A. pseudoplatanus* than the respective sun leaves.

Leaf dark respiration on a mass basis ($R_{d,m}$) was significantly higher in shade than in sun leaves in *T. cordata* and tended to do so in *C. betulus* as well (Fig. 2.4d). Concerning $R_{d,m}$, no species differences appeared in the sun leaves, while in the shade leaves, *T. cordata* reached significantly higher $R_{d,m}$ means than *F. excelsior*, *C. betulus* and *F. sylvatica*.

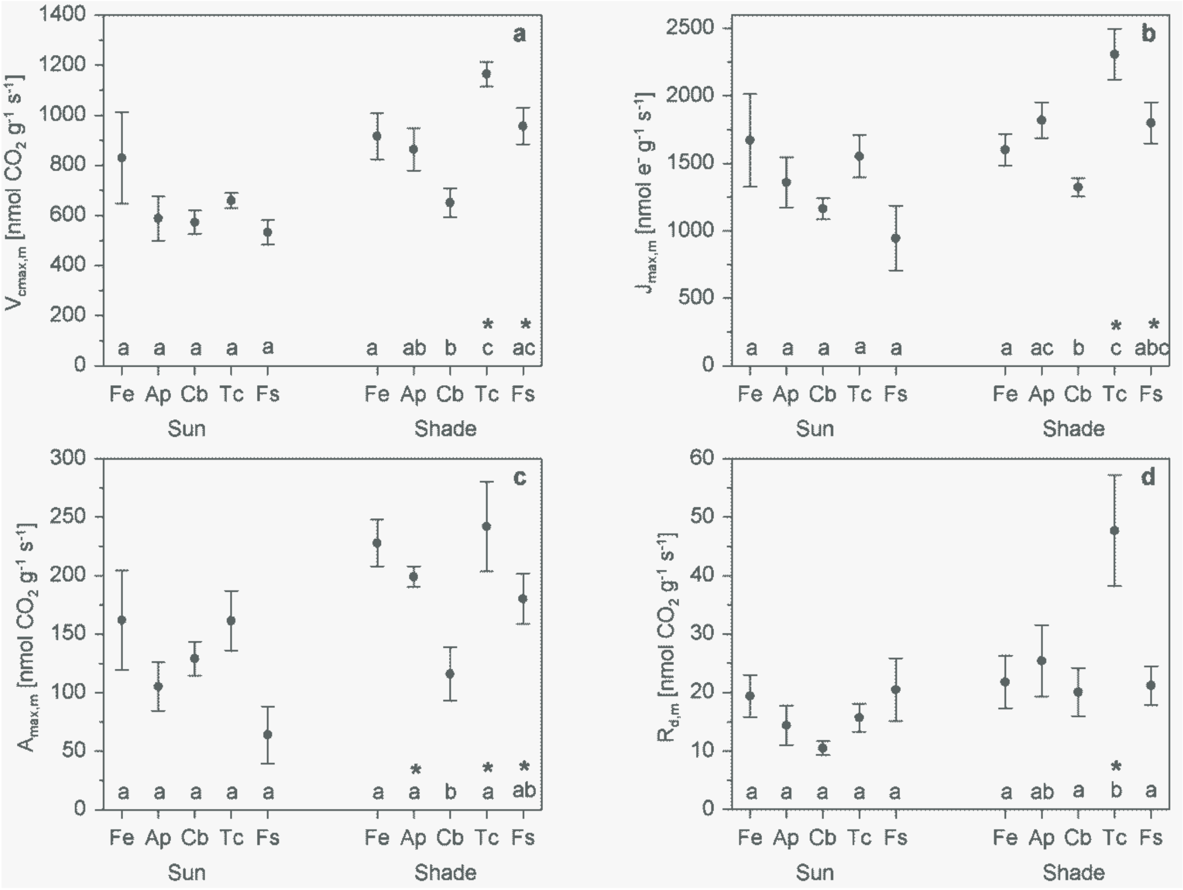

Figure 2.4: Parameters of leaf gas exchange for the sun and shade canopies of the five species expressed on a leaf mass basis. Only data from typical sun and typical shade leaves according to the definition based on canopy openness given in the Methods section are considered. $V_{cmax,m}$ - maximum carboxylation rate (a), $J_{max,m}$ – maximum electron transport rate (b), $A_{max,m}$ – light saturated net photosynthesis rate (c) and $R_{d,m}$ – leaf dark respiration rate (d). Given are means ± SE. For further explanation see Fig. 2.3.

Apparent photosynthetic nitrogen use efficiency

The five species were more similar in terms of their V_{cmax} and J_{max} rates scaled to leaf nitrogen than in the leaf area- or leaf mass-related photosynthetic activities. In fact, photosynthetic nitrogen use efficiency (PNUE) did not show any significant differences among the five species, neither in the sun nor the shade leaves (exception: higher sun leaf $A_{max,N}$ values in *C. betulus* than in *F. sylvatica*; Fig. 2.5a-c). However, *Fagus* sun leaves reached only half of the N-related $A_{max,N}$ rate of that of *Fraxinus* sun leaves (difference not significant). In general, PNUE tended to be higher in the shade than in the sun leaves of a species; this sun-shade leaf difference was significant for *F. sylvatica* ($V_{cmax,N}$, $J_{max,N}$, $A_{max,N}$), *T. cordata* ($V_{cmax,N}$) and *A. pseudoplatanus* ($A_{max,N}$).

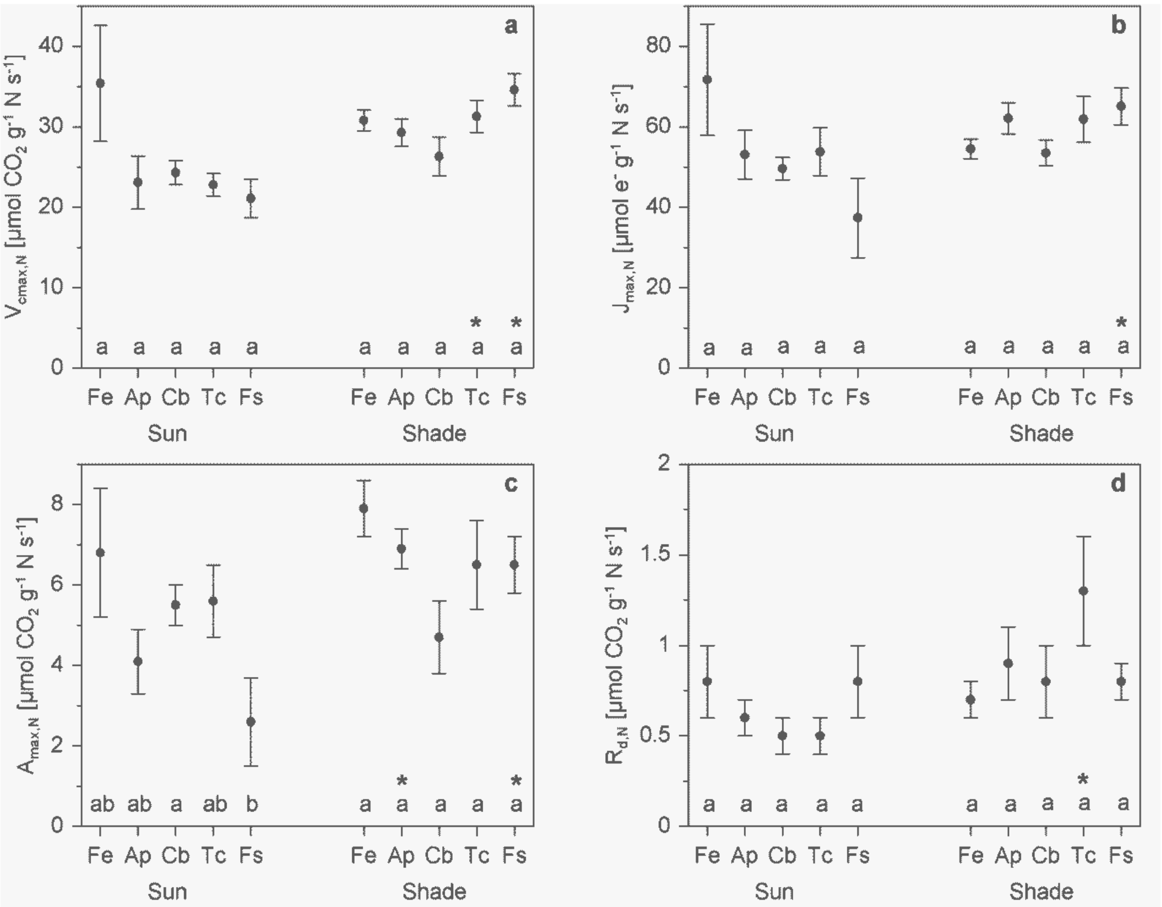

Figure 2.5: Parameters of leaf gas exchange for the sun and shade canopies of the five species expressed in relation to foliar N content. Only data from typical sun and typical shade leaves according to the definition based on canopy openness given in the Methods section are considered. $V_{cmax,N}$ - maximum carboxylation rate (a), $J_{max,N}$ – maximum electron transport rate (b), $A_{max,N}$ – light saturated net photosynthesis rate (c) and $R_{d,N}$ – leaf dark respiration rate (d). Given are means ± SE. For further explanation see Fig. 2.3.

Dark respiration expressed per leaf N ($R_{d,N}$, Fig 2.5d) was remarkably uniform among the five species (means of 0.45-1.13 µmol CO_2 g N^{-1} s^{-1}) with a significant difference only in *T. cordata* toward higher N-specific respiration rates in shade than in sun leaves.

2.5 Discussion

Species differences in the functional differentiation between sun and shade leaves

The within-canopy variation in leaf morphological traits indicates that *T. cordata*, *C. betulus* and *F. sylvatica* have a higher low-light acclimation potential than *F. excelsior* and *A. pseudoplatanus*. Probably the most influential leaf morphological property that distinguishes *F. excelsior* and *A. pseudoplatanus* from the former three species is the within-canopy variability of specific leaf area (Niinemets et al. 1998). The shade leaves of ash and maple never exceeded SLA values of 200 cm^2 g^{-1}, even though typical sun leaves of all five species were more or less similar with respect to SLA (80 to 120 cm^2 g^{-1}). *F. excelsior* and *A. pseudoplatanus* trees lack not only shade leaves with very high SLA but also cast less shade than *T. cordata*, *C. betulus* and *F. sylvatica.* It must remain open whether a higher shade canopy light transmissivity as found in ash and maple is primarily narrowing the SLA range of a species, or whether inherent shade leaf architectural constraints are primarily restricting the leaf area in the shade crown of the species, thus reducing below-canopy shade intensity.

The five species also differed markedly with respect to the leaf size difference between sun and shade canopy. Much larger shade than sun leaves were found in *T. cordata* (on average 87 % larger) and *F. sylvatica* (67 %, both differences significant) while only small (non-significant) or no differences existed in *A. pseudoplatanus* and *C. betulus* (<5 %). Remarkably, in *F. excelsior*, we found a larger, and not smaller, average leaf size in the sun than in the shade canopy (30 % larger area of all leaflets; difference not significant). Leaf size gradients in the canopy often reflect the vertical decrease in light availability in the crown. However, they can also be an expression of variable stress intensities in different parts of the canopy imposed by gradients in the atmospheric saturation deficit and the hydraulic conductivity of the axes in the crown. The surprising leaf size increase in *F. excelsior* may either indicate that ash sun leaves have a low susceptibility to drought and/or heat stress, or that the hydraulic architecture of this ring-porous species largely reduces the risk of water shortage and hydraulic failure in top canopy branches. Experiments are needed to distinguish between light and water status effects on leaf size development. Irrespective of the underlying causes, the specific leaf size patterns in ash are further support for the conclusion that this species has no morphologically distinct shade canopy and is exhibiting an intermediate position between typical pioneer and mid-successional trees.

The rather sharp distinction in terms of leaf morphological acclimation between *F. excelsior* and *A. pseudoplatanus* on the one side, and *T. cordata*, *C. betulus* and *F. sylvatica* on the other side, is only partly reflected by the data on photosynthetic capacity. Four of the five species (including *F. excelsior*) showed pieces of evidence for an effective acclimation of leaf photosynthetic activity and/or leaf dark respiration rate to the reduced light availability in the lower canopy, either by exhibiting relatively high $A_{max,m}$ rates or reduced $R_{d,a}$ rates (as in *F. excelsior*). Both traits may help to improve the C balance of the shade leaves. An exception was *C. betulus* which appeared to be poorly acclimated to low light in its leaf physiology despite much thinner (but not larger) shade than sun leaves. Thus, physiological acclimation to low light may occur even when only moderate or low leaf morphological modification occurs (as in *F. excelsior* and *A. pseudoplatanus*), but morphological acclimation may also take place without distinct physiological modifications (as in *C. betulus*).

Exposed sun leaves of *Fraxinus*, *Tilia*, *Carpinus* and *Acer* at 25-30 m height in the canopy reached mean $A_{max,a}$ rates between 12.7 and 15.8 µmol CO_2 m^{-2} s^{-1} which is higher than photosynthetic capacities reported for late-successional temperate broad-leaved trees (6-12 µmol CO_2 m^{-2} s^{-1}) but is in the lower range of $A_{max,a}$ rates thought to be characteristic for fast-growing pioneer species (12-25 µmol CO_2 m^{-2} s^{-1}; Ellenberg & Leuschner 2010, Larcher 1994). Other studies with mature trees of the four mentioned genera showed comparable sun leaf-$A_{max,a}$ rates in the case of temperate *Fraxinus* species (9-20 µmol CO_2 m^{-2} s^{-1}; Bassow & Bazzaz 1997, Hölscher 2004, Le Goff et al. 2004), but somewhat lower rates in case of temperate *Tilia* species (9-13 µmol CO_2 m^{-2} s^{-1}; Hölscher 2004, Leuzinger et al. 2005, Urban et al. 2007), *Carpinus betulus* (8-14 µmol CO_2 m^{-2} s^{-1}; Hölscher 2004, Leuzinger et al. 2005) and *Acer* species (7-13 µmol CO_2 m^{-2} s^{-1}; Bassow & Bazzaz 1997 Hölscher

2004, Jones & Thomas 2007, Urban et al. 2007). Not all of the cited studies measured $A_{max,a}$ in the exposed uppermost branches of the sun canopy of tall trees, as in the present study. This discrepancy may be one reason for the somewhat lower sun leaf values reported on average in the literature.

The relatively low sun leaf $A_{max,a}$ rates found for *F. sylvatica* in our study (mean: 7.6 µmol CO_2 m^{-2} s^{-1}) match only partly with the available literature data, where a wide range of values between 6 and >16 µmol CO_2 m^{-2} s^{-1} has been reported for adult beech trees (Lebaube et al. 2000, Leuzinger et al. 2005, Lichtenthaler et al. 1981, Matyssek et al. 2006, Schulze 1970, Urban et al. 2007). The relatively low $A_{max,a}$ values in the Hainich forest might in part be the result of photoinhibition or drought-induced stomatal limitation of photosynthesis in the sun crown of *Fagus*. We found a comparatively low leaf conductance in beech sun leaves (< 0.1 mol H_2O m^{-2} s^{-1}) on several measuring days.

The among-species variation in $A_{max,a}$ was larger in the shade leaves than in the sun leaves (range of species means: 4.2-14.0 vs. 7.6-15.8 µmol CO_2 m^{-2} s^{-1}). Relatively high shade leaf photosynthetic capacities were reached by early/mid-successional ash but also by the mid/late-successional species *A. pseudoplatanus*. One factor that certainly has contributed to the apparent A_{max} uniformity in the sun canopies of the five species is that the light climate is more similar among the species in the uppermost sun crown than in the lower shade canopies.

The foliar $\delta^{13}C$ signatures support the view that the gas exchange patterns of the foliage must be more similar among the species than leaf morphology. $\delta^{13}C$ showed no clear difference between the two groups of species, neither in the sun nor the shade leaves, and all species had by 2-3 ‰ lower $\delta^{13}C$ values in their shade leaves compared to the sun leaves. This apparent uniformity may indicate that the leaves of the five species are exposed to rather similar microclimatic gradients from canopy top to bottom which seems to overrule any species-specific differences in leaf physiology.

Within-canopy variation in photosynthetic capacity

We found two general assumptions of the sun/shade leaf paradigm (e.g. Niinemets 2010, Valladares & Niinemets 2008, Walters 2005) not or only partly supported by our data. First, contrary to the frequent observation that mass-specific photosynthetic parameters vary only little with light availability (Ellsworth & Reich 1993, Niinemets et al. 1998, Poorter et al. 2009), $V_{cmax,m}$ and $J_{max,m}$ were generally higher in the shade than in the sun leaves of our species (significant in two species, tendencies in one further species) indicating higher concentrations and activity of photosynthetic enzymes per leaf dry mass in the shade foliage. A generally higher mass-specific shade leaf photosynthetic activity was also found for $A_{max,m}$, i.e. photosynthetic capacity under the influence of environmental constraints. With respect to mass-specific A_{max}, the literature gives no coherent picture of sun/shade leaf differences in temperate trees. While several authors reported higher rates in sun leaves, e.g. Lichtenthaler et al. (1981) in *F. sylvatica* and Jones & Thomas (2007) in *Acer saccharum*, others reported the opposite. For example, Masarovicova & Stefancik (1990) found in *F. sylvatica* a slightly higher $A_{max,m}$ in sun than in shade leaves.

Second, due to the comparatively high $A_{max,m}$ rates measured in the shade leaves, three species (*F. excelsior*, *A. pseudoplatanus* and *F. sylvatica*) had equally high area-specific A_{max} rates in the shade and the sun leaves despite a substantially smaller SLA of the latter. Sun leaf photosynthetic activity per leaf area was only in *T. cordata* and *C. betulus* significantly higher than shade leaf activity.

Several explanations for this surprising result might be possible:

(1) the A_{max}/N ratio (instantaneous photosynthetic N use efficiency) of shade leaves was significantly higher than that of sun leaves in two species, and tended to be higher in another one, perhaps due to a smaller mesophyll resistance to CO_2 diffusion in shade leaves with thinner cell walls (Tholen & Zhu 2011). There is a need for more empirical data on mesophyll conductance for CO_2 comparing different leaf types and tree species.

(2) Drought-sensitive species such as *F. sylvatica* (Köcher et al. 2009) may suffer from a temporarily reduced photosynthetic capacity due to photoinhibition and/or drought stress in the sun canopy. Leaf conductance measurements in sun canopy leaves of beech during summer dry spells showed temporary reductions in leaf conductance and actual photosynthetic capacity on hot summer days in the Hainich forest as it was observed in the uppermost sun leaves of other Central European

F. sylvatica stands (e.g. Kutsch et al. 2001). However, we obtained no indication of a lasting reduction in J_{max} or V_{cmax} in dry spells, i.e. a reduction in the quantity and activity of photosynthetic enzymes in the leaf.

(3) Sun flecks tend to weaken the vertical within-canopy gradients of light availability and photosynthetic capacity on clear days, thereby reducing the contrast between sun and shade leaves (dePury & Farquhar 1997). This effect should be relevant in particular in climates with low cloudiness in summer as in the Hainich region, but it might act in a similar way in all investigated tree species.

An unexpected result was that the dark respiration rate per leaf mass and also per unit N tended to be higher, and not lower, in shade than in sun leaves in three species (*T. cordata*, *A. pseudoplatanus* and *C. betulus*), which caused area-specific R_d to be relatively high (though lower than in sun leaves). A possible explanation is the generally higher mass-specific photosynthetic activity in the shade than in the sun leaves in these species which may well have stimulated the demand for respiratory energy. However, it must be taken into account that the respiration data were estimated from the A/C_i curves; these values usually have a relatively low accuracy.

Factors that may determine the formation of a shade canopy

Different plant traits might determine a tree species' capability to produce and maintain acclimated shade leaves which can operate with a positive C balance under very low irradiances (< approx. 10 % of incident radiation) and simultaneously are casting deep shade on the forest floor (Ellenberg & Leuschner 2010, Hagemeier 2002). Producing adapted shade leaves may have advantages with respect to productivity because trees with a distinct shade canopy typically produce larger leaf areas (Falster & Westoby 2003) which may result in larger carbon gain and higher relative growth rates (Sims et al. 1994, Valladares & Niinemets 2008). Further, a shade canopy can be a very effective means for suppressing competitors (Ellenberg & Leuschner 2010). However, the formation of a shade canopy may also have disadvantages for the tree, notably a higher drought sensitivity or increased susceptibility to leaf herbivory (Hallik et al. 2009, Valladares & Niinemets 2008).

It appears that different temperate broad-leaved tree species possess contrasting upper SLA limits (e.g. 200 or 400 $cm^2\,g^{-1}$) that cannot be exceeded because a minimum of sclerenchymatic structure in the lamina is needed for stability, for counteracting herbivore attack and for withstanding drought. The production of very thin (and often large) shade leaves with highly efficient light harvesting may indeed conflict with a species' water and nutrient economy. Screening of data bases revealed that temperate tree species that produce leaves with high SLA are typically more shade tolerant and more effective in light-harvesting but they are also more drought susceptible (Hallik et al. 2009). In support of such a trade-off, *F. sylvatica* with its well-developed shade canopy is known to be more drought-sensitive than *F. excelsior*, *C. betulus* and *T. cordata* (Köcher et al. 2009) with the latter species' distribution ranges extending toward the summer-dry, more continental regions of Europe (Ellenberg & Leuschner 2010).

The acquisition and utilisation strategies for nitrogen may differ substantially between co-existing broad-leaved tree species which possibly may have consequences for the capability to produce shade leaves (Ellenberg & Leuschner 2010, Wallenda et al. 2000). In our study, the shade leaves of all five species had higher mass-specific N contents than the respective sun leaves (data not shown). Thus, when the fraction of shade leaf mass in total leaf mass is increased, a higher N demand for leaf area development is a consequence.

We speculate that it may be a question of N availability whether the formation of an extended shade canopy is possible or not, even though two of the five species (*A. pseudoplatanus* and *F. sylvatica*) had higher apparent photosynthetic N use efficiencies ($A_{max,N}$) in their shade leaves as compared to the sun leaves. The role of N availability for the competitive ability of trees that form distinct shade canopies is not clear yet, however. Niinemets (2010) suggested that trees with continuous leaf production (as many pioneer trees) should be capable of only moderate low-light acclimation because the average leaf is shorter lived than in trees with a single leaf flush, and continuous leaf death inevitably results in losses of chlorophyll and N. While N-limited environments should promote plants with longer lived leaves and thus with a greater light-acclimation potential, N shortage could also restrict the development of a distinct shade crown, when this canopy type is associated with a higher leaf area index and thus with higher C and N investments in the canopy per ground area.

It is possible that the constancy of the light climate is a more decisive factor for shade leaf production than N availability. Fast-growing canopies should mainly produce sun leaves with higher leaf turnover allowing for a more dynamic response to changing light climates during ontogenesis than is possible in trees with distinct shade canopies. This may suggest that the formation of distinct shade canopies should only be possible in stands where intensive light competition has already resulted in a stabilised community composition with only reduced temporal variation in light availability inside the canopy. In our tree species sample, ash is a species which often grows in stand development stages with dynamic change in light availability where highly adapted shade leaves may not be an advantage (Gregor & Seidling 1997).

Any generalisation about functional differences between sun- and shade-acclimated leaves must consider the time horizon of low-light acclimation. Different results may be obtained when comparing the leaves of juvenile trees that were grown under different irradiances, or when contrasting sun leaves with shade leaves within the canopy of a single tall tree. In the first case, the low-light acclimation of independent leaves with similar position on the shoot of different plants is analysed, while the second approach compares leaves growing on the same tree individual with presumed physiological interactions between sun and shade canopy. A further distinction is needed between trees that produce their leaves in a single leaf flush at the beginning of the growing season (such as the five species of the study), and fast-growing pioneer trees with continuous leaf development (e.g. *Populus*). The former possess sun and shade leaves of similar age along a steep within-canopy light gradient, while, in the latter, the shade leaves typically have a higher age than the sun leaves because the leaves at lower canopy height were produced earlier and are increasingly overtopped by newly formed branches and shaded by more recent sun leaves.

Our study investigated the within-canopy light acclimation potential of the leaves of tall trees in a closed stand, i.e. under natural conditions. The leaves were mostly of similar age because all species were mid- to late-successional species with single-flush leaf phenology. While we found clear species differences in the low-light acclimation potential, we recognise that the steepness of the vertical light gradient in the canopy differs between the five species, because radiation extinction in the canopy is largely determined by species-specific foliage distribution and light interception properties. We see a strength of our study in the fact that all 26 examined trees of different species grew in close proximity to each other in a closed stand which ensures similar overall climatic and edaphic conditions and thus allows to identify species differences in light acclimation under natural conditions. Clearly, every tree creates a specific environment in its crown through its specific canopy architecture and competitive ability for resources which sets ultimate limits for the comparison of tree species and their adaptive potential to low light.

Conclusions

From our results it appears that all five investigated species, be they early/mid-, mid/late- or late-successional species, show certain modifications in leaf morphology or physiology in response to reduced light availability in the lower canopy. The following six leaf-related criteria were found to be particularly informative for quantifying the degree of sun/shade leaf differentiation in these species: (i) shade leaf SLA does exceed 200 cm^2 g^{-1}; sun and shade leaves differ 2-3 fold in SLA; (ii) typical shade leaves are at least 20 % larger than sun leaves; (iii) the $A_{max,a}$ rate of shade leaves is similarly high, or only slightly lower, than that of the sun leaves; (iv) $A_{max,m}$ is higher in shade than in sun leaves; (v) the apparent photosynthetic N use efficiency is higher in shade than in sun leaves; and (vi) the specific dark respiration rate of shade leaves is low ($R_{d,a}$ lower in shade than in sun leaves; $R_{d,m}$ similar in sun and shade leaves). None of the five species met all six criteria, but *F. sylvatica* was certainly the species with the ‘most complete’ leaf-level acclimation to low light in its lower canopy. How the other four species can be ranked according to the degree of their shade leaf acclimation, depends on how leaf morphological and physiological modifications are weighted.

When classifying tree species according to their low-light acclimation in the lower canopy, it may be straightforward to consider not only leaf-level traits but to consult whole-canopy and stand-level properties as decision criteria as well (Niinemets 2010). The canopy architecture in the lower crown may be an important attribute. The existence of a ‘monolayer’-type branching system in the shade canopy with regular spatial foliage distribution and more efficient light harvesting as compared to the 'multilayer' system may be a useful parameter indicating a marked sun/shade canopy differentiation within a canopy. Typical monolayer branching patterns in the shade canopy are characteristic for *F. sylvatica* and *T. cordata* and, to a lesser extent, for *A. pseudoplatanus* and *C. betulus*. In contrast, the canopy of *F. excelsior* reveals a multilayer structure not only in the upper but also the lower canopy section.

Canopy transmissivity for light is another useful criterion for identifying trees with a high degree of low light-acclimation. Measurements of transmitted photosynthetically active radiation under closed monospecific stands of *F. sylvatica*, *T. cordata* and *C. betulus* gave average irradiances in the range of 0.5-3 % relative to incident radiation (Ellenberg & Leuschner 2010, Hagemeier 2002), which is somewhat lower than under *A. pseudoplatanus* canopies (approximate range 2-5 %) and much lower than under *F. excelsior* stands (>5 %; Leuschner, unpubl. data). This information from canopy architecture and radiation interception studies may indicate that the five species are representing the following sequence of decreasing low-light acclimation in their shade crowns: *F. sylvatica > T. cordata, C. betulus > A pseudoplatanus > F. excelsior*.

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CHAPTER 3

Within-canopy variation in photosynthetic capacity, SLA and foliar N in temperate broad-leaved trees of contrasting shade tolerance

N. Legner, S. Fleck & C. Leuschner

Keywords: *Acer pseudoplatanus*, adult trees, A_{max}, *Carpinus betulus*, *Fagus sylvatica*, *Fraxinus excelsior*, relative irradiance, shade adaptation, specific leaf area, *Tilia cordata*.

3.1 Summary

1. The leaf morphology and photosynthetic capacity of trees are remarkably plastic in response to intra-canopy light gradients. While most studies examined seedlings, it is not well understood how plasticity differs in mature trees among species with contrasting shade tolerance.

2. We studied light-saturated net photosynthesis (A_{max}), maximum carboxylation rate (V_{cmax}), electron transport capacity (J_{max}) and leaf dark respiration (R_d) along natural light gradients in the canopies of 26 adult trees of five broad-leaved tree species in a mixed temperate old-growth forest (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia cordata* and *Fagus sylvatica*, representing a sequence from moderately light-demanding to highly shade-tolerant species). We searched for species differences in the dependence of photosynthetic capacity on relative irradiance (RI), specific leaf area (SLA) and nitrogen per leaf area (N_a).

3. The three shade-tolerant species (*C. betulus, T. cordata, F. sylvatica*) differed from the two more light-demanding species by the formation of shade leaves with particularly high SLA but relatively low N_a and consequently lower area-based A_{max}, and a generally higher leaf morphological and functional plasticity across the canopy. Sun leaf morphology and physiology were more similar among the two groups.

4. The three shade-tolerant species differed in their shade acclimation strategies which are primarily determined by the species' plasticity in SLA. Under low light, *T. cordata* and *F. sylvatica* increased SLA, mass-based foliar N and leaf size, while *C. betulus* increased solely SLA exhibiting only low intra-crown plasticity in leaf morphology and N allocation patterns.

6. This study with mature trees adds to our understanding of tree species differences in shade acclimation strategies under the natural conditions of a mixed old-growth forest.

3.2 Introduction

Trees represent the plant life form with highest competitive ability for light due to their capability of overgrowing smaller-statured plants. The formation of a tree canopy requires the construction of a high number of structural elements for foliage exposure and it demands for plastic leaf responses to the highly variable irradiance in the canopy (Niinemets 2007). One of the most obvious problems of plants capable of overgrowing their competitors is that the shade cast by their canopy is not only restricting the light access of competitors but also that of the own foliage in the shade crown. While the sun leaves of trees are frequently exposed to full sun light, shade leaves at the canopy base often have to function with less than 5 percent of incident light (Walter & Torquebiau 1997, Hagemeier 2002, Ellenberg & Leuschner 2010, Niinemets 2010). This dramatic intra-canopy light gradient induces acclimation at the leaf-, branch- and canopy-levels which may vary with species, age, social position in the stand, and environment.

Given the high diversity in leaf forms, leaf life spans, branching patterns and crown dimensions among different tree species (Hallé et al. 1978), it is likely that not a single, but a multitude of competitive strategies for exploring canopy space, capturing light and assimilating CO_2 at the stand level do exist. In mixed forests, species with contrasting strategies for capturing aboveground resources often are co-existing under similar environmental conditions. In temperate forests, this can be members of the genera *Fagus, Tilia, Acer, Carpinus, Fraxinus* and *Quercus* with different phylogenies and functional features. However, we are only beginning to understand how species differences in leaf morphology and physiology, and in the plasticity of leaf functioning are determining the trees' strategies for capturing light and CO_2 in species-rich temperate and tropical forests (Rozendaal et al. 2006, Sack et al. 2006, Valladares & Niinemets 2008). Yet, this knowledge is important for a mechanistic understanding of forest dynamics in mixed forests and for the support of foresters in their search for tree species that can increase the yield of mixed stands.

Our current understanding of adult trees' competitive strategies for exploring canopy space and assimilating CO_2 is still based on the concept of light-demanding and shade-tolerant species (e.g. Liburnau 1918). However, the concept's limitations have also been recognised since long time (e.g. Fricke-Beutnitz 1904) as it is well known that shade-tolerant species often get more light-demanding when growing older while they demand less light when occurring at fertile and warmer sites (Liburnau 1918, Portsmouth & Niinemets 2007). An alternative concept for a functional classification of trees is related to the observed successional status of the species (e.g. Bazzaz 1979). However, key processes in this concept are dispersal, seedling establishment and the competitive success of the offspring which are only partly related to the strategy of light capture and canopy carbon gain in the adult stage.

Tree species differ largely in their capacity to modify leaf morphology, leaf physiology and canopy structure in response to low light (Rozendaal et al. 2006, Sack et al. 2006). Strategies of light-demanding early-successional species might result from genetically-determined thresholds that constrain the development of highly shade-tolerant foliage by restricting the plasticity of leaf morphology and limiting maximum canopy leaf area, or from a putative maximum leaf area index at the stand level, as it appears, for example, in the pioneer species *Pinus sylvestris* and *Betula pendula* from over-regional LAI surveys (Ellenberg & Leuschner 2010, Niinemets 2010, Bequet et al. 2012). While the development of shade-tolerant foliage is closely linked to efficient light harvesting, which requires the allocation of carbon and nitrogen over larger leaf areas (Niinemets 2010), certain woody species might well face inherent limitations in the maximum leaf size achievable per amount of C and N invested in leaf tissue. Thus, a key factor controlling the adaptability of a tree’s foliage is the intra-crown plasticity in leaf area per leaf mass (SLA).

While the majority of Central European tree species can adapt or acclimate to only moderate shade intensities (Ellenberg & Leuschner 2010), a few species such as *Fagus sylvatica* (European beech) and *Abies alba* (Silver fir) are able to adjust their foliage to nearly the full spectrum of light availability occurring in forests, i.e. from 100 to c. 1 % of full sun light (Tognetti et al. 1997, Valladares et al. 2002, Robakowski et al. 2004). However, most of the broad-leaved trees of this flora do not produce shade leaves at irradiances <10 % of incident radiation (e.g. *Betula*, *Populus*, *Quercus* and *Fraxinus* species) or do not tolerate <5 % relative irradiance (e.g. *Alnus* and *Acer* species) (Hagemeier 2002, Niinemets & Valldares 2006). Why these functional differences between the species do exist, is not sufficiently understood.

Controversial results have been reported concerning the influence of shade tolerance (or successional status) on the light-dependent plasticity in leaf morphology of tree species. For the leaf morphological plasticity of seedlings, either higher plasticity (e.g.

Valladares et al. 2002) or lower plasticity (e.g. Oguchi et al. 2005, Strauss-Debenedetti & Bazzaz 1996) in shade-tolerant late-successional species as compared to light-demanding species, or highest plasticity in mid-successional species (Abrams & Mostoller 1995), was found.

For mature trees, it has been postulated that shade-tolerant species should have higher plasticity in traits important for light harvesting (such as SLA and chlorophyll:N ratio) while species adapted to high irradiance should have higher plasticity in leaf traits related to CO_2 assimilation (such as N_a) (Valladares et al. 2002). However, it is generally assumed that overall plasticity is lower in shade-tolerant species (Valladares & Niinemets 2008) even though this is not fully supported by a number of studies with adult trees (e.g. Rozendaal et al. 2006, Sack et al. 2006). Other factors than shade tolerance may also influence leaf plasticity. For example, Niinemets (2010) postulated that trees with a relatively short leaf life span, which is characteristic for stands with high resource supply (light, water, nutrients), should not be able to produce foliage with distinct shade acclimation.

Progress in our understanding of tree species differences in shade acclimation or adaptation is linked to deeper insights into those factors that promote or limit leaf and canopy modification under low light. Typical morphological changes along the intra-canopy light gradient are increases in leaf size, SLA and chlorophyll content per unit dry mass, and reductions in leaf thickness, the number of palisade mesophyll cell layers, and stomatal density (Lichtenthaler et al. 1981, Givnish 1988, Niinemets 2010). Relevant functional changes with light reduction include a greater fractional investment of N in molecules involved in light harvesting, implying higher light absorptance per dry mass in shade than sun leaves, a reduction in area-specific leaf dark respiration, and reduced investment in light-protecting chemicals associated with the xanthophyll cycle (Niinemets 2007, Valladares & Niinemets 2008). Despite these modifications, tree sun leaves often have been found to reach two- to fourfold higher photosynthetic capacities per leaf area (A_{max}) than shade leaves (Hölscher 2004, Le Goff et al. 2004, Urban et al. 2007).

Generally accepted patterns of the functionality of tree crowns are that irradiance is decreasing exponentially with increasing canopy depth (Monsi & Saeki 1953), while irradiance shows a linear positive relation to leaf mass per area (LMA; or a negative hyperbolical one to its inverse, SLA) and also a linear positive relation to nitrogen per leaf area (N_a) (Fleck et al. 2004, Niinemets 2007). Area-related photosynthetic capacity ($A_{max,a}$) increases with N_a either linearly (e.g. Ellsworth & Reich 1993), or as observed in *Fagus sylvatica* and *Quercus petraea* trees (Fleck 2002), asymptotically. Attempts to explain the marked changes in leaf morphology and function along the intra-canopy light gradient prove to be difficult, mostly because SLA (and its inverse, LMA) and N_a as likely key determinants of $A_{max,a}$ are closely related to each other and thus change in parallel with light availability (Meir et al. 2002).

A major methodological problem in the identification of species-specific strategies of canopy light capture and carbon gain in the adult stage is that purely experimental approaches are hardly possible due to the long time span needed for a tree to reach the upper canopy layer in a stand. Observational studies in old-growth mixed stands are a promising alternative tool for comparing the strategies of different tree species under *ceteris paribus* conditions and they have the advantage that crown structure and vertical light gradient in the canopies are in a quasi steady state, thus reflecting the species' strategy of space filling under the influence of decade-long competitive interactions with neighbouring trees.

We started from the hypothesis that the known general pattern of the $A_{max,a}$ dependence on irradiance, SLA and N_a is modified by the environment (e.g. N and water availability) and species-specific traits such as leaf morphological plasticity. We examined the alteration of photosynthetic capacity, SLA, and foliar N content in five co-occurring temperate broad-leaved species in a mixed stand under rather homogenous microclimatic and edaphic conditions and thus were able to search for species differences in the light and nitrogen control of canopy photosynthesis with only minor influence of potentially confounding factors. Moreover, by considering tree species with markedly different shade tolerance of their most basal leaves (highly shade tolerant to moderately light-demanding), which is linked to different positions in forest dynamics (late-successional to early-/mid-successional), we attempted to recognize relationships between shade tolerance (or successional status) and the control of canopy photosynthesis by irradiance, SLA and N_a.

In conjunction with the study's principal goal, i.e. the search for species-specific strategies of light capture and CO_2 assimilation, we tested the following hypotheses: trees capable of producing highly shade-tolerant leaves (1) exhibit a greater leaf morphological plasticity with larger sun-shade leaf differences in lamina size and

SLA, and (2) maximize leaf area in the shade crown through a lower N_a/SLA slope as compared to trees lacking characteristic shade leaves; the latter vary less in leaf morphology and tend to maximize N accumulation per leaf area in sun leaves through a steep N_a/SLA slope. We further hypothesized (3) that trees producing highly shade-tolerant leaves show higher shade leaf photosynthetic capacities per C and N investment (A_{max} or V_{cmax} per leaf mass or per unit leaf N) than trees lacking characteristic shade leaves. Our analysis bases on the comparative analysis of co-variation in leaf morphology, foliar N, photosynthetic capacity (A_{max}, V_{cmax}, J_{max}) and leaf dark respiration (R_d) across the canopies of 26 adult trees (~30 m tall) from five species of the genera *Fagus, Tilia, Carpinus, Acer* and *Fraxinus* (each five or six representative trees) in an old-growth mixed forest.

3.3 Materials and methods

Study site

The study was carried out in 2008 and 2009 in Hainich National Park in western Thuringia, Germany. The national park on the south-eastern side of the Hainich mountain range is part of the largest unfragmented deciduous forest in Germany with a size of 160 km². The study site consists of a transect of approximately 200 m length and 30 m width in the south-east of the national park near the location Thiemsburg (51° 05’ 00’’ N, 10° 30’ 27’’ E) at 350 m a.s.l.. The soil type is a Luvisol developed in loess over Triassic Limestone with the topsoil pH (H_2O) ranging between 4.5 to 6.8 (C. Langenbruch, personal communications). With up to 14 tree species per hectare, the mixed broad-leaved forest communities of Hainich National Park are among the species-richest Central European forests. While European beech (*Fagus sylvatica* L.) is the most common species in the Hainich forest, species of the genera *Tilia*, *Acer*, *Carpinus*, *Fraxinus*, *Quercus*, *Prunus*, *Ulmus* and others are also present. The more abundant species besides beech are *Tilia cordata* Mill. (small-leaved lime), *Carpinus betulus* L. (European hornbeam), *Fraxinus excelsior* L. (European ash) and *Acer pseudoplatanus* L. (sycamore maple); all five species were selected for study. These species are not only representatives of five different families (Fagaceae, Tiliaceae, Betulaceae, Oleaceae and Aceraceae), but also differ with respect to their natural role in forest dynamics (*Fagus* is late-successional, *Acer*, *Carpinus* and *Tilia* mid- to late-successional, and *Fraxinus* early- to mid-successional), physiology and crown morphology (Köcher et al. 2009, Ellenberg & Leuschner 2010). The shade tolerance scores given by Niinemets & Valladares (2006) rank the five species in a similar manner as was already postulated by Liburnau (1918), with *F. sylvatica* as the most shade tolerant species (score: 4.56), followed by *T. cordata* (4.18), *C. betulus* (3.97) and *A. pseudoplatanus* (3.73) and finally *F. excelsior* (2.66) as the most light-demanding species.

The growing season 2008 (April 1st to September 30th) was characterised by a mean temperature of 14.6 °C and 234 mm of precipitation, that in 2009 by 15.1 °C and 469 mm (data from the weather station Weberstedt/Hainich, Meteomedia, Gais, Switzerland). The average temperature in the year 2008 was 9.5 °C, that in 2009 8.9 °C (long-term mean: 7.7 °C). The precipitation total was 500 mm in 2008 and 774 mm in 2009 (long-term mean: 590 mm yr^{-1}).

Sampling design and measurements

Each five individuals per species (six in the case of *F. excelsior*) that were similar with respect to demographic status and tree height, were selected for study (Table 3.1). All 26 selected trees were co-dominant mature individuals with their sun crowns reaching the upper canopy layer. The diameter at breast height (DBH at 1.3 m, recorded with D1 dendrometer bands, UMS, Munich, Germany) varied between the five species (species means of 36-50 cm, Table 3.1), since we attempted to select representative trees of a species in the upper canopy (height ~30 m), and the species differed in their diameter-height relation. The age of the trees ranged between 80 and 120 years (Gebauer et al. 2012) and tree height between 26 m and 31 m (tree height measured with a Vertex inclinometer, Vertex IV, Haglöf Inc., Langsele, Sweden; Table 3.1). We used a mobile lift (Denka model DL30, Rotlehner Arbeitsbühnen GmbH, Massing-Oberdietfurt, Germany) to access the sun and shade canopies of the trees up to a height of 30 m.

Table 3.1: Some characteristics of the five species. Shade tolerance score after Niinemets & Valladares (2006). Position in succession after observations in various forest communities in Central Europe after Ellenberg & Leuschner (2010). DBH is diameter at breast height. DBH and tree height are for the sample trees (means ± SE).

Tree species	No. of tree individuals	Shade tolerance score	Position in succession	DBH [cm]	Tree height [m]
Fraxinus excelsior	6	2.66	Early/mid	36.2 ± 2.6	27.6 ± 0.9
Acer pseudoplatanus	5	3.73	Mid	58.3 ± 7.1	30.3 ± 0.9
Carpinus betulus	5	3.97	Mid/late	45.8 ± 4.7	26.7 ± 0.7
Tilia cordata	5	4.18	Mid/late	43.5 ± 5.8	27.0 ± 1.1
Fagus sylvatica	5	4.56	Late	50.0 ± 3.2	29.5 ± 0.6

Due to difficult canopy access and the time-consuming establishment of the light response and A/C_i curves, we preferred replicates at the tree level over leaf replicates in the canopy of the same tree which represent pseudo-replicates. The five (six) investigated trees of a species were treated as true replicates because they were 10 up to > 20 m distant to each other (except for two individuals of *F. excelsior* with 5 m distance to each other). All measurements were done on sunny or overcast days (8 am to 5 pm) in the summers 2008 (Jun 20th – Aug 22nd) and 2009 (May 29th – Aug 29th). On every tree, we investigated fully expanded non-detached leaves under *in situ* conditions in three different canopy layers: uppermost sun canopy layer (canopy openness >0.25 %), middle canopy (in between upper sun and lower shade canopy, and lower shade canopy (canopy base, canopy openness <0.25 %). For all leaves, we examined the light and CO_2 response of photosynthesis, estimated integrated relative irradiance and determined SLA and N_a. Thus, each three leaves per tree were investigated resulting in about 75 leaves examined in total. Since one or two data points had to be excluded, 13-15 leaves per species were considered in the subsequent analysis: 13 in *F. excelsior* and *A. pseudoplatanus,* 14 in *C. betulus* and *F. sylvatica* and 15 in *T. cordata*). The gas exchange measurements were conducted with a portable LI-6400XT IRGA system (LI-COR Inc., Lincoln, Nebraska, USA) equipped with a standard leaf chamber and a LED red/blue light source (type 6400-02B) in intact, attached leaves. We investigated fully expanded healthy and non-senescent leaves of most distal insertion on exposed peripheral twigs in the sun and middle canopy sections, while the leaves of the shade crowns were positioned on branches in the interior of the lower canopy. In the pinnate leaves of *F. excelsior*, a leaflet in the middle part of the leaf was investigated. The CO_2 response was investigated through three A/C_i curves per leaf established at leaf temperatures of 19, 25 and 29 °C (± 1°C) under a photosynthetic photon flux density (PPFD) of 2000 µmol m^{-2} s^{-1}. The three measurements may be viewed as replicates at the leaf level, since only one photosynthesis rate was derived by interpolation from the three measurements (for the 25 °C level). Incident PPFD was increased stepwise to full light and the leaves were allowed to adapt to these conditions for at least 10 min for allowing photosynthesis to stabilise. The IRGA channels were matched before every measuring point. For every A/C_i curve, leaf internal CO_2-concentration (C_i) was varied in 10-steps in the order: 370, 30, 70, 100, 200, 370, 1200, and 2000 ppm CO_2. The second measurement at 370 ppm was repeated until the measured assimilation rate was approximately the same as in the first measurement at 370 ppm. On the same leaves, a light response curve (at 25 °C and 370 ppm CO_2) was established in 10 steps: 2000, 1200, 500, 200, 100, 50, 20, 0, 0, and 0 µmol m^{-2} s^{-1} PPFD (in 2008 in reverse order). The vapour pressure deficit was held constant at ambient conditions during the measuring campaign on a leaf.

A hemispherical photograph (Nikon Coolpix 8400 with Nikon Fisheye Converter FC-E9) was taken precisely at the position of each leaf for calculation of canopy openness in the zenith above the leaf and for deriving an estimate of the integrated relative irradiance received by the leaf during summer. The leaves were brought to the laboratory, scanned, dried (70 °C, 48 h) and weighed for determination of leaf size (software Winfolia, Regents Instruments, Quebec, Canada) and specific leaf area (SLA). The leaf dry mass was analysed for the concentration of N.

We preferred SLA as a leaf morphological parameter over the more widely used LMA (leaf mass per area) because SLA is more variable in absolute terms in the shade canopy which was in the focus of the study. Both quantities may easily be converted into each other since LMA equals 1/SLA.

Data analysis

For characterizing the photosynthetic capacity of the leaves, we chose light saturated net photosynthesis rate (A_{max}), maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) as parameters. In addition, respiration rate in the darkness (R_d; Atkin et al. 2000) was calculated from the A/C_i curves. The gas exchange data on the light and CO_2 dependence were analysed with nonlinear least-square regressions implemented in Mathematica (version 3.0, Wolfram Research, Champaign, Illinois, USA). For the fitting of the A/C_i curves, the program RACCIA (Fleck 2002) was used which is based on the equations of Farquhar et al. (1980), Harley & Tenhunen (1991) and Ball et al. (1987). Hence, the rates of V_{cmax} and J_{max} were calculated with the following equations:

$$V_{c\max} = \frac{\left(A + R_d\right)\left(C_i + K_c\left(\frac{1+O}{K_c}\right)\right)}{\left(1 - \frac{\Gamma_*}{C_i}\right)C_i} \tag{1}$$

$$J_{\max} = \frac{\left(A + R_d\right)\left(4C_i + 8\Gamma_* C_i\right)}{4\left(C_i - \Gamma_*\right)} \tag{2}$$

with A being assimilation rate, R_d leaf dark respiration rate, C_i the intercellular CO_2 concentration, K_c the Michaelis-Menten constant for carboxylation, O the oxygen concentration at the site of fixation and Γ_* the CO_2 compensation point without consideration of mitochondrial respiration. From the three A/Ci curves established at 19, 25 and 29 °C, V_{cmax} and J_{max} at 25 °C were calculated accordingly. The stomata model of Ball et al. (1987) was also included in the calculations.

Light response curves were fitted with a non-rectangular hyperbolic function (Ogren & Evans 1993, Thornley 2002) with the equation

$$A_{\max} = -\left(\frac{A\ \alpha\ PAR - \xi\ A^2}{A - \alpha\ PAR}\right) \tag{3}$$

where A is the assimilation rate at a given photosynthetically active radiation (PAR), ξ a factor which determines the sharpness in the knee of the non-rectangular hyperbolic curve (set to 0.9; Thornley 2002), and α the initial slope of the light response curve (quantum efficiency of photosynthesis).

In cases where more than one leaf was measured for gas exchange because the first leaf broke away due to strong wind, we used the N content and leaf size data of the leaf that was analysed for the 25 °C A/C_i curve. Most parameters were expressed not only in relation to leaf size but also to leaf mass. All photosynthetic parameters were analysed for a dependence on time (i.e. day of the year); none of the parameters showed such a dependency (data not shown).

Relative irradiance was derived from hemispherical photographs based on the method of Niinemets & Fleck (2002) and using the model of Roderick (1999) to estimate the proportion of diffuse radiation in global radiation. Global radiation measurements were performed on a tower in about 1 km distance to the study area. The coefficients used in the Roderick model were $X_0 = 0.21$, $X_1 = 0.71$, $Y_0 = 0.95$, and $Y_1 = 0.24$. The fraction of diffuse radiation in global radiation (f_{dif}) was 72.8 % and 64.6 % in the period of leaf unfolding of the years 2008 and 2009, respectively, and the fraction of direct radiation (f_{dir}), thus, 27.2 % and 35.4 %. Leaf unfolding was assumed to have occurred in the period of May 15th to June 30th in both years. The diffuse (I_{dif}) and direct site factor (I_{dir}) of the leaves were calculated for the relevant period with the program GLA (version 2.0, SFU, Burnaby, Canada), using a cloudiness index of 0.46 and a clearsky transmission coefficient of 0.6. Relative irradiance (RI) was then calculated as

$$RI = I_{dif} * f_{dif} + I_{dir} * f_{dir} \tag{4}$$

While most calculations were conducted with all leaves in the continuum from sun to middle and shade crown, a few analyses were conducted with the sub-populations of ‘sun leaves’ and ‘shade leaves’ in order to examine the size of the vertical gradient in the canopy. In this approach, we treated all leaves growing at a canopy openness <0.25 % as shade leaves and >0.25 % as sun leaves. The choice of a canopy openness threshold of 0.25 % is supported by the curvature of the SLA/relative irradiance plots which show marked slope alteration in this range (see Fig. 3.2a). The gas exchange data were tested for a dependence on the time of measurement (June, July or August). As no significant seasonal effect existed, we pooled the data.

Since not all data set met the assumptions for ANOVA, we applied a permutation test to test for significant differences between means among the five species and between sun and shade leaves (significance level: $P < 0.05$) using the software environment R, version 2.0.8 (R Development Core Team 2008). We used the package ‘perm’ (Fay & Shaw 2010) with permKS and permTS. Differences with a significance level of $0.05 < P < 0.1$ were treated in the text as ‘marginally significant’. Differences between the slopes of linear regression equations (ds) were tested for significance with the software environment SAS 9.2 (SAS Institute, Cary, NC, USA) using the linear model function. Regression analyses were conducted with the software SigmaPlot (version 11.0, Systat Software, Inc., San Jose, California, USA).

While most relationships between leaf properties were treated as being linear, non-linear models were calculated wherever the nature of the relationship is known from earlier investigation. Thus, the relation between height in the canopy and relative irradiance was treated as being exponential (Monsi & Saeki 1953), that one between RI and SLA as being hyperbolic (e.g. Niinemets et al. 2004), and that one between SLA and Na or parameters of area-related photosynthetic capacity as hyperbolic as well. The relationship between photosynthetic capacity and N_a was assumed to follow a sigmoid curve according to measurements done by Fleck (2002).

When regressing area-related A_{max}, V_{cmax}, J_{max} and R_d and mass-related A_{max} on RI, SLA or N_a for a relative comparison of influential factors, we tested both linear and non-linear models but presented only those with highest explanatory power. We did not include DBH or tree height as an influential variable in any of the analyses because light availability has been found to exert a much stronger effect on intra-canopy gradients of leaf morphology than tree height and related DBH (Sack et al. 2006, but see Thomas 2010).

Phenotypic plasticity (PI) was calculated as an index (ranging from 0 to 1) for each variable and species as the difference between the maximum and minimum value in the canopy divided by the maximum value (Valladares et al. 2002).

3.4 Results

Intra-canopy gradients of leaf morphology and foliar N in the five species

Relative irradiance (RI) as calculated from hemispherical photographs inside the crown showed the expected exponential decrease from canopy top to bottom with a similar shape of the curve in all five species (Fig. 3.1a and b). However, early- to mid-successional *F. excelsior* differed from the other four species in the lack of shade leaves at relative irradiances < ~ 0.1.

In all five species, SLA showed a linear increase with decreasing relative height in the canopy (R^2: 0.47-0.79; Fig. 3.1c) but the slope was more gentle in *F. sylvatica* (difference significant to all other species) and steepest in *F. excelsior* (Table 3.3: column 2). SLA decreased hyperbolically with increasing RI (R^2: 0.71-0.84, Fig. 3.2a) with a steeper slope in the more shade-tolerant species *F. sylvatica*, *C. betulus* and *T. cordata* than in the more light-demanding species *F. excelsior* and *A. pseudoplatanus*. This difference corresponded to narrower observed SLA ranges in *F. excelsior* and *A. pseudoplatanus* (60-221 cm² g^{-1}) than in the other three species (83-409 cm² g^{-1}; Figs 3.1c, 2a). Only the latter three species produced shade leaves with specific leaf areas well exceeding 250-300 cm² g^{-1} (Fig. 3.2a).

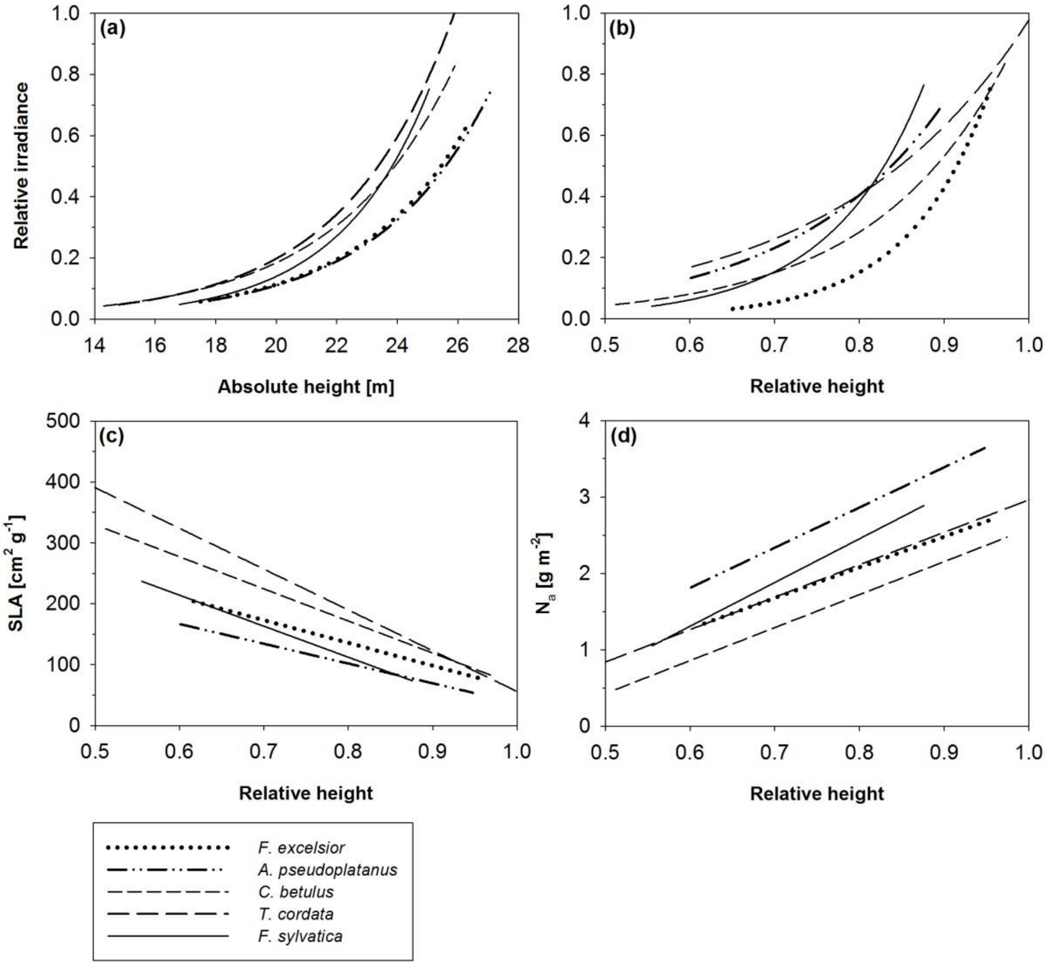

Figure 3.1: Change of relative irradiance (RI) with absolute height in the canopy (a), and of RI, SLA and N_a with relative height in the canopy (b, c and d) for the five species. The equations and their parameters are given in Table 3.3 (columns 1-3).

As an average over the whole canopy, the leaves of *A. pseudoplatanus* had higher N_a values (mean: 2.6, range: 1.5-4.2 g N m^{-2}) than those of *T. cordata* and *F. sylvatica* (means: 2.1 and 2.1, range: 0.9-3.3 and 0.9-3.5 g N m^{-2}, respectively; Figs 3.1d and 3.2b and Table 3.2; difference only partly significant at $P < 0.05$).

C. betulus differed from the four other species by relatively low N_a values with a more restricted range of variation (mean: 1.5, range 0.7-2.4 g m^{-2}; Fig. 3.2b).

N_a increased linearly with both RI (R^2: 0.63-0.89) and (though less tightly) with relative height in the canopy (R^2: 0.44-0.77; Figs 3.2b and 3.1d). The slope was steepest in *A. pseudoplatanus* (N_a vs. RI) and *C. betulus* (N_a vs. relative height) and showed no obvious relation to the shade tolerance or successional status of the species. Mass-related nitrogen content (N_m) was somewhat higher in *T. cordata* leaves ($P < 0.05$) but remarkably similar among the four other species (sun leaf N_m means between 22.2 and 25.9 mg N g^{-1}, shade leaf means: 24.7-28.4 mg g^{-1}, Table 3.2). In general, N_m remained relatively constant throughout the crown; in two species, however, we found a slight increase in N_m with a RI reduction (significant relation in *F. sylvatica*, a marginally significant one in *T. cordata*, Fig. 3.2c).

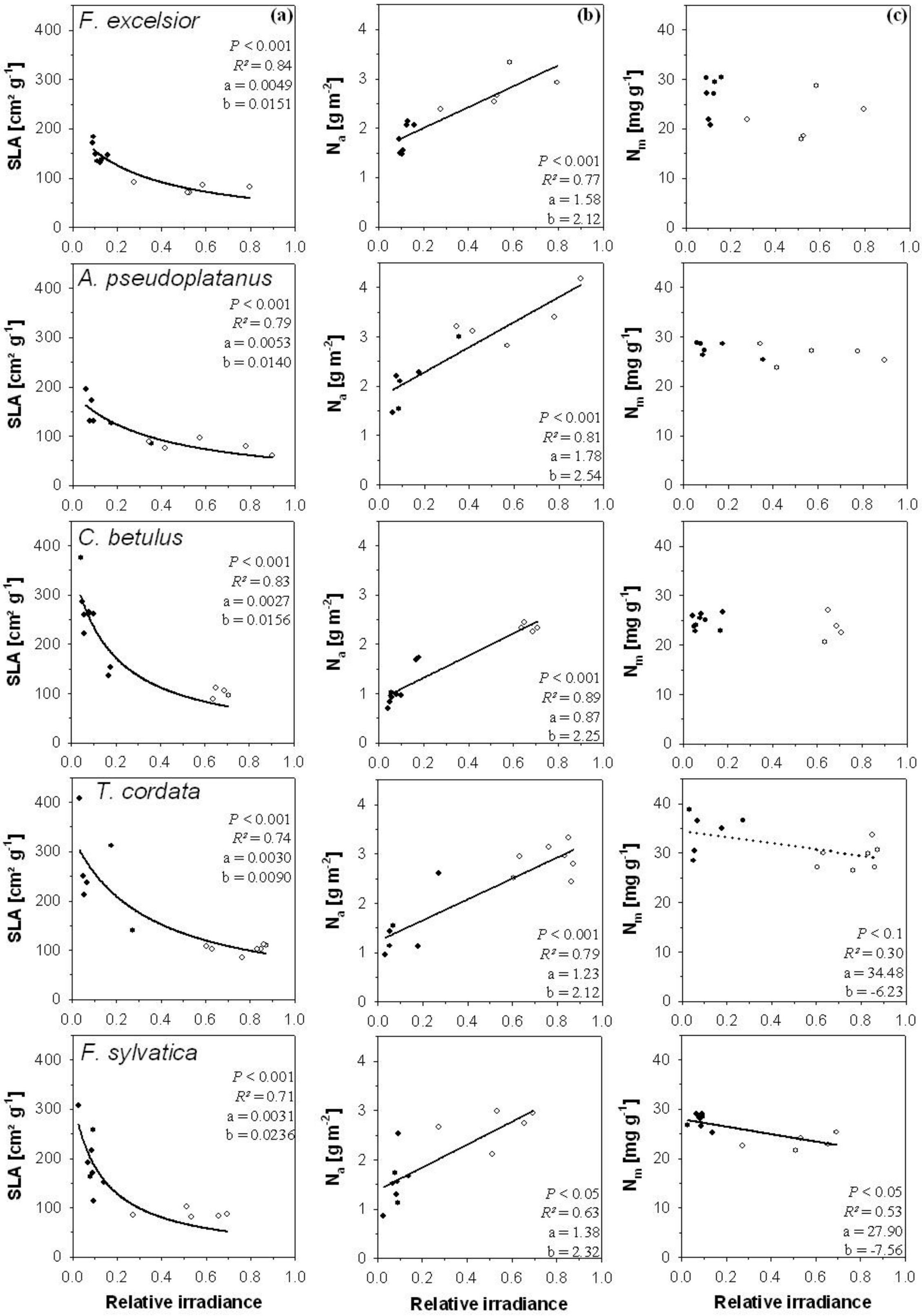

Figure 3.2: Relationship between relative irradiance (RI) and SLA (a), N_a (b) or N_m (c) for the sun (○) and shade (●) leaves of the five tree species. Given are *P*, *R²* and the coefficients a and b of the regression equations (SLA: y = 1 / (ax + b); N_a and N_m: y = ax + b). Solid lines mark significant relationships ($P < 0.05$), dotted lines those with $0.05 < P < 0.1$.

Table 3.2: Leaf morphololological and physiological parameters for 'sun leaves' and 'shade leaves' of the five species (means ± SE of n leaves). Sun leaves refer to leaves exposed to a canopy openness >25 %, shade leaves to an openness <25 %. PI is the plasticity index after Valladares et al. (2002). Different lower case letters indicate significant differences between the sun and shade leaves of a species (P<0.05. permutation test), differences between the sun leaves of the five species are marked with different uppercase letters, those between the shade leaves with different Greek letters (*P* < 0.05, permutation test).

Species	**n**	**Leaf size**	**SLA**	**N_a**	**N_m**	**Vcmax,a**	**Jmax,a**	**Amax,a**	**Rd,a**
		cm²	cm² g-1	g m^{-2}	mg g^{-1}	µmol CO_2 m^{-2} s^{-1}	µmol e- m^{-2} s^{-1}	µmol CO_2 m^{-2} s^{-1}	µmol CO_2 m^{-2} s^{-1}
Fe sun	5	246.5 ± 38.3 $^{a\,A}$	80.1 ± 4.3 $^{a\,A}$	2.8 ± 0.2 $^{a\,A}$	22.2 ± 2.0 $^{a\,A}$	73.6 ± 9.5 $^{a\,A}$	155.9 ± 14.0 $^{a\,A}$	14.3 ± 2.3 $^{a\,A}$	1.9 ± 0.3 $^{a\,A}$
Fe shade	8	201.9 ± 33.3 $^{a\,\Gamma}$	159.2 ± 10.9 $^{b\,\Gamma}$	1.8 ± 0.1 $^{b\,\Gamma\Phi}$	27.8 ± 1.7 $^{b\,\Gamma\Phi}$	56.3 ± 5.5 $^{b\,\Gamma}$	99.7 ± 7.7 $^{b\,\Gamma\Phi}$	14.3 ± 1.4 $^{a\,\Gamma}$	1.3 ± 0.1 $^{b\,\Gamma}$
PI		0.949	0.683	0.559	0.498	0.620	0.609	0.580	0.769
Ap sun	6	73.7 ± 8.8 $^{a\,B}$	79.2 ± 5.1 $^{a\,A}$	3.3 ± 0.2 $^{a\,B}$	25.9 ± 0.8 $^{a\,A}$	75.5 ± 6.4 $^{a\,A}$	175.3 ± 12.7 $^{a\,A}$	13.3 ± 1.9 $^{a\,A}$	1.8 ± 0.4 $^{a\,A}$
Ap shade	7	88.2 ± 7.4 $^{a\,\Theta}$	147.2 ± 15.5 $^{b\,\Gamma}$	2.0 ± 0.2 $^{b\,\Gamma}$	28.4 ± 1.0 $^{a\,\Gamma}$	61.5 ± 6.3 $^{a\,\Gamma}$	141.7 ± 18.9 $^{a\,\Gamma}$	13.3 ± 1.3 $^{a\,\Gamma\Phi}$	1.6 ± 0.3 $^{a\,\Gamma}$
PI		0.601	0.691	0.648	0.303	0.614	0.662	0.662	0.801
Cb sun	5	26.5 ± 3.4 $^{a\,C}$	100.7 ± 3.8 $^{a\,B}$	2.3 ± 0.0 $^{a\,C}$	23.5 ± 1.1 $^{a\,A}$	56.7 ± 3.7 $^{a\,A}$	115.8 ± 7.0 $^{a\,A}$	12.7 ± 1.1 $^{a\,A}$	1.1 ± 0.1 $^{a\,A}$
Cb shade	9	29.3 ± 1.8 $^{a\,\Delta}$	246.6 ± 23.8 $^{b\,\Delta\Phi}$	1.1 ± 0.1 $^{b\,\Delta}$	24.7 ± 0.5 $^{a\,\Phi}$	33.2 ± 5.6 $^{b\,\Delta}$	63.6 ± 9.3 $^{b\,\Delta}$	7.1 ± 1.7 $^{b\,\Delta}$	0.9 ± 0.1 $^{a\,\Gamma}$
PI		0.538	0.764	0.717	0.239	0.775	0.773	0.845	0.897
Tc sun	7	27.4 ± 3.5 $^{a\,C}$	102.5 ± 3.4 $^{a\,B}$	2.9 ± 0.1 $^{a\,AB}$	29.3 ± 1.0 $^{a\,B}$	64.6 ± 2.6 $^{a\,A}$	151.0 ± 14.4 $^{a\,A}$	15.8 ± 2.6 $^{a\,A}$	1.5 ± 0.2 $^{a\,A}$
Tc shade	8	47.6 ± 3.8 $^{b\,\Theta}$	293.9 ± 35.2 $^{b\,\Delta}$	1.3 ± 0.2 $^{b\,\Delta\Phi}$	35.3 ± 1.5 $^{b\,\Delta}$	44.7 ± 7.6 $^{b\,\Gamma\Delta}$	85.2 ± 14.9 $^{b\,\Delta\Phi}$	8.5 ± 1.9 $^{b\,\Phi}$	1.3 ± 0.2 $^{a\,\Gamma}$
PI		0.686	0.793	0.724	0.358	0.732	0.794	0.916	0.646
Fs sun	6	19.0 ± 2.3 $^{a\,C}$	86.9 ± 3.2 $^{a\,A}$	2.8 ± 0.2 $^{a\,AB}$	24.3 ± 1.1 $^{a\,A}$	64.5 ± 4.4 $^{a\,A}$	119.8 ± 23.2 $^{a\,A}$	7.5 ± 2.3 $^{a\,A}$	2.2 ± 0.6 $^{a\,A}$
Fs shade	8	29.9 ± 1.8 $^{b\,\Delta}$	196.4 ± 22.1 $^{b\,\Gamma\Phi}$	1.5 ± 0.2 $^{b\,\Gamma\Phi}$	27.6 ± 0.5 $^{b\,\Gamma}$	50.8 ± 4.8 $^{a\,\Gamma}$	93.6 ± 12.9 $^{a\,\Gamma\Delta}$	9.5 ± 1.1 $^{a\,\Delta}$	1.2 ± 0.2 $^{a\,\Gamma}$
PI		0.682	0.737	0.754	0.262	0.636	0.882	0.864	0.813

Table 3.3: Results of regression analyses for the dependence of RI, SLA and N_a on relative height (columns 1-3), for the relation between SLA and N_a or N_m (columns 4 and 5), and for the dependence of $V_{cmax,m}$ on SLA, $A_{max,N}$ on RI, and $A_{max,m}$ on N_m (columns 6-8) in the five species. Given are P, R^2, the equation parameters a und b, and the significance of species difference in the slope (ds) of the relationships. Significant relations in bold, marginally significant ones (0.05 < P < 0.1) in italics. Abbreviations: relative height (relH), relative irradiance (RI). n.s. – not significant, n.a. – not applicable due to non-linear relationship.

		(1)	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**
		RI vs. relH	SLA vs relH	N_a vs relH	SLA vs N_a	SLA vs N_m	$V_{cmax,m}$ vs. SLA	$A_{max,N}$ vs. RI	$A_{max,m}$ vs. N_m
equation		y = a exp(bx)	y = a+bx	y = a+bx	y = 1/(a+bx)	y = a+bx	y = a+bx	y = a+bx	y = a+bx
F. excelsior	P	**0.0023**	**0.0016**	**0.0129**	**0.0004**	**0.0045**	**0.014**	**0.0212**	**0.0035**
	R²	**0.62**	**0.61**	**0.44**	**0.69**	**0.54**	**0.44**	**0.46**	**0.59**
	a	**3.7 10-5**	**1.03**	**0.58**	**0.1812**	**14.98**	**298.61**	**122.33**	**-86.12**
	b	**10.39**	**-0.0016**	**0.11**	**0.0025**	**0.0829**	**3.71**	**-81.59**	**10.51**
	ds	na	**Fs *** **	n.s.	n.a.	**Tc *.** *Fs* **	n.s.	**Fs *** **	n.s.
A. pseudo-platanus	P	**0.0143**	**0.0008**	**0.0032**	**<0.0001**	**0.0069**	**0.0163**	**0.0106**	**0.0493**
	R²	**0.50**	**0.66**	**0.56**	**0.96**	**0.5**	**0.42**	**0.53**	**0.31**
	a	**0.005**	**0.99**	**0.48**	**0.0657**	**22.5**	**410.5**	**98.69**	**-140.7**
	b	**5.57**	**-0.002**	**0.11**	**0.0030**	**0.041**	**2.84**	**-56.05**	**10.62**
	ds	na	**Fs *** **	*(Cb)*	n.a.	n.s.	n.s.	n.s.	n.s.
C. betulus	P	**<0.0001**	**0.0007**	**<0.0001**	**<0.0001**	0.1569	0.6998	0.8122	0.1697
	R²	**0.80**	**0.63**	**0.77**	**0.96**	0.16	0.01	0.01	0.16
	a	**0.002**	**0.99**	**0.48**	**0.0723**	22.7	629.17	80.18	-121.88
	b	**6.28**	**-0.0012**	**0.18**	**0.0036**	0.008	0.21	7.18	10.76
	ds	na	**Fs ** **	*(Ap. Fs)*	n.a.	n.a.	n.a.	n.a.	n.a.
T. cordata	P	**0.0177**	**0.0002**	**0.0036**	**<0.0001**	**0.0013**	**0.0033**	0.8895	0.1794
	R²	**0.58**	**0.79**	**0.63**	**0.95**	**0.56**	**0.5**	0.002	0.14
	a	**0.012**	**1.01**	**0.47**	**0.0907**	**26.7**	**598.87**	84.10	-35.95
	b	**4.40**	**-0.0012**	**0.15**	**0.0025**	**0.029**	**1.56**	-4.65	7.1
	ds	na	**Fs ** **	n.s.	n.a.	**Fe * **	n.s.	n.a.	n.a.
F. sylvatica	P	**<0.0001**	**0.0092**	**0.0016**	**<0.0001**	*0.0723*	**0.0046**	*0.0722*	0.1121
	R²	**0.90**	**0.47**	**0.61**	**0.92**	*0.24*	**0.53**	*0.26*	0.2
	a	**0.0003**	**0.86**	**0.51**	**0.0604**	*23.5*	**446.67**	*92.14*	-209.05
	b	**9.11**	**-0.0009**	**0.11**	**0.0033**	*0.018*	**2.22**	*-79.08*	12.96
	ds	na	**all species**	*(Cb)*	n.a.	*Fe ** *	n.s.	*Fe *** *	n.a.

Examining the inter-relationships between N_a or N_m and SLA as likely determinants of photosynthetic capacity showed that N_m was positively related to SLA in four species (significant in *F. excelsior*, *A. pseudoplatanus* and *T. cordata*, marginally significant in *F. sylvatica*, no relation in *C. betulus*; Fig. 3.3b and Table 3.3: column 5). Across all species, N_m showed a closer relation to SLA than to relative irradiance (Table 3.3: column 5 and Fig. 3.2c). Nevertheless, the N_m/SLA relation was less tight than the negative hyperbolical relation between N_a and SLA (Fig. 3.3a and Table 3.3: column 4) which was the closest relationship between any two of the leaf traits investigated ($P < 0.001$ in all species, R^2 values of 0.69 to 0.96). The slope parameter b ranged between 0.0025 and 0.0036 in the five species and showed no clear relation to the shade tolerance of the species.

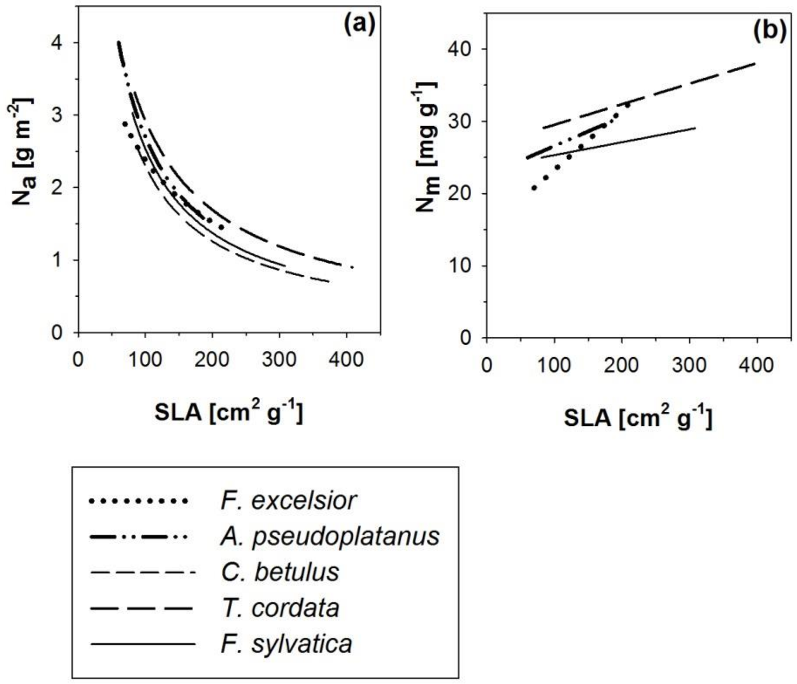

Figure 3.3: Relationships between SLA and N_a (a), and SLA and N_m (b) in the canopies of the five tree species. Only significant relations are printed. The equations and their parameters are given in Table 3.3 (columns 4 and 5).

While all species had higher N_a and smaller SLA values in their sun than shade leaves (Table 3.2), the sun leaves of four species had also a smaller size than the shade leaves (difference significant in *T. cordata* and *F. sylvatica,* non-significant trend in *A. pseudoplatanus* and *C. betulus*). Early- to mid-successional *F. excelsior* differed from the other species by a non-significant tendency for larger, and not smaller, sun than shade leaves (Table 3.2). SLA increased and N_a decreased with increasing leaf size in *T. cordata* and *F. sylvatica* but no such relationship was found in the other three species (Table 3.4). Only in these two moderately to highly shade tolerant species, leaf size showed a significant negative dependence on relative irradiance. N_m decreased with increasing leaf size in *F. excelsior*, but increased in *F. sylvatica* (Table 3.4). The plasticity index after Valladares et al. (2002) for SLA and N_a was higher for the shade-tolerant than for the more light-demanding species (Table 3.2).

Table 3.4: Results of linear regression analyses between leaf size as dependent variable and relative irradiance (RI), SLA, N_a or N_m. Given are *P*, *R²* and the direction of the relationship (+ positive, - negative). Significant relations in bold, marginally significant ones ($0.05 < P < 0.1$) in italics.

		RI	**SLA** $cm^2\ g^{-1}$	**N_a** $g\ m^{-2}$	**N_m** $mg\ g^{-1}$
F. excelsior	*P*	0.8736	*0.0765*	0.8546	**0.0050**
	R²	0.003	*0.26*	0.003	**0.53**
	direction	+	-	+	**-**
A. pseudo-platanus	*P*	0.1437	0.7128	0.3672	0.2459
	R²	0.22	0.01	0.07	0.12
	direction	-	+	-	-
C. betulus	*P*	0.6357	0.9168	0.8895	0.1301
	R²	0.02	0.0009	0.002	0.18
	direction	-	+	-	+
T. cordata	*P*	**0.0019**	**0.0021**	**0.0002**	0.1652
	R²	**0.60**	**0.53**	**0.68**	0.14
	direction	**-**	**+**	**-**	+
F. sylvatica	*P*	**0.0045**	**0.0333**	**0.0234**	**0.0343**
	R²	**0.53**	**0.32**	**0.36**	**0.32**
	direction	**-**	**+**	**-**	**+**

Intra-canopy gradients of photosynthetic capacity and leaf dark respiration and their relation to RI, N_a and SLA

The species differences in the area-related photosynthetic capacity of sun leaves (i.e. leaves exposed to >25 % canopy openness) were only moderate and not significant in our species sample (Table 3.2). However, shade-tolerant *F. sylvatica* tended to have a lower $A_{max,a}$ mean and *F. sylvatica* and *C. betulus* a lower $J_{max,a}$ mean in the sun canopy than the other species (differences not significant at $P < 0.05$). The species differences were more pronounced in the shade leaves (<25 % canopy openness) where the species with higher light demand (*F. excelsior* and *A. pseudoplatanus*) had higher $A_{max,a}$ and $J_{max,a}$ means (differences to the other species mostly significant) and tended to have higher $V_{cmax,a}$ means than the more shade-tolerant *C. betulus, T. cordata* and *F. sylvatica* (Table 3.2). The plasticity index of Valladares et al. (2002) for J_{max} and A_{max} was higher in the shade-tolerant than in the more light-demanding species (Table 3.2).

While the $V_{cmax,a}/J_{max,a}$ ratio tended to be higher in shade than in sun leaves of *F. excelsior* (not significant) and *T cordata* (significant at P <0.05), no difference was found in *A. pseudoplatanus, C. betulus* and *F. sylvatica* (Table 3.5). The $V_{cmax,a}/J_{max,a}$ ratio showed neither a relation to the shade tolerance of the species nor to the morphological sun/shade leaf difference.

Table 3.5: $V_{cmax,a}/J_{max,a}$ ratio (in mol mol^{-1}) of sun and shade leaves of the five tree species and the total leaf sample. Different lower case Latin letters indicate significant differences between sun and shade leaves for a species, different upper case Latin letters give significant species differences for sun leaves and ‘all leaves’, different Greek letters species differences for shade leaves.

	Sun leaves	**Shade leaves**	**All leaves**
F. excelsior	1.86 ± 0.10^{aA}	$2.26 \pm 0.14^{a\Gamma}$	2.11 ± 0.11^{AB}
A. pseudoplatanus	1.82 ± 0.31^{aA}	$1.78 \pm 0.08^{a\Gamma}$	1.80 ± 0.14^{A}
C. betulus	1.98 ± 0.17^{aA}	$2.06 \pm 0.15^{a\Gamma}$	2.03 ± 0.11^{AB}
T. cordata	1.80 ± 0.17^{aA}	$2.12 \pm 0.09^{b\Gamma}$	1.97 ± 0.10^{AB}
F. sylvatica	2.47 ± 0.41^{aA}	$2.52 \pm 0.43^{a\Gamma}$	2.50 ± 0.30^{B}

Table 3.6 presents the results of regression analyses on the dependence of photosynthetic capacity (area-related V_{cmax}, J_{max} and A_{max} and mass-related A_{max}) and (area-related) leaf dark respiration on RI, SLA and N_a. The expected positive relation between relative irradiance and photosynthetic capacity was found to be significant for V_{cmax}, J_{max} and A_{max} only in two species (*C. betulus and T. cordata*); in *A. pseudoplatanus* and *F. excelsior*, only the RI-J_{max} relation was significant but not the relation to A_{max} and V_{cmax} (marginally significant for *F. excelsior*). In *F. sylvatica*, only $V_{cmax,a}$ increased significantly (and $J_{max,a}$ marginally significantly) with increasing irradiance (Table 3.6).

Table 3.6: Results of regression analyses between relative irradiance (RI), SLA or N_a, and five gas exchange parameters. Given are *P*, *R²* and the direction of the relationship (+ positive, - negative). Equations for RI: linear equations except for cases marked by * (non-linear regression equation: $y = a (1- \exp^{(-bx)})$); equation for SLA: $y = 1 / (a + bx)$; equation for N_a: $y = a x^b / (x^b + c)$; linear equation for R_d (SLA and N_a). ^{A} marks parameters with a significant linear regression to LMA.

		$V_{cmax,a}$	$J_{max,a}$	$A_{max,a}$	$A_{max,m}$	$R_{d,a}$
Relative irradiance RI						
F. excelsior	*P*	_0.0853*_	__0.0026*__	0.7273*	**0.0479**	__0.0448*__
	R²	*0.27*	**0.61**	0.01	**0.37**	**0.34**
	direction	+	**+**	+	**-**	**+**
A. pseudo-platanus	*P*	__0.0223*__	__0.0001*__	0.2972*	**0.0052**	0.1843*
	R²	**0.46**	**0.82**	0.12	**0.60**	0.19
	direction	**+**	**+**	+	**-**	+
C. betulus	*P*	__< 0.0001*__	__< 0.0001*__	__0.0001*__	0.9832	_0.0841*_
	R²	**0.78**	**0.80**	**0.78**	$4.7\ 10^{-5}$	*0.25*
	direction	**+**	**+**	**+**	-	+
T. cordata	*P*	__0.0047*__	__0.0019*__	__0.0178*__	0.5791	0.1512*
	R²	**0.53**	**0.60**	**0.45**	0.03	0.18
	direction	**+**	**+**	**+**	-	+
F. sylvatica	*P*	__0.0154*__	_0.0699*_	0.6340*	**0.0279**	0.5211*
	R²	**0.46**	*0.29*	0.02	**0.37**	0.04
	direction	**+**	+	+	**-**	+
SLA						
F. excelsior	*P*	0.1813	**0.0056** ^{A}	0.6897	**0.0183** ^{A}	0.2482
	R²	0.15	**0.52**	0.02	**0.44**	0.12
	direction	-	**-**	-	**+**	-
A. pseudo-platanus	*P*	**0.0335**	**0.0085** ^{A}	0.3087	**0.0128** ^{A}	0.3243
	R²	**0.34**	**0.48**	0.09	**0.44**	0.09
	direction	**-**	**-**	-	**+**	-
C. betulus	*P*	**0.0002** ^{A}	**< 0.0001** ^{A}	**0.001** ^{A}	0.5516	**0.0137**
	R²	**0.74**	**0.80**	**0.66**	0.03	**0.41**
	direction	**-**	**-**	**-**	-	**-**
T. cordata	*P*	**0.0002** ^{A}	**0.0002** ^{A}	**0.0071** ^{A}	0.3661	0.5453
	R²	**0.70**	**0.69**	**0.47**	0.07	0.03
	direction	**-**	**-**	**-**	+	-
F. sylvatica	*P*	**0.0021** ^{A}	*0.0686*	0.8543	**0.0221** ^{A}	*0.0644* ^{A}
	R²	**0.61**	*0.27*	0.003	**0.36**	*0.27*
	direction	**-**	-	+	**+**	-

Table 3.6 continued		$V_{cmax,a}$	$J_{max,a}$	$A_{max,a}$	$A_{max,m}$	$R_{d,a}$
N_a						
F. excelsior	*P*	**0.0312**	**0.0033**	0.4514	0.2714	0.1374
	R^2	**0.50**	**0.68**	0.16	0.25	0.19
	direction	**+**	**+**	+	+	+
A. pseudo-platanus	*P*	**0.0084**	**0.0067**	0.4304	**0.0049**	0.4046
	R^2	**0.62**	**0.63**	0.16	**0.66**	0.06
	direction	**+**	**+**	+	**+**	+
C. betulus	*P*	**< 0.0001**	**0.0001**	**< 0.0001**	0.2976	*0.0973*
	R^2	**0.87**	**0.81**	**0.87**	0.22	*0.21*
	direction	**+**	**+**	**+**	+	+
T. cordata	*P*	**< 0.0001**	**0.0005**	**0.0207**	0.6587	0.1407
	R^2	**0.79**	**0.72**	**0.51**	0.07	0.16
	direction	**+**	**+**	**+**	+	+
F. sylvatica	*P*	**0.0019**	*0.0709*	0.4908	**0.0014**	**0.0051**
	R^2	**0.71**	*0.41*	0.12	**0.70**	**0.53**
	direction	**+**	+	-	**+**	**+**

$V_{cmax,a}$ and $J_{max,a}$ showed significant negative relations to SLA and positive relations to N_a in all species (except for V_{cmax} in *F. excelsior*: non-significant relation to SLA; and J_{max} in *F. sylvatica*: marginally significant relations to SLA and N_a). The SLA and N_a influence was generally weaker on $A_{max,a}$ than on $V_{cmax,a}$ and $J_{max,a}$: this relation was significant only in *C. betulus* and *T. cordata* but non-significant in the other three species (*F. excelsior, A. pseudoplatanus* and *F. sylvatica*). In these species, SLA, N_a and also RI significantly influenced mass-related A_{max} instead of area-related A_{max}.

We compared the five species with respect to three measures of photosynthetic performance across the intra-canopy light gradient, the $V_{cmax,m}$-SLA relation, the $A_{max,m}$-N_m relation, and the dependence of $A_{max,N}$ on RI (Fig. 3.4). (1) Maximum carboxylation rate per leaf mass ($V_{cmax,m}$) decreased with a decrease in SLA (relationship significant in all species except for *C. betulus*) but showed steeper slopes (2.8 and 3.7 µmol m^{-2} s^{-1}) in the more light-demanding species *A. pseudoplatanus* and *F. excelsior* than in the more shade-tolerant *T. cordata* and *F. sylvatica* (1.6 and 2.2 µmol m^{-2} s^{-1}; Table 3.3: column 6 and Fig. 3.4a); however, this difference was not significant. (2) $A_{max,m}$ increased with foliar N concentration (N_m) in *F. excelsior* and *A. pseudoplatanus* while N_m had no influence on the $A_{max,m}$ variation in the canopies of the more shade-tolerant species (Table 3.3: column 8 and Fig. 3.4c). (3) Instantaneous photosynthetic N use efficiency (PNUE or $A_{max,N}$)

increased linearly with a decrease in irradiance in *F. excelsior, A. pseudoplatanus* and (marginally significant) *F. sylvatica* (Fig. 3.4b and Table 3.3: column 7) but revealed no relation in the other species.

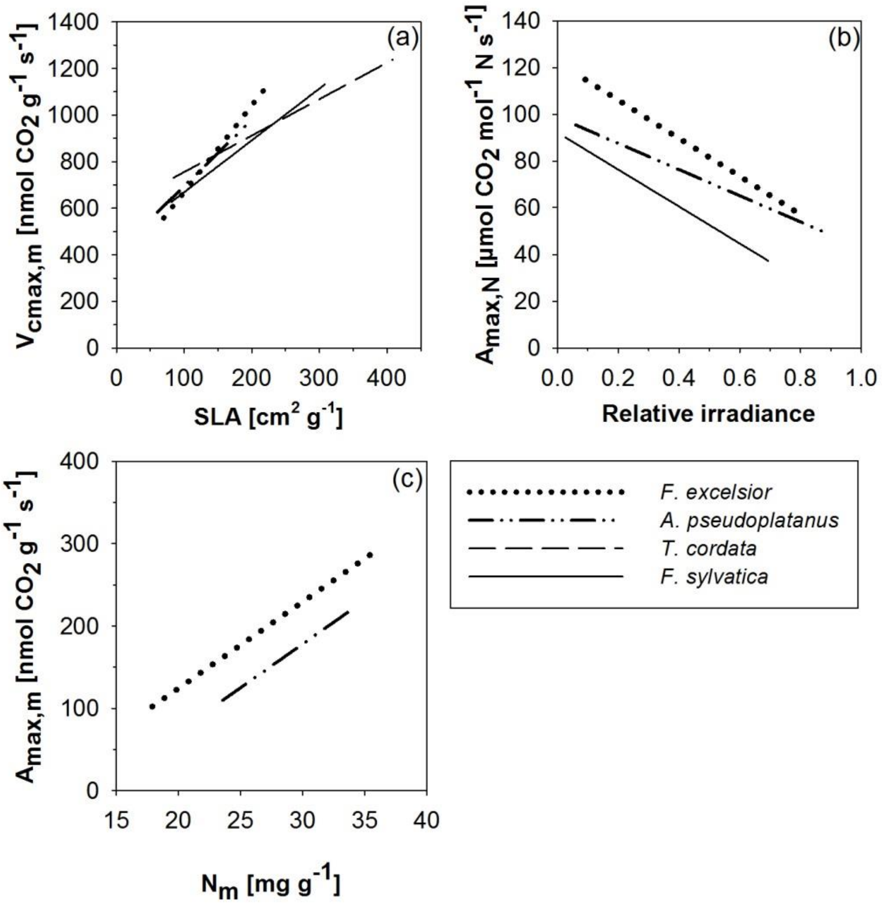

Figure 3.4: Dependence of $V_{cmax,m}$ on SLA (a), of $A_{max,N}$ (photosynthetic N use efficiency) on relative irradiance (b), and of $A_{max,m}$ on N_m in the canopies of the five species. Only significant relationships are printed. The equations and their parameters are given in Table 3.3 (columns 6-8).

Leaf dark respiration as estimated from the intercept of the A/C_i curve with the y-axis showed no clear picture of inter-relationships with relative irradiance, SLA and N_a among the five species (Table 3.6). The expected positive relation between N_a and area-related leaf dark respiration was found in only one species (*F. sylvatica*) together with a marginally significant relation in *C. betulus*. However, leaf dark respiration expressed on a leaf mass basis ($R_{d,m}$) scaled positively with N per leaf mass (N_m) in three species (*F. excelsior*, *T. cordata*, *F. sylvatica*) and with SLA in two species (*F. excelsior*, *T. cordata*, data not shown) indicating a higher mass-specific dark respiration of the shade leaves in these species, which contrasts with the generally lower area-specific respiration of the shade leaves (see Table 3.2).

3.5 Discussion

Species differences in low-light adaption: leaf-morphology and foliar N

Our comparison of the five tree species revealed larger species differences in leaf morphology and physiology in the shade crown than in the sun crown. Leaves exposed to a canopy openness >0.25 (‘sun leaves’) showed only moderate species differences in SLA, nitrogen per area and mass, photosynthetic capacity per area (V_{cmax}, J_{max} and A_{max}) and leaf dark respiration. For the majority of parameters, these differences were not significant and no clear relation to the species’ shade tolerance or successional status was visible. A marked exception was only sun leaf size with a high variation among the species. Thus, the five species revealed more or less convergent patterns in the morphology and functioning of the sun leaves despite large differences in phylogeny, crown morphology, shade tolerance, and physiology (Köcher et al. 2009). One factor that certainly has favoured convergence in the sun foliage are the uniform microclimatic and edaphic conditions under which the species existed in the Hainich mixed forest.

The situation is different in the shade canopy (here defined as canopy openness <0.25 %, RI typically <0.2) where the species can be arranged into two groups according to SLA, N_a and the photosynthetic performance of the shade leaves, the first group with higher light demand (*F. excelsior, A. pseudoplatanus*), the second with moderate to high shade tolerance (*C. betulus, T. cordata, F. sylvatica*). A key variable determining the formation of adapted shade leaves is certainly SLA that reached in the first group maximum values of only ~200 $cm^2\ g^{-1}$, which is considerably less than the maximum value found in the more shade-tolerant second group. Since *Fraxinus* and *Acer* have on average much larger shade (and also sun) leaves than *C. betulus*, *T. cordata* and *F. sylvatica* (*A. pseudoplatanus*: two- to fourfold, *F. excelsior*: four- to twelvefold larger, Table 3.2), it is likely that specific leaf area cannot further be increased in the large *Fraxinus* and *Acer* leaves. The limits of maximising leaf area by increasing SLA and reducing leaf thickness are set by the mechanical requirements of the foliage and its exposure to additional stresses such as drought, herbivory and frost (Valladares & Niinemets 2008). This explanation is supported by our observation that the lowest irradiance levels measured in proximity to *F. excelsior* and *A. pseudoplatanus* shade leaves were higher (RI not below 0.05 or 0.03) than those recorded near typical shade leaves of the more shade tolerant three species (RI minima of 0.02 or 0.01, see Fig. 3.2a). This suggests that ash and maple are indeed less shade-tolerant than the other three species as is also indicated by the scores of relative shade tolerance of Niinemets & Valladares (2006).

The N_a minima in the shade leaves were much lower in *C. betulus*, *T. cordata* and *F. sylvatica* than in *F. excelsior* and *A. pseudoplatanus*. While the large leaves of ash and maple may be costly in terms of supporting structures, those of *T. cordata* are characterised by particularly high N investments per leaf mass (significantly higher N_m values than in the other species). Lime shade leaves also had the highest SLA values of all species examined; thus, with respect to morphology, these leaves must be considered as the most distinct shade leaves in our species sample. The large SLA variation in the leaves of *T. cordata* was associated with a high plasticity in leaf size; lime shade leaves were nearly twice as large as sun leaves.

Due to their small size and relatively low N concentration, *F. sylvatica* and *C. betulus* shade leaves are apparently the least costly leaves in terms of N investment and supporting structures. However, the two species differ in that *F. sylvatica* manages to reach high N_a values in its sun leaves due to a much higher plasticity in leaf size, while *C. betulus*, which apparently is neither flexible in leaf size nor in N investment per leaf mass, produces the sun leaves with lowest N_a values of all species investigated. Thus, most leaves in the canopy of *C. betulus* have to be considered as shade leaves in terms of SLA and N_a, while the leaves of *T. cordata* and *F. sylvatica* cover a wide range of morphological types with sun leaves of these shade-tolerant species being similar to the sun leaves of light-demanding species.

As expected, N_a and SLA were closely related to each other in a negative hyperbolical way in all species (Fig. 3.3a). This relation resulted not only from the intra-canopy gradient in lamina thickness (or SLA) but it is partly also caused by changes in mass-specific N content (N_m) from the sun to the shade crown. We found significant N_m increases with increasing SLA in *F. excelsior*, *A. pseudoplatanus* and *T. cordata*, and a tendency for an N_m increase in *F. sylvatica*. Correspondingly, N_m decreased significantly with increasing relative irradiance in *F. sylvatica* (and marginally significant also in *T. cordata*), evidencing higher N concentrations in shade than sun leaves in three of the investigated species. This matches with results obtained by Niinemets (1997) in four broad-leaved tree species who assumed that N_m should be more responsive to decreasing irradiance in shade-tolerant than in light-demanding species because an increase of light-harvesting compounds per leaf mass and thus in the specific absorptivity of shade leaves is one strategy to relieve light limitation imposed on photosynthesis. This assumption is supported by our data where the N_m increase with decreasing RI was only found in the highly (or moderately) shade-tolerant species *F. sylvatica* and *T. cordata*. In these species, shade leaves represent a high-priority sink for nitrogen.

Our results on leaf morphological plasticity within the canopies contradict the assumption that shade-tolerant tree species should generally be less plastic than light-demanding species (Valladares & Niinemets 2008). A larger within-canopy plasticity of the shade-tolerant species is not only visible in the higher plasticity indices for SLA, N_a, J_{max} and A_{max} in this group, but also in the steeper SLA increase with increasing depth in the canopy in these species as compared to more light-demanding *F. excelsior* and *A. pseudoplatanus*.

It has been pointed out that leaf plasticity in trees depends on ontogeneity, tree size and also radiation regime (Rozendaal et al. 2006, Valladares & Niinemets 2008). Empirical studies on within-canopy gradients in leaf morphology, foliar N and photosynthetic capacity in mature closed forests are rare (e.g. Kull & Niinemets 1998, Niinemets et al. 1999, Meir et al. 2002). One should expect that the shade exposure of the most basal leaves is higher, and the trait differences between sun and shade leaves larger, in closed stands with tall trees than in younger stands or isolated trees. That tree size affects the intra-crown plasticity in leaf morphology is suggested from a comparison of the Hainich data with other published results that found lower plasticity in the foliage. For example, the 27 m-tall *T. cordata* trees of our study had an up to four times higher SLA in shade than in sun leaves while Niinemets et al. (2004) reported an only twofold difference in 4-17 m tall lime trees. Differences in the radiation regime may also be influential; this could explain the apparent discrepancy between our results and those of Sack et al. (2006) from six temperate broad-leaved tree species. These authors found no relation between intra-canopy leaf plasticity and the species' light requirements for regeneration, which are typically related to the shade tolerance of the adult trees. Sack et al. (2006) studied 13-18 m high solitary trees in an arboretum and not ~30 m tall trees in a closed forest as we did.

Species differences in low-light adaptation: photosynthetic capacity and leaf respiration

As for leaf morphology, we found larger species differences in the physiology of shade than sun leaves. The lowest shade leaf photosynthetic and respiratory activity among the five species was found in *C. betulus*, the species with the least variable leaves in terms of mass-specific N investment (N_m); this species' sun leaf activity was also relatively small. The limited plasticity in N_m, leaf size and also in mass-specific A_{max} and the lacking relation of $A_{max,m}$ to relative irradiance, SLA or N_a in *C. betulus* indicates that this species seems to be relatively inflexible with respect to the allocation of photosynthesis-relevant compounds to leaf tissues. This species achieves acclimation or adaptation to variable light availabilities in the crown mainly through alteration in SLA, and not by modifying N_m and/or leaf size, which is an important strategy in the other four species.

T. cordata has in common with *C. betulus* that SLA variation plays an important role for achieving photosynthetic acclimation across the light availability gradient as is indicated by the lacking influence of RI, SLA and N_a on mass-based A_{max} in both species, whereas RI, SLA and N_a had a strong influence on area-based A_{max}. However, *T. cordata* was much more flexible with respect to N_m and also leaf size than *C. betulus* resulting in higher photosynthetic capacities per area (and also per mass) in the sun leaves of lime than hornbeam.

F. excelsior, A. pseudoplatanus and *F. sylvatica* have in common that area-based A_{max} was, contrary to our expectation, not dependent on relative irradiance, SLA and N_a while mass-based A_{max} showed a significant relation to these determinants of photosynthetic capacity. This indicates that the increase in leaf thickness (i.e. the SLA decrease) from the shade to the sun leaves was not large enough in these three species to compensate the decline in mass-specific photosynthetic capacity from the shade to the sun leaves, as it is indicated by the negative $A_{max,m}$–RI relation in Table 3.6. Three factors may be discussed as potential causes of a reduced mass-based photosynthetic capacity in the trees' sun leaves, (i) a smaller investment of N in leaf structures involved in light harvesting in sun leaves as compared to shade leaves (which explains the reduced photosynthetic N use efficiency of sun leaves, Fig. 3.4b), (ii) a reduced N_m concentration (as found in *F. sylvatica*), and (iii) higher leaf-internal diffusion limitation (Niinemets 2007) and reduced light availability in the interior of the thicker sun leaves.

From the $V_{cmax,m}$ increase with SLA in Fig. 3.4a, it appears that the light-demanding species *F. excelsior* and *A. pseudoplatanus* are more efficiently increasing the CO_2 net flux into the leaf with a growth in leaf area when the leaves become thinner (higher SLA) as compared to the more shade-tolerant species *F. sylvatica* and *T. cordata*, even though the latter reached higher $V_{cmax,m}$ values in absolute terms in their shade leaves (see Fig. 3.4a).

Our data further suggest a shift in the major abiotic determinants of photosynthetic capacity, RI, SLA and N_a, from the more light-demanding to the shade-tolerant species. In the most light-demanding species *F. excelsior*, all three factors correlated closely with $J_{max,a}$ (and to a lesser degree with V_{cmax}), while the closest correlations were found with $V_{cmax,a}$ (and only weakly with J_{max}) in the most shade-tolerant species *F. sylvatica*. In the other three species with intermediate shade tolerance, RI, SLA and N_a were correlated with both $V_{cmax,a}$ and $J_{max,a}$. This might imply that electron transport capacity was optimized with respect to light availability in the more light-demanding species while it was carboxylation capacity that was optimized in the more shade-adapted species.

The inspection of three parameters characterising photosynthetic capacity per unit of invested carbon or nitrogen gave, however, no indication that the shade leaves of the more shade-tolerant species (*C. betulus, T. cordata* and *F. sylvatica*) were generally more efficient in terms of resource use than those of the more light-demanding species: neither mass-specific V_{cmax} or A_{max}, nor photosynthetic N use efficiency ($A_{max,N}$) were generally higher in extreme shade leaves of the group of the more shade-tolerant species (see Figs. 3.4 a-c). This was only the case in *T. cordata* with significantly higher $V_{cmax,m}$ and $J_{max,m}$ rates in the shade leaves than in the other species (Legner et al., unpubl. results). For achieving a more general picture of physiological shade leaf adaptation in temperate trees, a larger number of tree species have to be investigated.

Determinanats of photosynthetic capacity

N_a was in all species (except for J_{max} in *A. pseudoplatanus*) a better predictor of V_{cmax} and J_{max} (R^2 values of 0.41-0.87) than relative irradiance or SLA (R^2: 0.27-0.82). In contrast, a relation of $A_{max,a}$ to these three parameters existed only in *C. betulus* and *T. cordata*, but was non-significant in the other three species. This result is evidence for significant species differences in the strategies of leaf morphological and functional adaptation to light availability gradients. Tree species which only increase SLA (such as *C. betulus*) may be contrasted with species that are capable of increasing SLA and also foliar N concentration (such as *T. cordata* and *F. sylvatica*). The increase in N_m under low light is probably a main driver of the observed linear increase in mass-related maximum carboxylation rate ($V_{cmax,m}$) with SLA in four of the five species of our study, but it was lacking in *C. betulus* with its inflexible N allocation strategy. A corresponding increase in $V_{cmax,m}$ towards the shade leaves was found by Meir et al. (2002) in the canopies of tall temperate broad-leaved and tropical trees.

It is unexpected that only two species (*C. betulus*, *T. cordata*) showed a dependence of $A_{max,a}$ on N_a but three did not. Other studies on intra-canopy light gradients found a linear correlation between N_a and A_{max} (e.g. Ellsworth & Reich 1993). However, there are some reasons to assume that photosynthetic capacity is not always closely related to the absolute amounts of N per leaf area along intra-canopy light gradients. Maximum photosynthesis in deep shade may depend more on SLA, leaf angles and the mode of N partitioning between chemicals used either for light-harvesting or for carboxylation (Meir et al. 2002) than on absolute amounts of N per leaf area; these effects could weaken the N_a influence on A_{max}. In the species without a clear N_a influence on A_{max} in our study (*F. excelsior, A. pseudoplatanus* and *F. sylvatica*), we instead found a significant positive relationship between mass-specific A_{max} and N_a. This may be viewed as an indication that N partitioning must have played a prominent role for determining the intra-canopy variation in photosynthetic capacity, while a larger effect of N_a than of N_m on photosynthetic capacity may point at a key role of SLA. This implies that leaf structural modifications are not the only means by which temperate trees are adjusting to low light, but that alteration in N partitioning can also be influential which is not in line with the assumption of Niinemets (2007) that trees modify mostly SLA.

The generally higher N_m values of the shade leaves as compared to the sun leaves in the species examined may in part explain why mass-specific photosynthetic capacity ($V_{cmax,m}$; $J_{max,m}$; $A_{max,m}$) in four of the five species (exception: *C. betulus*) was higher in shade than in sun leaves in the Hainich forest (see plot of $V_{cmax,m}$ vs. SLA in Fig. 3.4a) which contrasts with the area-specific rates. Our findings contradict earlier studies in broad-leaved trees that found mass-specific J_{max} and A_{max} to be relatively invariant along the intra-canopy light gradient (e.g. Ellsworth & Reich 1993, Niinemets et al. 2004) but which are consistent with the higher mass-specific photosynthetic capacities in shade than in sun leaves reported by Niinemets et al. (1998). However, these studies investigated smaller trees and thus shorter intra-canopy light gradients than we did. A factor that might also be influential is the rather high fertility of the Hainich soils; we argue that high soil N availability could promote relatively high shade leaf N concentrations as were found in our study.

Respiratory losses per dry mass were generally higher in shade than in sun leaves corresponding to the elevated N concentrations. As a consequence, area-related leaf dark respiration rate did not significantly decrease with increasing shade tolerance of the species, not supporting the prediction of the carbon gain hypothesis formulated by Givnish (1988).

Other causes of intra-canopy leaf modification

An examination of canopy architecture and the general ecology of the five species (Frech et al. 2003, Ellenberg & Leuschner 2010) indicates that traits related to canopy architecture may also play an important role in determining the degree of shade adaptation in these five species. In the Hainich forest, Frech (2006) found a longer vertical crown extension in the species with moderate to high shade tolerance (*C. betulus, T. cordata, F. sylvatica*) than in light-demanding *F. excelsior* which concentrated the foliage in the upper third of canopy space. Possible explanations for this discrepancy are that leaves and branches in the lower part of the ash canopy are missing because (i) the C and N resources needed to build the foliage are preferentially invested in the sun crown for maximising carbon gain in full light, or (ii) the species is inherently limited in its potential to produce shade leaves with higher

SLA and better low-light adaptation (Sack et al. 2006, Niinemets 2007, Valladares & Niinemets 2008).

The inter-relationship between leaf morphology, N partitioning and photosynthetic capacity is further complicated by the fact that the intra-canopy light gradient is typically associated with vertical gradients in atmospheric water vapour saturation deficit (VPD), leaf water status, wind speed and leaf temperature, factors that can modify the light influence on leaf morphology and function. Elevated VPD may not only limit photosynthesis through a reduction of stomatal conductance (Gries 2004) but it can also influence leaf expansion growth and may determine final leaf size in trees (Fender et al. 2011). Further abiotic stressors such as excess radiation, restricted water supply and high leaf temperatures can reduce the assimilation rate of sun leaves and may have negative effects on leaf expansion (Niinemets et al. 1999, Chaves et al. 2002, Niinemets 2007). Experiments under field conditions would be needed to prove the importance of these factors for leaf morphology and function.

Conclusions

In our species sample, the three shade-tolerant species *C. betulus, T. cordata and F. sylvatica* differed from the two more light-demanding species in a number of leaf- and canopy-level traits relevant for low-light acclimation. Among the most important differences are a greater vertical canopy extension and, in support of hypothesis (1), a higher intra-canopy SLA variation in the shade-tolerant species, which is reflected in a relatively steep RI/SLA slope and in the formation of shade leaves with high SLA (exceeding values of ~200 cm^2 g^{-1}), supporting hypothesis (2). Shade leaf N_a was relatively low in the shade-tolerant species due to a high SLA, even though two species increased mass-specific N content (N_m) with decreasing light. In shade-tolerant temperate broad-leaved trees, a plurality of low-light adaptation strategies seems to exist. In fact, the three shade-tolerant species *C. betulus*, *T. cordata* and *F. sylvatica* differed markedly with respect to the relative importance of light-induced modifications in either SLA or N allocation patterns to leaf tissues. Species-specific restrictions in the capability of achieving high SLA values are certainly a key trait. We found only weak support for our hypothesis (3) that the shade leaves of the more shade-tolerant species should be more efficient in terms of C and N use in photosynthesis than those of the light-demanding species.

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CHAPTER 4

Photosynthetic capacity of Central European broad-leaved trees: variation with light demand and tree age, and alteration since the 1960s

N. Legner & C. Leuschner

Keywords: adult trees, N deposition, photosynthetic capacity, saplings, successional status.

4.1 Summary

The photosynthetic capacity of trees is an important input variable of terrestrial biosphere models but reliable data from adult trees are scarce. We compiled a data base of A_{max} (light-saturated net photosynthesis), V_{cmax} (maximum carboxylation efficiency) and J_{max} (maximum electron transport rate) data from Central European broad-leaved tree species (19 taxa; 302 data sets; grouped by successional status, tree age and leaf position). We tested the hypotheses that (1) photosynthetic capacity decreases with increasing shade tolerance, (2) sun leaves of adult trees have higher capacities than those from juveniles, and (3) sun/shade leaf differences in photosynthetic capacity increase with higher shade tolerance. For five Central European broad-leaved tree species, differences in A_{max}, V_{cmax} and J_{max} of mature trees and saplings were studied in depth. Both approaches revealed large among-species variations in photosynthetic capacity but only weak differences between early- and late-successional species, contradicting earlier studies. Photosynthetic capacity was generally not higher in the sun leaves of mature trees than in juvenile trees grown in high light. The sun/shade leaf difference in the photosynthetic capacity of mature trees was not larger in late- than early-successional trees. 17 data sets from mature *Fagus sylvatica* trees show a doubling of sun leaf A_{max} since the late 1960s. We conclude that parameterisation of terrestrial biosphere models for simulating canopy photosynthesis should not be done with group means of photosynthetic capacity in early-, mid- and late-successional trees and should not use data from juveniles, urging to complete data bases with a focus on mature trees.

4.2 Introduction

Central Europe's temperate broad-leaved forests are composed of c. 45 tree species, but only about 18 taxa are more widespread in the natural forest communities and eleven or so species (*Fagus sylvatica, Tilia cordata, Quercus robur* and *Q. petraea, Fraxinus excelsior, Acer pseudoplatanus, Betula pendula* and *B. pubescens, Salix alba, Alnus glutinosa* and *A. incana*) may achieve dominance, or at least a high cover, in certain forest communities (Ellenberg & Leuschner 2010); all other species are only admixed with low cover values. However, despite being rather species-poor, the woody flora of Central Europe represents a remarkable diversity in terms of phylogeny and tree functional types being present. The 17 or so most important broad-leaved tree species of natural forest vegetation belong to seven families (Fagaceae, Tiliaceae, Betulaceae, Oleaceae, Aceraceae, Ulmaceae, Salicaceae) with contrasting systematic relatedness, and represent early- or early- to mid-successional species (c. six taxa), mid- or mid- to late-successional species (c. nine taxa), and late-successional species (two taxa) with contrasting light demand at the juvenile stage and canopy structure at maturity. Furthermore, the species pool consists of taxa with constrating physiological and morphological adaptations including species with diffuse- or ring-porous xylem, ecto- or arbuscular mycorrhiza, high or low litter decomposability, and high or low drought sensitivity (Bartels 1993, Köcher et al. 2009, Roloff & Schütt 2006). Much research interest has recently focused on tree functional traits because they are indispensable for predicting species responses to environmental change and are fundamental for understanding effects of species identity and species diversity on ecosystem processes in forests (Reich et al. 1998).

One of the most important tree functional traits is photosynthetic capacity because it is one of the determinants of forest primary productivity and a key input variable of global terrestrial biosphere models (TBM). In the photosynthesis model of Farquhar et al. (1980), photosynthetic capacity is expressed by V_{cmax} (maximum rate of carboxylation at standard temperature) and J_{max} (maximum rate of electron transport at standard temperature). More widely used in field studies is the maximum rate of net photosynthesis (A_{max}) measured under ambient [CO_2] and favourable environmental conditions (light saturation, optimal temperature, no limitation by soil water deficits or elevated water vapour saturation deficits). Progress in parameterisation of TBMs for forest biomes is hampered by the limited availability of suitable data on the photosynthetic capacity of mature trees in temperate, boreal and tropical forests. Numerous observations exist for A_{max} of juvenile trees (seedlings and saplings) measured outdoors under variable light conditions (e.g. Dreyer et al. 2001, Valladares et al. 2002, Wittmann et al. 2001) but it is doubtful whether this information can simply be extrapolated to mature trees in the field because physiological activity and leaf morphology and chemistry may change from the juvenile to the adult stage (Cornelissen et al. 2003, Valladares & Niinemets 2008). However, not many studies have examined differences in photosynthesic capacity of juvenile and mature tree species in a systematic way (e.g. Grulke & Retzlaff 2001, Hölscher 2004, Thomas & Winner 2002).

For the large majority of temperate and boreal tree species, only very few or no observations on A_{max} at maturity do exist, which is partly caused by difficult canopy access. The lack of data is even more severe in the case of V_{cmax} and J_{max} because these parameters require more time-consuming measuring approaches than A_{max}. The few existing reviews of photosynthetic capacity data for temperate trees often do not distinguish between juvenile and mature trees (e.g. Ellsworth et al. 2004, Hallik et al. 2009, Wullschleger 1993) or include data obtained with older measuring techniques that are thought to be less reliable (e.g. Larcher 1969). In the absence of suitable data, leaf area-based A_{max} has often been predicted from leaf nitrogen content (Evans 1989, Lambers et al. 2008, Wright et al. 2004) which, however, can give only a rough estimate of light-saturated net photosynthesis rate. Moreover, photosynthetic capacity typically shows large variation across tree canopies in close association with light availability which has strong influence on leaf N content per area and specific leaf area, the two principal determinants of area-related photosynthetic capacity which determines leaf N content per area and specific leaf area, the two principal determinants of area-related photosynthetic capacity (Ellsworth et al. 2004, Niinemets 2007, Reich et al. 1998). Consequently, data on the photosynthetic capacity of trees and leaf N-derived estimates of A_{max} require a careful check with respect to their representativeness for the canopy before they can be used in modelling exercises.

Here, we present the results of a comparative study on the photosynthetic capacity of five important broad-leaved tree species of Central Europe (genera *Fagus, Tilia,* *Carpinus, Acer* and *Fraxinus*) under well-defined environmental conditions in which mature and juvenile trees were examined. We investigated A_{max}, V_{cmax} and J_{max} of exposed sun leaves and typical shade leaves of tall (~30 m high) trees in close neighbourhood to each other in a mixed stand and also examined the photosynthetic capacity of 2-3 yr-old saplings grown under high light. In a second step, we compiled a data base of published and unpublished A_{max}, V_{cmax} and J_{max} data of these five and other Central European broad-leaved tree species for compiling species means of photosynthetic capacity for sun and shade leaves of mature trees, and juvenile trees of as many Central European tree species as possible. We addressed the following questions: how different are the photosynthetic capacities (1) of light-demanding early-successional and shade-tolerant late-successional species, (2) of the sun leaves of mature trees and juvenile trees, and (3) of sun and shade leaves of mature trees? We carefully checked the literature data for comparability of site and measuring conditions in order to generate relatively homogenous A_{max}, V_{cmax} and J_{max} data sets in terms of leaf origin (upper sun or typical shade canopy of mature trees, juveniles older than 1 year), measuring conditions (optimal light and temperatures in the range of 20-25 °C, light response curves examined at ambient [CO_2]), equipment used (open gas exchange systems), and geographical range (only temperate broad-leaved tree species of Central and Western Europe).

Using this comprehensive data base, we tested the hypotheses that (i) late-successional species have a lower area-related photosynthetic capacity of their sun and shade leaves than early-successional species as stated by Kutsch et al. (2009) and others (e.g. Ceulemans & Saugier 1991, Lambers et al. 2008), (ii) the sun leaves of mature trees show higher photosynthetic capacities than tree juveniles in high light as found by Thomas & Winner (2002), and (iii) the sun-shade leaf difference in area-related photosynthetic capacity increase with increasing shade tolerance.

4.3 Material and methods

In-depth study of five common broad-leaved tree species

For examining the dependence of photosynthetic capacity on tree age and the light demand or successional status of the species, we conducted a comparative study in five abundant and wide-spread Central European broad-leaved tree species with contrasting phylogeny and ecology. The species *Fraxinus excelsior* L. (European ash), *Acer pseudoplatanus* L. (sycamore maple), *Carpinus betulus* L. (European hornbeam), *Tilia cordata* Mill. (small-leaved lime) and *Fagus sylvatica* L. (European beech) were selected in the Hainich National Park (Thuringia, Germany), where they were the most abundant species in a species-rich temperate broad-leaved mixed forest (oak-hornbeam forest community). Even though these species from five different families co-exist in this old-growth stand under similar environmental conditions, they represent largely different tree functional types with respect to canopy architecture, light demand, successional status, hydraulic architecture, drought sensitivity and type of mycorrhiza (see Table 4.1; Köcher et al. 2009).

Table 4.1: Morphological and functional traits of the five species of the in-depth study according to a relative categorisation of species properties in Ellenberg & Leuschner (2010), Roloff & Schütt (2006), Bartels (1993) and others. Extreme values of tree longevity are given in brackets.

	Fraxinus excelsior	***Acer pseudo-platanus***	***Carpinus betulus***	***Tilia cordata***	***Fagus sylvatica***
Family	Oleaceae	Aceraceae	Betulaceae	Tiliaceae	Fagaceae
Max. tree height (m)	< 40	< 40	< 35	45	50
Canopy architectural model	Rauh	Scarrone	Troll	Troll	Troll
Tree longevity (years)	250 - 300	150 - 600	150 - 300	400 (-1000)	350 (-900)
Shade intensity[1]	3	4	4	4	5
Light demand of saplings[2]	5-8	~5	~3	~3.5	~2
Leaf area index	5.8	5.2	8.3	7.1	7.4
Xylem anatomy[3]	Ring	Diffuse	Diffuse	Diffuse	Diffuse
Type of mycorrhiza	Arbuscular	Arbuscular	Ecto	Ecto	Ecto
Successional status	Early/mid	Mid/late	Mid/late	Late	Late

[1] Relative assessment of shade intensity below mature tress (3 – moderate, 4 – high, 5 – very high); [2] estimated minimum canopy transmissivity (in %) required for survival; [3] Ring-porous, diffuse-porous

Measurements of photosynthetic capacity under standard conditions were conducted in the sun and shade canopy of tall trees with up to 30 m in height in the Hainich forest and also in 2-3 year old saplings of theses species that were grown under high light and uniform nutrient and water availabilities in the Experimental Botanical Garden of the University of Göttingen. In the Hainich forest, each five mature trees per species (*F. excelsior*: six trees) were selected in a transect of approximately

200 m length and 30 m width located in the south-east of the national park near the village Weberstedt close to the location Thiemsburg (51° 05’ 00’’ N, 10° 30’ 27’’ E) at 350 m a.s.l.. The soil type is a Luvisol developed from loess over Triassic limestone. Tree age ranges between 80 and 120 years (Gebauer et al. 2008). Canopy access was achieved with a mobile lifter (Denka Lifter model DL30, Rotlehner Arbeitsbühnen GmbH, Massing-Oberdietfurt, Germany) that allowed reaching the uppermost sun leaves at 30 m. The five (six) trees were treated as true replicates in the analysis because they were at least 10 m (in most cases >20 m) apart from each other (except for two ash trees: 5 m). The measurements took place on sunny or overcast days (8 am to 5 pm) in the summers 2008 (Jun 20th – Aug 22nd) and 2009 (May 29th – Aug 29th). The weather during the summer 2008 was characterised by 14.6 °C mean temperature and 234 mm of precipitation in the growing season (April 01st – Sep 30th) while the summer 2009 was somewhat warmer and wetter (15.3 °C and 469 mm; data from Weberstedt/Hainich weather station, meteomedia).

Light- and CO_2-response curves were established in each 15 fully expanded leaves per species on the five trees of a species (i.e. three leaves measured per tree) covering the whole within-canopy light gradient from the uppermost sun canopy top to the bottom of the shade crown. The each three leaves per tree were always chosen in the uppermost sun canopy, in the middle of the canopy (close to the centre of the vertical crown axis) and in the lowermost shade canopy. Since one to two data points per species had to be omitted, we calculated with each 13 leaves of *F. excelsior* and *A. pseudoplatanus*, 14 leaves of *C. betulus* and *F. sylvatica*, and 15 of *T. cordata* in the subsequent analysis.

The *in situ* gas exchange measurements were conducted on intact leaves in natural position in the canopy using a portable LI-6400XT IRGA system (LI-COR Inc., Lincoln, Nebraska, USA) equipped with a standard leaf chamber and a LED red/blue light source (type 6400-02B). In the composed leaves of *F. excelsior*, one leaflet in the middle part of the leaf was examined. We selected the parameters A_{max}, V_{cmax} and J_{max} for characterising photosynthetic capacity in both adult and juvenile trees. On every leaf, the CO_2 response was investigated through three A/C_i curves established at leaf temperatures of 19, 25 and 29 °C (± 1 °C) under a photosynthetic photon flux density (PPFD) of 2000 µmol m^{-2} s^{-1}. After clamping the leaf into the leaf chamber and prior to each A/C_i- or light response curve, incident PPFD was stepwise increased to the maximum (2000 µmol m^{-2} s^{-1}) and the leaves were allowed to adapt to these conditions for at least 10 min in order to avoid stomatal limitation of gas exchange. The IRGA channels were matched before every measuring point. For every A/C_i curve, ambient CO_2-concentration was varied in the following steps in the order: 370, 30, 70, 100, 200, 370, 1200, and 2000 ppm CO_2. The second measurement at 370 ppm was repeated twice until the measured assimilation rate had approached the value of the first measurement under natural CO_2 conditions (370 ppm). Subsequently, a light response curve (at 25 °C and 370 ppm CO_2) was established in 10 steps: 2000, 1200, 500, 200, 100, 50, 20, 0, 0, and 0 µmol m^{-2} s^{-1} PPFD (in 2008 in reverse order) on the same leaves. The vapour pressure deficit was held constant at ambient conditions during the measuring campaign on a leaf. The classification of the measured leaves into sun and shade leaves was done using hemispherical photographs that were taken at exactly the same position were the leaves grew. A threshold value of 25 % of canopy openness was used to separate sun (>25 %) and shade leaves (<25 %).

A sapling study with the five species was conducted in summer 2011 in the Experimental Botanical Garden of the University of Göttingen for measuring the same photosynthetic parameters in 2-3 year old juvenile trees. The plants were obtained from a local tree nursery (Billen Forst GmbH, Bösinghausen, Germany) and planted in late April 2011 in 65 L pots filled with 50 L unfertilised medium-grained sand. Each five saplings of a species with height ranging between 37 and 62 cm were placed together in a pot with the pots replicated 15-fold. The pots were randomly placed outdoors under a mobile transparent plexiglass roof to allow for constant and uniform growing conditions with respect to soil moisture. Thus, the plants were exposed to full sunlight and the pots were watered once a week to keep soil moisture constant at 95% of field capacity. The soil was fertilized twice (Jun 28th and July 04th 2011) with the NPK fertilizer Wuxal super (Bayer, Leverkusen, Germany) to simulate the fertile soil conditions of the field site. To exclude a possible edge effect on the microclimate in the experimental setup, the pots were rearranged in a random manner mid of August 2011.

Gas exchange measurements at the saplings were conducted from July 27th to Aug 31st 2011, on four to six leaves per species using two portable LI-6400 systems in analogy to the measurement protocol used in the mature trees. The measured leaves were all fully expanded and sun-exposed and grew close to the top of the saplings. In contrast to the measuring campaigns in the forest, we established only one A/C_i curve per leaf at 25 °C (the temperature sometimes increased to 26 or 27 °C in full sun; in two leaves, the temperature had to be adjusted to 29 °C).

Data processing

The data from both measuring tasks were analysed with nonlinear least-square regression models implemented in Mathematica (version 3.0, Wolfram Research, Champaign, Illionois, USA) to extract A_{max}, V_{cmax} and J_{max} from the light- and CO_2-response curves. We used the program RACCIA (Fleck 2002) for fitting of the A/C_i curves which bases on the equations of Farquhar et al. (1980), Harley & Tenhunen (1991) and Ball et al. (1987):

$$V_{c\max} = \frac{(A+R_d)\left(C_i + K_c\left(\frac{1+O}{K_c}\right)\right)}{\left(1-\frac{\Gamma_*}{C_i}\right)C_i} \tag{1}$$

$$J_{\max} = \frac{(A+R_d)(4C_i + 8\Gamma_* C_i)}{4(C_i - \Gamma_*)} \tag{2}$$

where the assimilation rate (A), leaf day respiration rate (R_d), the intercellular CO_2 concentration, the Michaelis-Menten constant for carboxylation (K_c) and the CO_2 compensation point without consideration of mitochondrial respiration (Γ_*) are inserted. The light response curves were fitted with a non-rectangular hyperbolic function (Ögren & Evans 1993, Thornley 2002) in the same software environment:

$$A_{\max} = -\left(\frac{A\ \alpha\ PAR - \xi\ A^2}{A - \alpha\ PAR}\right) \tag{3}$$

with the photosynthetically active radiation (PAR), a factor (ξ) which determines the sharpness in the knee of the non-rectangular hyperbolic curve (set to 0.9; Thornley 2002) and the initial slope of the light response curve (α).

Literature data analysis on the photosynthesis capacity of Central European broad-leaved tree species

We compiled a data base of A_{max}, V_{cmax} and J_{max} data from Central and Western European broad-leaved tree species by screening the relevant literature and including additional unpublished results from various sources (Tables A1 to A3 in the appendix). The data base consists of 77 V_{cmax}, 60 J_{max} and 165 A_{max} data sets covering 19 species from six families. Only data from gas exchange measurements conducted under well-defined environmental conditions were considered. Gas exchange data obtained from detached branches were marked with the symbol ‘c’ in the Tables A1 to A3 of the appendix. Estimates of photosynthetic activity reached by down-scaling from stand-level eddy flux measurements, data derived from chlorophyll fluorescence measurements and photosynthesis measurements with older technology taken before the late 1960s (as summarised in Larcher 1969) were excluded. We collected data from three different objects, (i) sun leaves and (ii) shade leaves in the canopy of mature trees (age >20 years) and (iii) tree saplings with a minimum age of 1 year, while seedling studies (age <1 year) were not included. All data refer to measurements under saturating photon flux densities (typically >1200 µmol photons m^{-2} s^{-1}), optimal or near-optimal temperatures (mostly in the range of 18 to 25 °C), ambient CO_2 concentration and conditions of more or less favourable soil water availability, if indicated in the source. When photosynthesis data were taken from carbon dioxide-, temperature-, moisture- or ozone-manipulation studies, they always refer to the control treatment. In a few cases, no data were given and approximate mean values had to be read from the graphics; these values are marked by the symbol ‘~’ in the Tables A1 to A3. If a standard deviation was given in the studies, we calculated a standard error based on the number of measurements (n_M, see Tables A1 to A3 in the appendix).

In our analysis of the literature data, we treated every arithmetic mean of A_{max}, V_{cmax} or J_{max} given in a study for a certain species and location as a single independent value. Thus, our species means for the three photosynthetic parameters are based on one to 17 means from different locations and studies; those data are presented in box-whisker plots of the Figs 4.2, A1 to A2 with species mean, 25- and 75-percent quartiles and minimum and maximum values. In order to obtain a weighted species mean, the study means were weighted by the number of measurements used in the study for averaging (1 to >90). Where no number of samples was given, we calculated with the one data point. We classified the 19 species according to their successional status (early-, mid- and late-successional) using existing information on their occurrence in natural forest communities and the light demand of their offspring as specified in relative and absolute terms in Ellenberg & Leuschner (2010) and other sources. Accordingly, we classified the *Populus, Salix, Betula* and *Fraxinus* species and *Quercus pyrenaica* as early-successional, the *Alnus, Quercus, Acer, Carpinus* species and *Tilia platyphyllos* as mid-successional, and *Tilia cordata* and *Fagus sylvatica* as late-successional, resulting in eight early-successional, nine mid-successional and only two late-successional species in the analysis. Based on the two to nine species means in the three successional groups, we tested for significant differences in A_{max}, V_{cmax} and J_{max} between these groups and for differences between sun leaves (mature trees), shade leaves (mature trees) and saplings within the three successional groups using GLM and Scheffé's test as post-hoc test. In cases of non-normally distributed data or inhomogeneity of variances, we conducted a Wilcoxon test. All statistical analyses were conducted with the program SAS 9.2 (SAS Institute, Cary, NC, USA). To test for significant differences between the five species and between sun leaves of mature and juvenile trees in the in-depth study, we applied a permutation test in the software environment R, version 2.0.8. (R Development Core Team 2008). We used the package 'perm' (Fay & Shaw 2010) with permKS and permTS. We tested for a significant difference in *F. sylvatica* A_{max} between juvenile beech trees reared under full light (Acronym: ju,su) and juveniles reared under reduced sunlight or partial shade (ju,sh) but found no difference (P=0.09, Wilcoxon test); in other species, only very few ju,sh-data were available. We thus treated all juvenile data in the literature survey as one collective in the analysis irrespective of the light regime. A significance level of $P < 0.05$ was used throughout the analysis.

4.4 Results

Influence of successional status and tree age on the photosynthetic capacity of five common tree species

The sun leaves of the five mature tree species (*F. excelsior, A. pseudoplatanus, C. betulus, T. cordata* and *F. sylvatica*) differed not significantly in the photosynthetic capacity of the in-depth-study, even though they belong to different successional groups (early, mid or late); this is valid for V_{cmax}, J_{max} and also A_{max} (Fig. 4.1). However, late-successional *F. sylvatica* tended to have a lower A_{max}, but the difference to the other species was not significant. Leaves of juvenile trees grown in high light differed significantly in photosynthetic capacity from the respective sun leaves of mature trees only in a few cases: *T. cordata* had a lower J_{max}, and *A. pseudoplatanus* and *F. sylvatica* showed higher A_{max} rates in the juveniles than in the mature trees. Nevertheless, A_{max} tended to be lower in the sun leaves of mature trees than in the juveniles in all five species. It appears that the species differences in photosynthetic capacity were larger in the juvenile stage than in the sun leaves of the mature trees. *F. excelsior* and *A. pseudoplatanus* had significantly higher V_{cmax} rates than the saplings of late-successional *T. cordata* and *F. sylvatica,* and *F. excelsior* saplings showed higher J_{max} rates than *C. betulus, T. cordata* and *F. sylvatica* saplings (Fig. 4.1). No significant differences were found between the species with respect to the A_{max} rates of the juvenile trees.

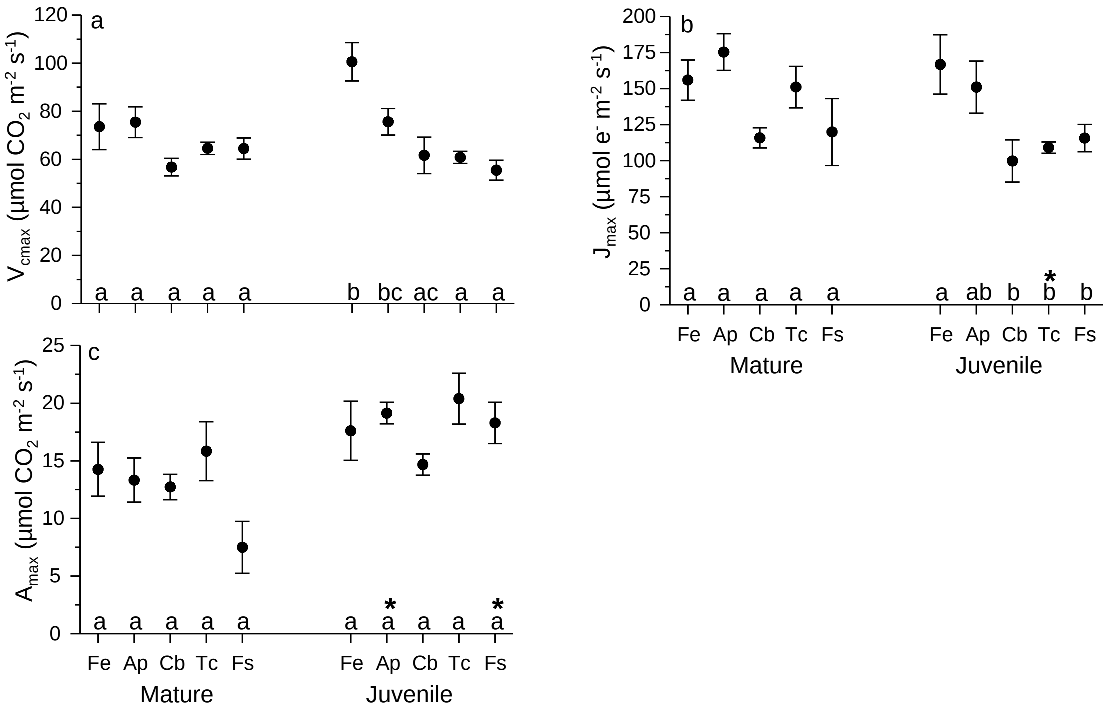

Figure 4.1: Means ± SE of V_{cmax} (a), J_{max} (b) and A_{max} (c) in sun canopy leaves of mature trees and in leaves of saplings (2-3 yr-old) of the five species of the in-depth study. Fe - *Fraxinus excelsior*, Ap - *Acer pseudoplatanus,* Cb - *Carpinus betulus*, Tc - *Tilia cordata* and Fs - *Fagus sylvatica*. n (replicate leaves investigated) = 5-7 (mature trees), 4-6 (juveniles). Different small letters in the figure indicate significantly different means among the five species in an age class; asterisks mark significant mature-juvenile differences within a species ($P < 0.05$).

Data base study: photosynthetic capacity of early-, mid- and late-successional trees

The tables A1 to A3 in the appendix list the V_{cmax}, J_{max} and A_{max} means of the studies included in the data base. The largest number of literature data exists for A_{max} and for juvenile trees. Based on this compilation and our own measurements, species means of V_{cmax}, J_{max} and A_{max} were calculated (Fig. 4.2 and Figs A1 to A2) with the species arranged from early- to late-successional. For about half of the species, more than three independent studies were available (maximum: 17 for *F. sylvatica*) and the data could be presented in box-whisker plots, while only one or two studies were available in the remaining taxa. Table A4 lists the weighted species means of V_{cmax}, J_{max} and A_{max} and the related SE by averaging over the existing studies that were weighted by the number of observations. The two groups of early- and late-successional species differed not significantly from each other in terms of A_{max} and its partial determinants V_{cmax} and J_{max}, neither in the sun or shade leaf activity of mature trees, nor in the photosynthetic capacity of juvenile trees (Table 4.2).

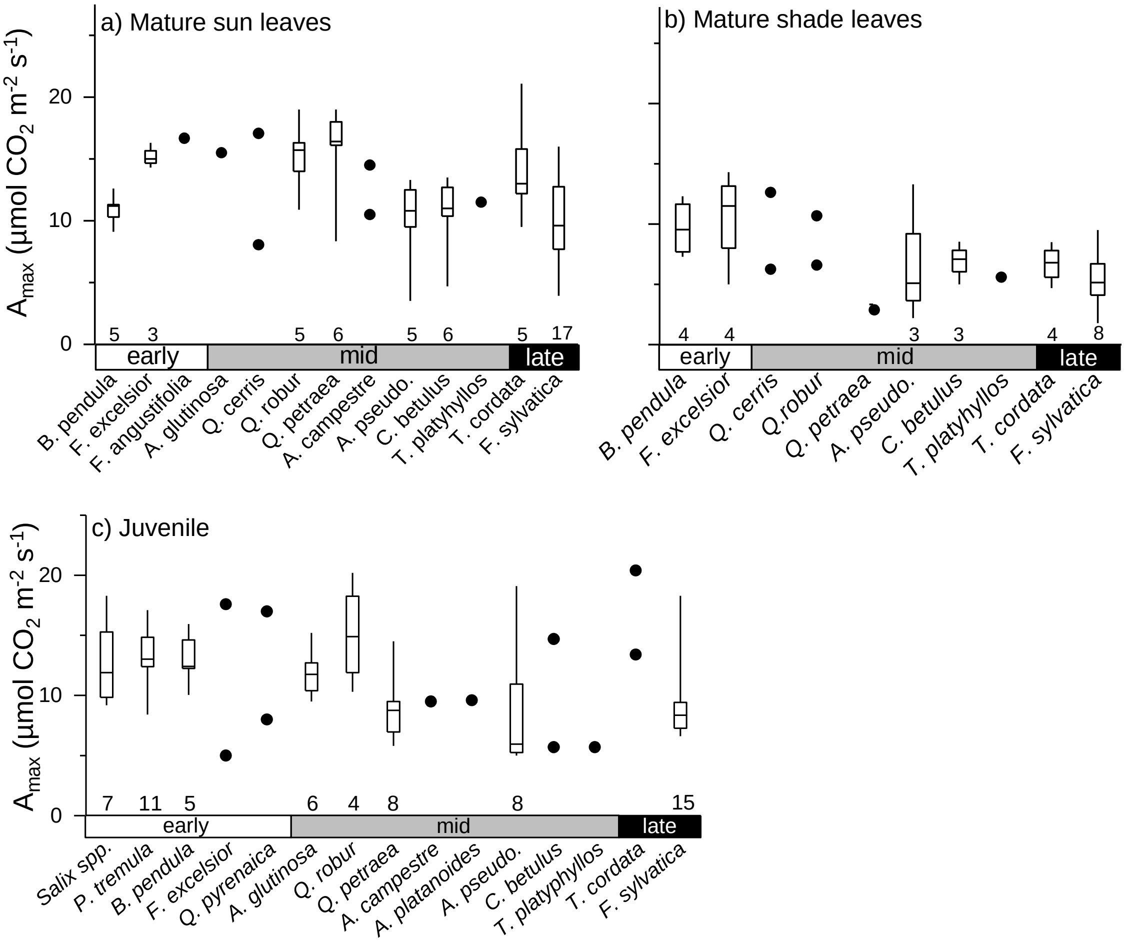

Figure 4.2: A_{max} of sun leaves (a) or shade leaves (b) of mature trees, or juvenile trees (c) grouped as early-, mid- or late-successional (data points stand for means of a given study and location; box-whisker-plots give the non-weighted average, the 25- and 75-percent quartiles and maxima and minima of the study means). The numbers in the figure bottom indicate the number of studies per species. For significant differences between the three successional groups see Table 4.2.

We obtained species means of sun leaf-A_{max} for early-, mid- and late-successional trees (three, eight and two species) of 14.1, 12.9 and 14.3 µmol CO_2 m^{-2} s^{-1}, respectively. Only in two cases, the A_{max} means differed significantly between any of the successional groups, (1) between the shade leaves of early- and mid-successional trees with smaller values in the latter (*P*=0.021) and (2) in the J_{max} means of juvenile trees (*P*=0.0495), but the difference could not be localised.

Table 4.2: Results of GLM combined with Scheffé's test as post-hoc test on differences in V_{cmax}, J_{max} or A_{max} between the groups of early-, mid- and late-successional trees analysed separately for sun and shade leaves (mature trees) and juvenile trees. Given are the *P* values (significant values in bold, marginally significant ones in italics) and the successional groups with significant contrasts.

	Leaf type	*P*	Groups with differences
V_{cmax}	Sun	0.384	
	Shade	0.411	
	Juvenile	0.467	
J_{max}	Sun	0.272	
	Shade	0.817	
	Juvenile	**0.050**	--
A_{max}	Sun	0.652	
	Shade	**0.021**	early - mid
	Juvenile	0.176	

Table 4.3: Results of GLM combined with Scheffé's test as post-hoc test on differences in V_{cmax}, J_{max} and A_{max} between sun, shade leaves (mature trees) and juvenile trees analysed separately within the groups of early-, mid- and late-successional trees. Given are *P* values (significant value in bold, marginally significant ones in italic) and the leaf types (sun or shade leaves of mature trees, juveniles) with significant contrasts.

		Sun Mean ± SE	Shade Mean ± SE	Juveniles Mean ± SE	*P*	Significant leaf type contrasts	
V_{cmax}	Early	83.4 ± 4.3	43.2 ± 5.0	67.0 ± 3.9	0.221		
	Mid	76.0 ± 3.0	28.4 ± 3.2	75.3 ± 4.9	**0.008**	sun - shade	shade - juvenile
	Late	58.3 ± 3.5	31.5 ± 3.2	53.3 ± 2.1	*0.060*		
J_{max}	Early	166.5 ± 8.0	79.9 ± 5.9	160.1 ± 9.1	**0.008**	sun - shade	shade - juvenile
	Mid	154.2 ± 10.0	86.2 ± 14.1	140.3 ± 10.5	*0.078*		
	Late	129.9 ± 15.0	64.3 ± 8.0	95.7 ± 3.5	**0.023**	sun - shade	
A_{max}	Early	14.1 ± 0.4	12.7 ± 0.8	12.3 ± 1.8	0.550		
	Mid	12.9 ± 1.6	6.4 ± 0.5	9.6 ± 0.7	**0.0004**	sun - shade	shade - juvenile
	Late	14.3 ± 1.1	6.1 ± 0.6	13.2 ± 1.1	0.165		

The A_{max} means of shade leaves in early-, mid- and late-successional trees amounted to 12.7, 6.5 and 6.1 µmol CO_2 m^{-2} s^{-1} (Table 4.3). When plotting the species means of V_{cmax}, J_{max} and A_{max} (sun and shade leaves of mature trees) against the estimated below-canopy shade intensity of adult trees, only V_{cmax} of sun leaves showed a significant negative relationship, i.e. a decrease with increasing shade production (P=0.038, R^2=0.54; Fig. 4.3c and Table 4.4); marginally significant relations existed also for J_{max} of sun leaves (P=0.080, R^2=0.42) and A_{max} of shade leaves (P=0.080, R^2=0.38).

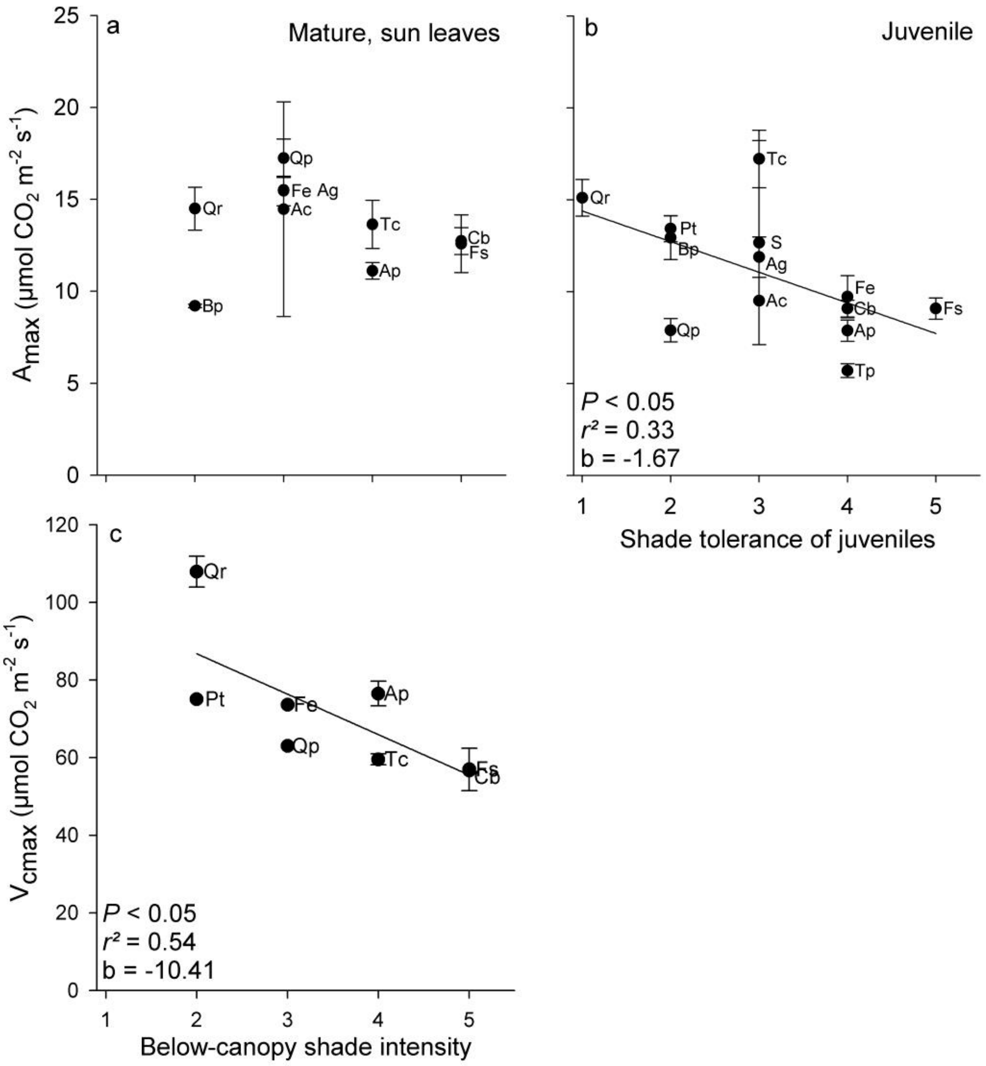

Figure 4.3: Relationship between the species means of (a) sun leaf A_{max} and the corresponding shade intensity below the canopy of the species, (b) relation between the A_{max} of juvenile trees and the light demand of the species' offspring, and (c) relation between the sun leaf V_{cmax} of mature trees and shade intensity below the canopy. The species means of photosynthetic capacity (± SE) were obtained by weighting the individual studies by the number of observations per study. The classification of the species with respect to below-canopy shade intensity and the light demand of the juveniles follows Ellenberg & Leuschner (2010), see Table A4 (1 = very low, 5 = very high). Solid regression lines indicate significant (P < 0.05) relationships, broken lines marginally significant (P < 0.1) relationships. Further results of the correlation analysis between photosynthetic capacity and light demand or shade production of the species are presented in Table 4.4. Species abbreviation: Ac *Acer campestre*, Ag *Alnus glutinosa*, Ap *Acer pseudoplatanus*, Bp *Betula pendula*, Cb *Carpinus betulus*, Fs *Fagus sylvatica*, Fe *Fraxinus excelsior*, Pt *Populus tremula*, Qp *Quercus petraea*, Qr *Quercus robur*, S *Salix* sp., Tc *Tilia cordata*, Tp *Tilia platyphyllos.*

Contrary to expectation, A_{max} of sun leaves was not related to the below-canopy shade intensity (*P*=0.277; Fig. 4.3a). We found a significant decrease in A_{max} of juvenile trees (and a marginally significant decrease in J_{max}) with a decrease in the estimated light demand of the offspring (*P*=0.041, R^2=0.33 and *P*=0.072, R^2=0.39, respectively; Fig. 4.3b and Table 4.4).

Table 4.4: Results of a linear regression analysis on the relationship between three parameters characterising photosynthesis (V_{cmax}, J_{max}, A_{max}) and the shade intensity below the canopy (for the photosynthetic capacity of sun and shade leaves of mature trees) or the light demand of the offspring (for the photosynthetic capacity of juveniles). Given are the *P* value (significant relations in bold, marginally significant ones in italics), R^2 and the slope b and intercept a of the linear regression. The species means of photosynthetic capacity were calculated by weighing the means of the individual studies by the number of observations per study. Three selected relationships are plotted in Fig. 4.3.

	Leaf type	*P*	R^2	a	b
V_{cmax}	Sun	**0.038**	0.5390	107.59	-10.41
	Shade	0.845			
	Juvenile	0.425			
J_{max}	Sun	*0.080*	0.4240	200.10	-13.84
	Shade	0.582			
	Juvenile	*0.072*	0.3895	181.69	-14.91
A_{max}	Sun	0.277			
	Shade	*0.080*	0.3745	14.12	-1.87
	Juvenile	**0.041**	0.3252	16.06	-1.67

Data base study: photosynthetic capacity of juveniles and mature trees

The photosynthetic capacity of sun leaves of mature trees tended to be higher than that of juvenile trees, but the difference was not significant, neither for V_{cmax} and J_{max} , nor for A_{max} (Table 4.3).

Across all species, the sun leaves of mature trees had on average roughly twice as high V_{cmax}, J_{max} and A_{max} rates than the corresponding shade leaves. However, the sun-shade leaf contrast was significant only in part of the data set, i.e. in the early-successional group for J_{max}, in the mid-successional group for V_{cmax} and A_{max}, and in the late-successional group for J_{max} (Table 4.3). The sun/shade leaf difference in photosynthetic capacity was not higher in the late-successional shade-tolerant species, contradicting our hypothesis three. A significantly higher photosynthetic capacity of juvenile trees as compared to the shade leaf capacity of mature trees was found for J_{max} in early-successional trees, and for V_{cmax} and A_{max} in mid-successional trees.

Long-term change in the photosynthetic capacity of F. sylvatica

Fagus sylvatica is the only species for which a large number of independent observations of photosynthetic capacity do exist since the late 1960s (30, 26 and 40 data sets for V_{cmax}, J_{max} and A_{max}). Plotting the mean A_{max}, V_{cmax} and J_{max} values of the studies against the year of measurement revealed significant increases in light-saturated net photosynthesis rate and maximum carboxylation rate during the observation period (Table 4.5 and Fig. 4.4). In the more than 40 years elapsed since the first gas exchange measurements with open systems and climatised chambers, the A_{max} of mature tree sun leaves seems to have doubled while the increase in shade leaf activity was less pronounced but significant as well (Fig. 4.4c and Table 4.5). Despite a shorter observation period (18 years), our data compilation also points to an increase in the V_{cmax} rates (significant for the whole *F. sylvatica* data set and the shade leaves, Fig. 4.4a), while no trend was detected for J_{max} (Fig. 4.4b, Table 4.5). The significant increase in A_{max} since the 1960s/70s in *F. sylvatica* was also evident when data obtained with different gas exchange systems were analysed separately (Fig. 4.5). Measurements with various open gas exchange systems manufactured by Walz GmbH (Effeltrich, Germany) since the late 1960s gave a nearly identical and significant A_{max} increase as that observed with measurements taken with other systems (slope: 0.25 for Walz systems and ‘Other systems’, Fig. 4.5). A_{max} data for *F. sylvatica* obtained with systems of Licor Inc. are available only since 1994; but they show a significant increase (*P*=0.029, slope: 0.37).

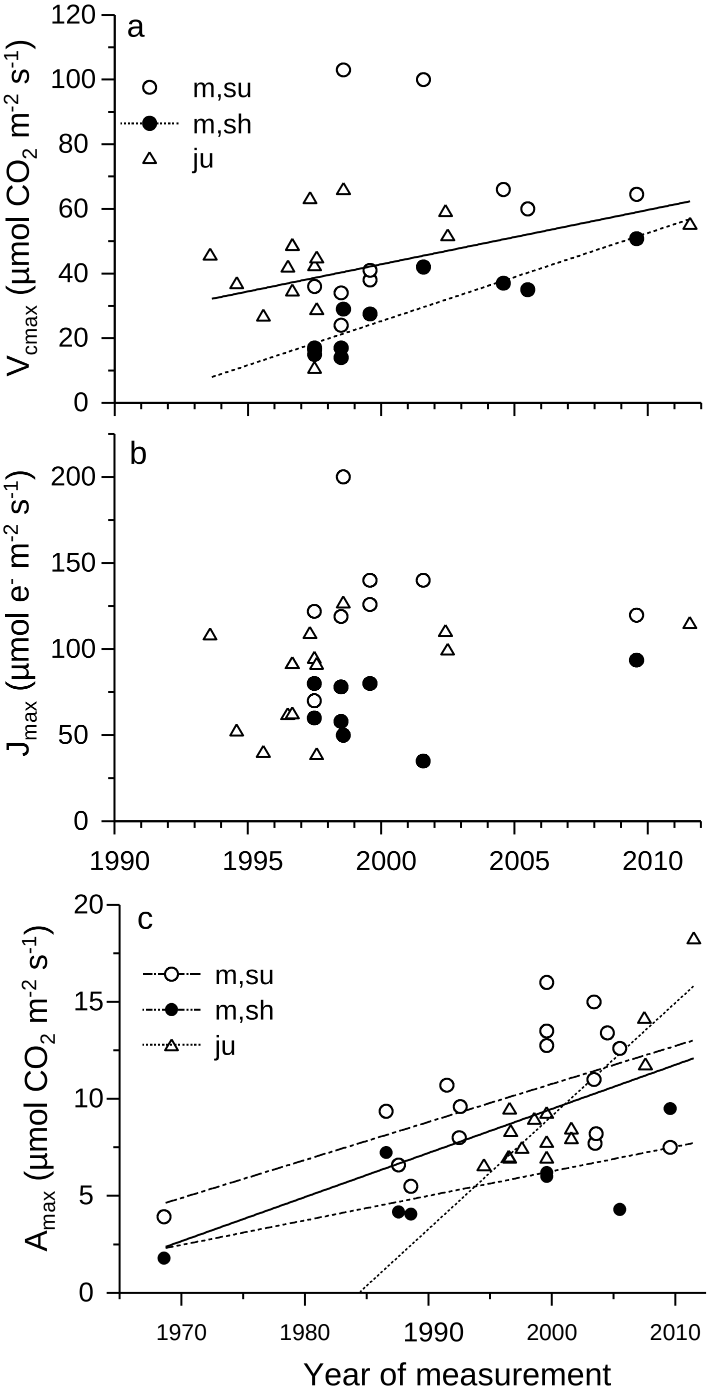

Figure 4.4: Variation over time in the means of V_{cmax} (a), J_{max} (b) and A_{max} (c) for *F. sylvatica* reported in various gas exchange studies since the late 1960s. Each data point is the mean of a study and location. Different symbols mark the sun leaves of mature trees (m,su), shade leaves of mature trees (m,sh) and juvenile trees (ju). The regression lines are plotted for significant relationships (solid line: all data; for the equation parameters see Table 4.5).

Table 4.5: Results of a linear regression analysis on the dependence of V_{cmax}, J_{max} and A_{max} of *F. sylvatica* on the year of measurement (1968 – 2011) analysed separately for sun or shade leaves (mature trees), or juvenile trees and all data pooled. The data are those depicted in Fig. 4.4. Given are *P* and R^2 values, intercept a and slope b (unit: µmol e^- m^{-2} s^{-1} yr^{-1} (J_{max}) or µmol CO_2 m^{-2} s^{-1} yr^{-1}) for the significant relationships.

		P	*R²*	a	b
V_{cmax}	All	**0.037**	0.14	27.44	1.71
	Sun	0.310			
	Shade	**0.0002**	0.88	14.42	2.71
	Juvenile	0.102			
J_{max}	All	0.135			
	Sun	0.904			
	Shade	0.131			
	Juvenile	0.113			
A_{max}	All	**0.0001**	0.36	2.11	0.23
	Sun	**0.015**	0.33	4.41	0.20
	Shade	**0.0486**	0.50	2.17	0.13
	Juvenile	**0.00005**	0.80	5.37	0.25

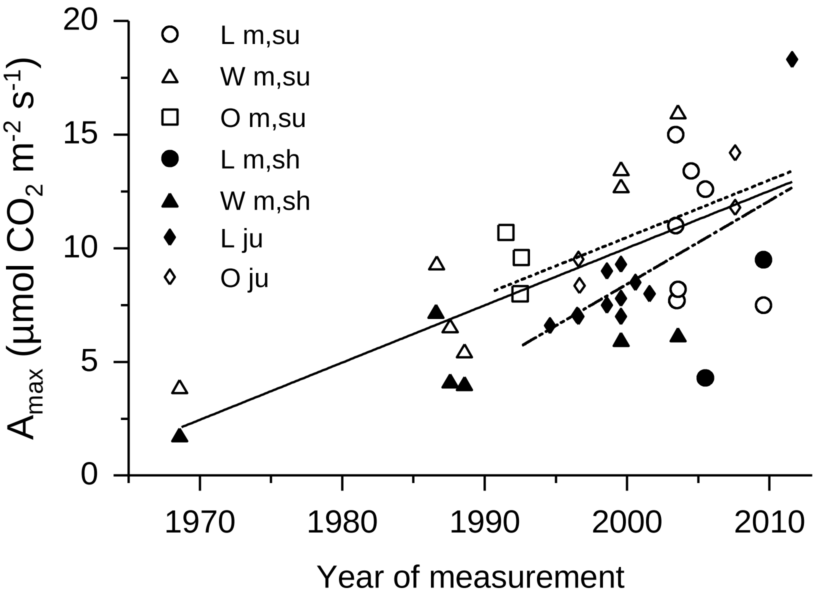

Figure 4.5: Variation over time in the A_{max} means of *F. sylvatica* as reported in different studies since the late 1960s. Different symbols stand for juvenile trees, and sun and shade leaves of mature trees, and indicate the type of gas exchange system used (three main groups distinguished: systems manufactured by Licor Inc., systems of Walz GmbH, and other systems). Data recorded with Licor systems are available only since 1994. Linear regression equations (y = a + bx; all leaf types pooled): Walz – y = 1.85 + 0.25x, *P*=0.0097, R^2=0.42; other systems – y = 8.10 + 0.25x, *P*=0.0496, R^2=0.41; Licor – y = 6.05 + 0.37x, *P*=0.029, R^2=0.25. Unit of the slope b: µmol CO_2 m^{-2} s^{-1} y^{-1}.

4.5 Discussion

Higher photosynthetic capacity in temperate early-successional trees?

In both temperate and tropical forests, shade-intolerant early-successional trees are assumed to reach on average higher A_{max} rates than shade-tolerant late-successional trees and to exhibit a larger within-species and between-species variation in photosynthetic capacity (e.g. Barnes et al. 1998, Bazzaz & Pickett 1980, Turner 2001). Supportive evidence for temperate broad-leaved trees and shrubs is provided by the A_{max} data compilations of Larcher (1969, 29 taxa), Ceulemans & Saugier (1991, 51 taxa) and Kutsch et al. (2009, 41 taxa) mostly from North American and European temperate forests. Kutsch et al. (2009) used the data base of Kattge et al. (2009) to examine A_{max} differences between early- and late-successional trees and found a significantly higher sun leaf photosynthetic capacity of mature early-successional trees as compared to late-successional species (11.4 vs. 7.5 µmol CO_2 m^{-2} s^{-1}). For seven temperate broad-leaves tree species in Japan, Koike et al. (2001) reported a large decrease in average A_{max} from early- to late-successional trees (12.5 – 14.8 vs. 3.1 µmol CO_2 m^{-2} s^{-1}). Increasing information is also available from tropical forests, where comparisons between shade-tolerant and –intolerant tree species with respect to photosynthetic capacity have been conducted, for example, by Strauss-Debenedetti & Bazzaz (1996) and Turner (2001).

These data compilations coherently reveal a negative A_{max}-shade tolerance relationship; however, the criteria for data selection often have not been rigid or were not specified at all. Most authors did not distinguish between data from mature trees, saplings and seedlings, and the precise canopy position of the leaves and the measuring conditions were often not given. Further, several authors have mixed tall canopy trees (such as *Fagus* species) and low-stature understorey trees or shrubs (such as *Cornus* species) in the shade-tolerant category (e.g. Barnes et al. 1998, Ceulemans & Saugier 1991, Kutsch et al. 2009), or have included measurements in fertilised plantation forests in the shade-intolerant group. Finally, in many sapling studies, the light regime and soil fertility have not been specified (Aasamaa & Söber 2001, Clemenz et al. 2008, Gardiner et al. 2009, Mäenpää et al. 2011). Thus, the significance of the negative shade tolerance-A_{max} relationship may be less clear than it appears from the existing analyses. We seeked to re-analyse the among-species variation in photosynthetic capacity of temperate broad-leaved trees in a more homogeneous data set after filtering the available data in a rigid way and by focussing on a defined biogeographical region for assessing the local relevance of a putative A_{max} decrease with higher shade tolerance.

The results obtained for the Central and Western European broad-leaved tree flora contrast with earlier findings in that early-, mid- and late-successional trees appear to have remarkably similar mean photosynthetic capacities. Our data do not evidence a significant decrease in the A_{max}, V_{cmax} or J_{max} rates from early- to late-successional trees, neither in upper sun crown leaves of mature trees nor in juvenile trees. A significant group difference was only detected for the shade leaves of mature trees with a lower A_{max} in mid- than early-successional trees, and for the J_{max} of juvenile trees which showed a significant difference between the three successional groups (this difference could not be assigned to a distinct group contrast). A non-significant trend for a decrease with increasing shade tolerance was observed for sun leaf V_{cmax} and J_{max}.

Our results agree with the conclusion of Körner (2005) that tree A_{max} is highly variable within groups of trees that are defined by their shade tolerance and/or successional status, but that the shade tolerance-A_{max} relationship is weak. Clearly, this outcome is partly a consequence of the limited number of species (2) included in the late-successional category; with a larger sample of late-successional species, some of the group differences, in particular those in sun leaf V_{cmax} and J_{max}, would probably have been significant. However, our analysis is complete in the sense that it includes nearly all dominant and abundant temperate broad-leaved tree species of the European sub-continent (except for *Alnus incana, Betula pubescens* and *Salix alba*) and thus covers the most widespread forest communities of Central and Western Europe's natural vegetation. In contrast to tropical forests, the tree flora of temperate Europe and North America includes only very few characteristic late-successional broad-leaved species with tall stature (in Europe only *Fagus sylvatica* and *Tilia cordata*, in North America about five to eight species). Since *F. sylvatica* is the dominant tree species of the natural forest vegetation of Central Europe (Ellenberg & Leuschner 2010), the relatively high photosynthetic capacity of beech sun leaves found by averaging over 17 studies (A_{max}: 14.3 µmol CO_2 m^{-2} s^{-1}) can only be interpreted in the sense that early- and late-successional tree species are in fact not very different in their sun canopy photosynthetic capacities. This matches with a comparison of foliar N concentrations between Central European early- and late-successional trees based on the data compiled by van den Burg (1985) which does not show a significantly higher N content per leaf mass in early- than in late-successional species (*P*=0.47, Wilcoxon test). Thus, if the first group of species indeed would develop a higher mean photosynthetic capacity, it should be linked to a higher sun leaf LMA as compared to late-successional trees which seems not to be the case in our five-species sample (Legner et al., unpubl. results). Rather, we speculate that the astonishing similarity between early- and late-successional species in photosynthetic capacity may partly be a result of continued high N deposition that has resulted in elevated leaf-area based N contents in *F. sylvatica* in various regions of Central and Western Europe with the likely consequence of higher recent A_{max} rates and thus a further reduction in group differences in photosynthetic capacity. Unfortunately, information on possible A_{max} increases in early-successional other tree species in recent time is not available.

Ontogenetic variation in photosynthetic capacity

Our gas exchange measurements in the five intensively studied early-, mid- or late-successional tree species showed in only a few cases significant differences in the A_{max}, V_{cmax} and J_{max} rates between the exposed sun leaves of mature trees and the 2-3 yr-old juveniles grown under high light. The maximum assimilation rate of sun leaves of mature trees and juveniles differed typically by 15-43 % with significantly (twofold) higher A_{max} rates of the juveniles found in two species. No significant juvenile-mature difference was found for V_{cmax} and J_{max} (except for a lower juvenile J_{max} mean in *T. cordata*). Thus, the evidence for an ontogenetic shift in sun leaf photosynthetic capacity was only weak in our five-species sample and a more general pattern did not evolve. This conclusion is supported by our data base analysis where no significant tree age effect on A_{max}, V_{cmax} or J_{max} was detected and both higher and lower A_{max}, V_{cmax} and J_{max} means in adult trees as compared to juveniles were found in a sample of 15 broad-leaved tree species. In contrast, in a meta-analysis covering seven temperate broad-leaved tree species from North America, Thomas & Winner (2002) found significantly higher A_{max} rates for adult trees than for saplings in high light, which they mainly attributed to a higher LMA in the sun crown of adult trees than in saplings. However, decreases of area-related A_{max} from the juvenile to the adult stage have also been reported, most often for conifers, but also for other woody plants (Bond 2000, Thomas & Winner 2002). Whether A_{max} is increasing or decreasing with growing tree age, may depend not only on tree functional type and species, but probably also on nitrogen availability, drought regimes and further environmental factors. Direct comparisons between temperate broad-leaved tree seedlings in the dim light of the forest understory and the adult trees in the same stand have found sapling photosynthetic capacities to be equal to (*A. pseudoplatanus*, *T. platyphyllos*, *C. betulus*), or lower than (*F. excelsior*), the A_{max} of shade leaves of mature trees (Hölscher 2004, Kazda et al. 2004). The statement of Larcher (1969) is still valid that photosynthetic data from sapling studies should not be used to model the photosynthesis of mature trees.

Increased photosynthetic capacity in F. sylvatica since the late 1960s

Not many tree species are similarly well studied as *Fagus sylvatica*, the most widespread species of the temperate forests of Central Europe. With more than 40 years of gas exchange measurements conducted in mature trees and juveniles of this species, European beech offers the unique possibility to search for long-term trends in photosynthetic capacity in a temperate tree species. With 17 data sets for sun leaf-A_{max} of mature trees taken from towers or cranes in seven different beech forests in the period 1968-2009, this data compilation is probably the most comprehensive and most extended record of canopy photosynthetic capacity of a single tree species worldwide. The large increase in A_{max} of *F. sylvatica* sun leaves found for a 40-yr period in this data set is paralleled by a weaker, but also significant, increase in the photosynthetic capacity of shade leaves and an even steeper increase in the A_{max} of juvenile beech trees. It has to be taken into account that the equipment used for measuring photosynthetic capacity has changed in the last decades and every measuring systems and approach may introduce specific errors in the A_{max} estimate (Long & Bernacchi 2003). For example, Ceulemans & Saugier (1991) stress that early measurements with gas exchange systems (before 1975) frequently may have underestimated true A_{max} because of low cuvette ventilation and thus a higher than natural leaf boundary layer. However, even if the low A_{max} values (<5 µmol CO_2 m^{-2} s^{-1}) of the first data point in 1968 are exclude from our study, the regression line is indicating nearly a doubling of sun leaf A_{max} between the 1980s and 2009. This increase can neither be attributed to possible measuring errors or a sequence of alternative gas exchange systems used over the 40 years, nor to a tree age effect because the A_{max} increase was recorded independently with different measurement systems and age had no influence on A_{max} in a multiple linear regression analysis (results not shown). Most likely causes are increased foliar N concentrations due to continued high atmospheric N deposition, and a possible effect of the rising atmospheric CO_2 concentration since the 1960s. Model suggest that simulation of A_{max} by the slightly higher summer temperatures since the 1960s is not very likely in lowland beech forests (Schulze 1970, Terborg 1998).

Re-sampling studies and over-regional mapping of foliar N contents both show that N deposition has led to increased foliar N concentrations in *F. sylvatica* in various regions of Central Europe in the past decades. For example, Duquesnay et al. (2000) found a 12 % increase in the foliar N concentration of *F. sylvatica* trees in north-eastern France in the 26 years between 1969-71 and 1996-97; significant N concentration increases were also reported from Swiss beech forests in the period 1984–1995 (Flückiger & Braun 1998). Mapping studies showed particularly high leaf N concentrations (>3 % N of leaf dry mass) in certain beech forest regions with high N deposition (e.g. Heinsdorf 1997). In the data base of our study, foliar N data were available only for a minority of the studies included which allows only indirect conclusions on the importance of N depostition for the A_{max} increase. However, the close dependence of A_{max} on foliar N (e.g. Reich et al. 1994) makes it likely that assumed leaf N concentration increases in the range of 10-30 % must have resulted in a significant increase in photosynthetic capacity of *F. sylvatica* since the 1960s. Further support for an important role of N fertilisation is provided by the finding that V_{cmax} increased significantly in *F. sylvatica* sun leaves in the past three decades, but J_{max} did not. The amount of N allocated in sun leaves to Calvin cycle enzymes is usually higher than the partitioning to compounds associated with light harvesting and electron transport (Evans & Seemann 1984); a likely consequence is that a higher N supply should increase V_{cmax} before it will manifest in higher J_{max} rates. The increase of atmospheric CO_2 concentration by roughly 60 µmol mol^{-1} (i.e. by 20 %) since the late 1960s is the second factor that may have contributed to the observed A_{max} increase. However, it is unlikely that the CO_2 effect is equally important as the N effect, because long-term adaptation to elevated [CO_2] in trees seems to involve a reduction in stomatal conductivity and a down-regulation of carboxylation capacity (Ainsworth & Rogers 2007).

Conclusions

Both the in-depth study of five common broad-leaved tree species and the literature search for data of Central and Western European tree species showed a large among-species variation photosynthetic capacity while only weak evidence for a dependence of sun leaf photosynthetic capacity on the species' shade tolerance was found contradicting our first hypothesis. This implies that the parameterisation of terrestrial biosphere models for simulating canopy photosynthesis should not be done with group means of early-, mid- or late-successional species, but rather rely on species means if available. This emphasizes the need for extending existing tree functional trait data bases. The assumption of a decrease in sun leaf photosynthetic capacity with increasing shade tolerance of the species may be misleading, in particular when referring to the regional level where the woody floras of many temperate regions contain only a small number of late-successional species and N deposition may have reduced differences in photosynthetic capacity between functional groups. The relatively small difference between early- and late-successional trees in sun leaf photosynthetic capacity implies that a higher carbon gain cannot be the main cause of the assumed faster height growth of light-demanding temperate broad-leaved species (e.g. Ceulemans & Saugier 1991). Rather, differences in C allocation patterns, in total leaf area, and in the proportion of shade leaves in total leaf area must be responsible for differences in growth rate among early- and late-successional trees. No increase in the mature/juvenile ratio of photosynthetic capacity was found contradicting our second hypothesis. Rather, the species showed idiosyncratic pattern which demands great caution when attempting to extrapolate juvenile data to mature trees, or *vice versa*.

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4.7 Appendix

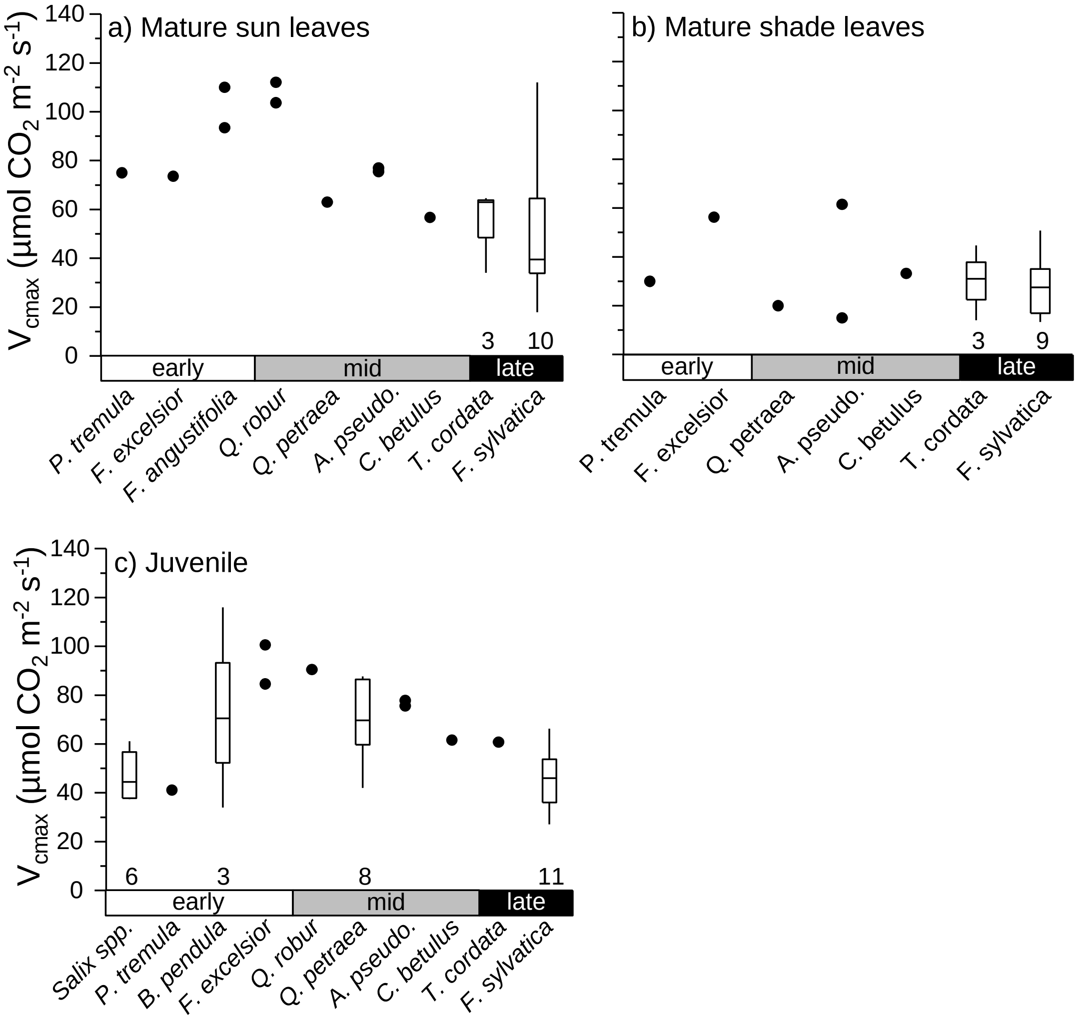

Figure A1: V_{cmax} of sun leaves (a) or shade leaves (b) of mature trees, or juvenile trees (c) grouped as early-, mid- or late-successional (data points stand for means of a given study and location; box-whisker-plots give the non-weighted average, the 25- and 75-percent quartiles and maxima and minima of the study means). The numbers in the figure bottom indicate the number of studies per species. For significant differences between the three successional groups see Table 4.3.

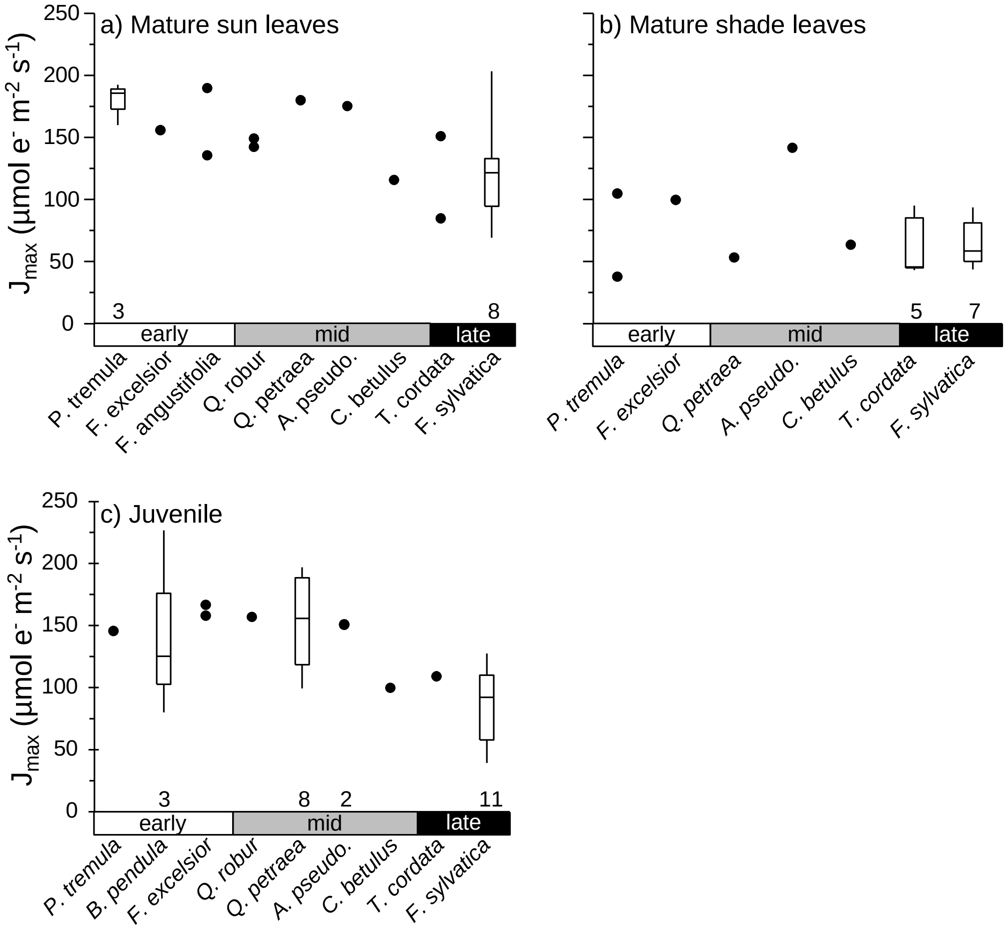

Figure A2: J_{max} of sun leaves (a) or shade leaves (b) of mature trees, or juvenile trees (c) grouped as early-, mid- or late-successional. For explanations see Fig. A1.

Table A1. V_{cmax} values (study means ± SE) reported from Central and Western European broad-leaved tree species. Abbreviations: m,su – sun leaves of mature trees; m,sh - shade leaves of mature trees; ju,su - leaves of juvenile trees grown at >1000 µmol m^{-2} s^{-1} PPFD; ju,sh – leaves of juvenile trees grown at PPFD <1000 µmol m^{-2} s^{-1}; ju – leaves of juvenile trees grown at unknown irradiance. The 'c' directly behind the V_{cmax} values indicates studies conducted with cut branches or twigs. n_M – number of measurements per study used for averaging. Gas exchange systems used: AD - CO_2 analyser of ADC Ltd., UK; ACD - ADC LCA2 infra red gas analyser; B3 - Binos 3 differential IR gas analyser; C - Ciras-PP Systems; C1 - Ciras-1 PP-Systems; C2 - Ciras-2 PP Systems; L62 - Licor Li6200; L625 - Licor Li6251 gas analyser; L626 - Licor Li6262 gas analyser; L64 - Licor Li6400; LA - LA2 infrared gas analyser, ADC, UK; LC - LC pro Analytical Development, UK; LC3 - LCA-3 Analytical Development Corporation, UK; SM - self-constructed measuring system; W - Walz; W130 - Walz CQP 130 and GMA3; W400 - Walz CMS-400.

Species	**V_{cmax}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measure-ment**	**Location**	**System used**	**Reference**
Acer pseudo-platanus	75.5 ± 6.4	m,su	6	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	77 ± 1.6 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	61.5 ± 6.3	m,sh	7	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	15 ± 1.2 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	75.6 ± 5.5	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
	77.8 ± 2.6	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Betula pendula	~ 116 ± 4	ju,su	6-20	13	Aug 1997	Glencorse Mains, UK	C1	Meir et al. (2002)
	~ 34 ± 3	ju,sh	2-8	13	"	"	"	"
	70.5 ± 3.0	ju,sh	5	1	Aug 1998	near Nancy, France	L64	Dreyer et al. (2001)

Species	V_{cmax} µmol CO_2 m^{-2} s^{-1}	Leaf type	n_M	Age of trees years	Date of measurement	Location	System used	Reference
Carpinus betulus	56.7 ± 3.7	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	33.2 ± 5.6	m,sh	9	80-120	"	"	"	"
	61.6 ± 7.6	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
Fagus sylvatica	64.5 ± 4.4	m,su	6	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 112 ± 9	m,su	6-20	70	Aug 1998	Dalkeith, UK	C1	Meir et al. (2002)
	66 ± 3.1	m,su	5	60	Aug 2004	Kranzberger Forst, Freising, Gemany	L64	Warren et al. (2007)
	60 ± 0.6 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	~ 17.9 ± 5.6 c	m,su	6-8	150	July 1997	Solling, Germany	W400	Gries (2004)
	~ 24.1 ± 4.1 c	m,su	6-8	150	July 1998	"	"	"
	~ 36.9 ± 6.2 c	m,su	6-8	110-125	July 1997	Göttinger Wald, Germany	W400	Gries (2004)
	~ 33.8 ± 10.3 c	m,su	6-8	110-125	July 1998	Göttinger Wald, Germany	W400	Gries (2004)
	34 - 42	m,su		100	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	36 - 46	m,su		100	"	"	"	"
	37 ± 7.6	m,sh	5	60	Aug 2004	Kranzberger Forst, Freising, Germany	L64	Warren et al. (2007)
	50.8 ± 4.8	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 28 ± 3	m,sh	2-8	70	Aug 1998	Dalkeith, UK	C1	Meir et al. (2002)
	35 ± 0.3 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)

Species	**V_{cmax}**	**Leaf type**	**n_M**	**Age of trees**	**Date of measurement**	**Location**	**System used**	**Reference**
	μmol CO_2 m^{-2} s^{-1}			years				
F. sylvatica	~ 16 ± 1 c	m,sh	6-8	150	July 1997	Solling, Germany	W400	Gries (2004)
(continued)	~ 18.5 ± 1.5 c	m,sh	6-8	150	July 1998	"	"	"
	~ 16.9 ± 0.4 c	m,sh	6-8	110-125	July 1997	Göttinger Wald, Germany	W400	Gries (2004)
	~ 13.3 ± 1.5 c	m,sh	6-8	110 -125	July 1998	"	"	"
	23 - 32	m,sh		100	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	55.5 ± 4.1	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
	46 ± 5	ju,su	6	2		Orsay, France	SM	Epron et al. (1995)
	59.5	ju,su	35	2	June 2002	Mont Ventoux, France	L64	Parelle et al. (2006)
	52.0	ju,su	36	2	July 2002	"	L64	"
	37.2 ± 3.6	ju,su	13	1	Aug 1994	Berlin, Germany	W400	Medlyn et al. (1999)
	27.1 ± 1.9	ju,su	24	1	Aug 1995	"	"	"
	42.3 ± 2.3	ju,su	9	1	July 1996	"	"	"
	29.2 ± 2.9	ju,su	13	1	Aug 1997	"	"	"
	66.3 ± 1.0	ju,sh	5	3	Aug 1998	near Nancy, France	L64	Dreyer et al. (2001)
	49.0 ± 8.5	ju,sh	3	1	Sep 1996	eastern France	L64	Liozon et al. (2000)
	34.9 ± 4.3	ju,sh	6	1	"	"	"	"
Fraxinus angustifolia	110 ± ~ 2	m,su	6-9	20	2002, beginn of summer	Po Valley, Italy	C1	Grassi & Magnani (2005), Grassi et al. (2005)
	93.5 ± ~ 3	m,su	6-9	20	2002, end of summer	"	"	"

Species	**V_{cmax}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measure-ment**	**Location**	**System used**	**Reference**
Fraxinus excelsior	73.6 ± 9.5	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	56.3 ± 5.5	m,sh	8	80-120	"	"	"	"
	100.6 ± 8.0	ju,su	4	2-3	summer 2011	Göttingen, Germany	L64	This study
	84.6 ± 1.92	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Populus tremula	~ 75 ± 1 c	m,su	2	27	Aug 1994	Ülenurme, Estonia	SM	Niinemets et al. (1998)
	~ 30 ± 4.5 c	m,sh	4	55	"	Tartu, Estonia	"	"
	41.1 ± 1.3	ju, su	30	1	June - Aug 2009	Solling, Germany	L64	Müller (2011)
Quercus petraea	~ 63 ± 1	m,su	6-20	65	Aug 1996	near Alice Holt, UK	C1	Meir et al. (2002)
	~ 20 ± 1	m,sh	2-8	65	"	"	"	"
	42 ± 3.61	ju,su	2	2	July 1996	Headly, Hampshire, UK	C	Medlyn et al (1999)
	61.4 ± 4.0	ju,su	4	1	May 1997	"	"	"
	75.3 ± 4.0	ju,su	4	1	June 1997	"	"	"
	64 ± 3.1	ju,su	4	1	July 1997	"	"	"
	86.6 ± 9.0	ju,su	4	1	Aug 1997	"	"	"
Q. petraea	57.9 ± 3.9	ju,su	4-5	1	May 2005	Madrid, Spain	LC	Rodriguez-Calcer-rada et al. (2008)
	86.3 ± 10.6	ju,su	4-5	1	"	"	"	"
	87.7 ± 1.4	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)

Species	V_{cmax} µmol CO_2 m^{-2} s^{-1}	Leaf type	n_M	Age of trees years	Date of measurement	Location	System used	Reference
Quercus robur	112.1 ± ~ 3	m,su	6-9	20	2002, beginn of summer	Po Valley, Italy	C1	Grassi & Magnani (2005), Grassi et al. (2005)
	103.7 ± ~ 5	m,su	6-9	20	2002, end of summer	"	"	"
	90.5 ± 2.8	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Salix dasyclados	56.7 ± 4.6	ju,su	3	3	Sep 2000	Saare, Estonia	L64	Merilo et al (2006)
	37.4 ± 10.8	ju,sh	3	3	"	"	"	"
Salix viminalis	49.0 ± 1.9	ju,su	3	3	Sep 2000	Saare, Estonia	L64	Merilo et al (2006)
	61.1 ± 3.9	ju,su	3	3	„	„	„	„
	40.0 ± 10.2	ju,sh	3	3	"	"	"	"
	37.8 ± 5.6	ju,sh	3	3	"	"	"	"
Tilia cordata	64.6 ± 2.6	m,su	7	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~34 ± 2 c	m,su	3	55	Aug 1994	Tartu, Estonia	SM	Niinemets et al. (1998)
	63 ± 0.6 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	44.7 ± 7.6	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 14 c	m,sh	1	55	Aug 1994	Tartu, Estonia	SM	Niinemets et al. (1998)
	31 ± 2.4 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	60.8 ± 2.5	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study

Table A2: J_{max} values (study means ± SE) reported from Central and Western European broad-leaved tree species. For abbreviations see Table A1.

Species	**J_{max}** µmol e^{-} m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Acer pseudo-platanus	175.3 ± 12.7	m,su	6	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	141.7 ± 18.9	m,sh	7	"	"	"	"	"
	151.0 ± 18.1	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
	150.6 ± 3. 2	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Betula pendula	~ 226.7 ± 13.3	ju,su	6-20	13	Aug 1997	Glencorse Mains, UK	C1	Meir et al. (2002)
	~ 80 ± 10	ju,sh	2-8	13	"	"	"	"
	125.3 ± 2.9	ju,sh	5	1	Aug 1998	near Nancy, France	L64	Dreyer et al. (2001)
Carpinus betulus	115.8 ± 7.0	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	63.6 ± 9.3	m,sh	9	"	"	"	"	"
	99.8 ± 14.7	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
Fagus sylvatica	112-140	m,su		100	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	120-160	m,su		100	"	"	"	"
	~ 123.2 ± 12.6 c	m,su	6-8	110-125	July 1997	Göttinger Wald, Germany	W400	Gries (2004)
	~ 116.8 ± 15.8 c	m,su	6-8	110-125	July 1998	"	"	"
	~ 69.2 ± 24.2 c	m,su	6-8	150	July 1997	Solling, Germany	W400	"
	~ 72.3 ± 10.8 c	m,su	6-8	150	July 1998	"	"	"

Species	J_{max} µmol e^{-} m^{-2} s^{-1}	Leaf type	n_M	Age of trees years	Date of measure-ment	Location	System used	Reference
F. sylvatica	119.8 ± 23.2	m,su	6	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
(continued)	~ 203.3 ± 23.3	m,su	6-20	70	Aug 1998	Dalkeith, UK	C1	Meir et al. (2002)
	76 - 84	m,sh		100	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	~ 82.1 ± 1.6 c	m,sh	6-8	110-125	July 1997	Göttinger Wald, Germany	W400	Gries (2004)
	~ 53.3 ± 9.5 c	m,sh	6-8	110-125	July 1998	"	"	"
	~ 58.5 ± 6.2 c	m,sh	6-8	150	July 1997	Solling, Germany	W400	"
	~ 43.7 ± 4.6 c	m,sh	6-8	150	July 1998	"	"	"
	93.6 ± 12.9	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 46.7	m,sh	6-20	70	Aug 1998	Dalkeith, UK	C1	Meir et al. (2002)
	115.6 ± 9.4	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study
	53.1 ± 5.5	ju,su	13	1	Aug 1994	Berlin, Germany	W400	Medlyn et al (1999)
	40.7 ± 3.4	ju,su	24	1	Aug 1995	"	"	"
	62.5 ± 4	ju,su	9	1	July 1996	"	"	"
	39.3 ± 4.7	ju,su	13	1	Aug 1997	"	"	"
	127.5 ± 3.0	ju,sh	5	3	Aug 1998	near Nancy, France	L64	Dreyer et al. (2001)
	110.9	ju,su	35	2	June 2002	Mont Ventoux, France	L64	Parelle et al. (2006)
	100.0	ju,su	36	2	July 2002	"	"	"
	92.1 ± 18.5	ju,sh	3	1	Sept 1996	eastern France	L64	Liozon et al. (2000)
	63.0 ± 5.0	ju,sh	6	1	"	"	"	"
	109 ± 12	ju,su	6	2		Orsay, France	SM	Epron et al. (1995)

Species	**J_{max}** µmol e^- m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Fraxinus angustifolia	~ 189.8 ± 6.8	m,su	3	20	2002, beginn of summer	Po Valley, Italy	C1	Grassi & Magnani (2005), Grassi et al. (2005)
	~ 135.6 ± 3.4	m,su	3	20	2002, end of summer	"	"	"
Fraxinus excelsior	155.9 ± 14.0	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	99.7 ± 7.7	m,sh	8	80-120	"	"	"	"
	166.7 ± 20.6	ju,su	4	2-3	summer 2011	Göttingen, Germany	L64	This study
	158.0 ± 5.2	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Populus tremula	~ 185.7 ± 4.8 c	m,su	2	adult	100 days after bud-burst, 1995-97	Järvselja, Estonia	SM, L626	Niinemets et al. (2004)
	~ 160 c	m,su	1	adult	June - Aug 1995	Järvselja, Estonia	SM, L626	Niinemets et al. (1999)
	~ 192.4 c	m,su	1	27	Aug 1994	Ülenurme, Estonia	SM	Niinemets et al. (1998)
	~ 104.8 ± 2.4 c	m,sh	2	adult	100 days after bud-burst, 1995-97	Järvselja, Estonia	SM, L626	Niinemets et al. (2004)
	~ 37.8 ± 5.0 c	m,sh	4	55	Aug 1994	Tartu, Estonia	SM	Niinemets et al. (1998)
	145.6 ± 5.0	ju, su	30	1	June - Aug 2009	Solling, Germany	L64	Müller (2011)

Species	**J_{max}** µmol e$^-$ m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Quercus petraea	~ 180 ± 6.7	m,su	6-20	65	Aug 1996	near Alice Holt, UK	C1	Meir et al. (2002)
	~ 53.3	m,sh	2-8	65	"	"	"	"
	131 ± 3.8	ju,su	2	2	July 1996	Headly, Hampshire, UK	C	Medlyn et al (1999)
	99.3 ± 3.3	ju,su	4	1	May1997	"	"	"
	181 ± 15.5	ju,su	4	1	June 1997	"	"	"
	196 ± 17.6	ju,su	4	1	July 1998	"	"	"
	197 ± 15.1	ju,su	4	1	Aug 1998	"	"	"
	158 ± 11	ju,su	4-5	1	May 2005	Madrid, Spain	LC	Rodriguez-Calcerrada et al. (2008)
	106 ± 5	ju,sh	4-5	1	„	„	„	“
	153.7 ± 3.4	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Quercus robur	142.4 ± 13.6	m,su	3	20	2002, beginn of summer	Po Valley, Italy	C1	Grassi & Magnani (2005), Grassi et al. (2005)
	149.2 ± 13.6	m,su	3	20	2002, end of summer	"	"	"
	156.9 ± 7.6	ju,sh	5	1	July 1999	near Nancy, France	L64	Dreyer et al. (2001)
Tilia cordata	151.0 ± 14.4	m,su	7	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 84.8 ± 3.7 c	m,su	3	55	Aug 1994	Tartu, Estonia	SM	Niinemets et al. (1998)

Species	**J_{max}** µmol e$^-$ m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
T. cordata (continued)	~ 43.0 ± 3.4 c	m,sh	3	adult	100 days after budburst, 1995-97	Järvselja, Estonia	SM, L626	Niinemets et al. (2004)
	~ 95.1 c	m,sh	1	adult	"	"	"	"
	~ 45.6 ± 5 c	m,sh	4	55	Aug 1994	Tartu, Estonia	SM	Niinemets et al. (1998)
	85.2 ± 14.9	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 45 c	m,sh	1	adult	June - Aug 1995	Järvselja, Estonia	SM, L626	Niinemets et al. 1995
	109.1 ± 3.9	ju,su	5	2-3	summer 2011	Göttingen, Germany	L64	This study

Table A3: A_{max} values (study means ± SE) reported from Central and Western European broad-leaved tree species. For abbreviations see Table A1.

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Acer campestre	~ 14.5 ± 5.9	m,su	96	100	June 2003	Canopy crane site, Basel, Switzerland	L64	Leuzinger et al. (2005)
	~ 10.5	m,su	1	100	June 2003	"	L64	Zotz et al. (2005)
	8 - 11	ju,su		10-15	summer 1979/1980	Stadtsteinach, Bayreuth, Germany	SM, W	Küppers (1984)
Acer platanoides	~ 9.6 ± 0.4	ju	3-7	8-10	July 97	Tartu, Estonia	SM; L626	Aasamaa & Söber (2001)
Acer pseudo-platanus	12.5 ± 0.4	m,su	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	13.3 ± 1.9	m,su	6	80-120	summer 2008, 2009	Hainich NP, Germany	L64	This study
	~ 10.8 ± 0.3	m,su	25	50-100	1999, day 200	Wytham Woods, Oxfordshire, UK	ADC	Morecroft et al. (2008)
	3.5 ± 0.3	m,su		50-100	May - Nov 1996	"	ADC	Morecroft & Roberts (1999)
	9.5 ± 0.1 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	5.1 ± 0.3	m,sh	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	13.3 ± 1.3	m,sh	7	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
A. pseudo-platanus	2.2 ± 0.1 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
(continued)	19.1 ± 0.9	ju,su	6	2-3	summer 2011	Göttingen, Germany	L64	This study
	6.4 ± 0.3	ju,sh	10	saplings	July to Aug 2001	Hainich NP, Germany	L64	Hölscher 2003
	~ 15.5 ± 0.4	ju,sh	12	4	1996	western Austria, near German border	L64	Kazda et al. (2004)
	~ 6 ± 0.5	ju,sh	12	5	1997	"	"	"
	~ 5.5 ± 0.5	ju,sh	12	6	1998	"	"	"
	~ 5 ± 0.7	ju,sh	12	7	1999	"	"	"
	~ 5 ± 0.7	ju,sh	12	8	2000	"	"	"
	~ 5.9 ± 0.7	ju,sh	12	9	2001	"	"	"
Alnus glutinosa	15.5	m,su		adult		Bornhöveder Wald, Plön, Germany	W	Dilly et al. (2008)
	~ 12.5 ± 1.7	ju,su	6	3	June 2004	Freising, Germany	L64	Clemenz et al (2008)
	~ 9.5 ± 0.6	ju,su	6	3	"	"	"	"
	~ 12.7 ± 1.5	ju,su	6	3	July 2004	"	"	"
	~ 15.2 ± 1.5	ju,su	6	3	"	"	"	"
	~ 11.0 ± 0.7	ju,su	6	3	July 2005	"	"	"
	~ 10.4 ± 0.6	ju,su	6	3	"	"	"	"
Betula	9.1 ± 0.1	m,su	90	40	summer 1996	Kornik, Poland	LC3	Oleksyn et al. (2000)
pendula	11.2	m,su		30	May 1990	Lüneburger Heide, Germany	W	Greve (1991)

Species	**A_{max}**	**Leaf type**	**n_M**	**Age of trees**	**Date of measurement**	**Location**	**System used**	**Reference**
	μmol CO$_2$ m^{-2} s^{-1}			years				
B. pendula (continued)	12.6	m,su		30	June 1990	"	"	"
	11.3	m,su		30	Aug 1990	"	"	"
	10.3	m,su		30	Sep 1990	"	"	"
	12.3	m,sh		30	May 1990	Lüneburger Heide, Germany	W	Greve (1991)
	7.3	m,sh		30	June 1990	"	"	"
	11	m,sh		30	Aug 1990	"	"	"
	8.1	m,sh		30	Sep 1990	"	"	"
	12.2 ± 2.1	ju,su	5	1	Aug 1999	Goettingen, Germany	L64	Aspelmeier (2001)
	10.1 ± 1.2	ju,su	5	1	Aug 1999	"	"	"
	12.4 ± 1.4	ju,su	5	1	Aug 1999	"	"	"
	14.6 ± 0.7	ju,su	5	1	Aug 1999	"	"	"
	15.9 ± 0.4	ju	4	saplings	Aug 2007	Kuopio, Finland	L64	Mäenpää et al. (2011)
Carpinus betulus	10.5 ± 0.5	m,su	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	12.7 ± 1.1	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 4.7 ± 1.6	m,su	5	100	summer 2003	Canopy Crane site, Basel, Switzerland	L64	Hoch & Keel (2006)
	~ 13.5 ± 0.7	m,su	96	100	June 2003	Canopy crane site, Basel, Switzerland	L64	Leuzinger et al. (2005)
	~ 11.5 ± 1.2	m,su	3-4	100	June 2003	"	L64	Zotz et al. (2005)
	10.4	m,su	3	80	June - Aug 1987	Bab, Czechoslovakia	L62	Marek et al. (1989)
	5.0 ± 0.4	m,sh	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	7.1 ± 1.7	m,sh	9	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measure-ment**	**Location**	**System used**	**Reference**
C. betulus	8.5	m,sh	3	80	June - Aug 1987	Bab, Czechoslovakia	L62	Marek et al. (1989)
(continued)	14.7 ± 0.9	ju,su	6	2-3	summer 2011	Göttingen, Germany	L64	This study
	5.7 ± 0.2	ju,sh	10	saplings	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
Fagus sylvatica	3.9	m,su		115	1968	Solling, Germany	W	Schulze et al. (1977)
	9.4	m,su	4-10	135-140	summer 1986	Solling, Germany	W	Schulte (1992)
	6.6	m,su	4-10	135-140	summer 1987	"	"	"
	5.5	m,su	4-10	135-140	summer 1988	"	"	"
	12 - 15	m,su		adult	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	9 - 16.5	m,su		adult	"	"	"	"
	12.6 ± 0.1 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	7.5 ± 2.3	m,su	6	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	7.7 ± 0.6	m,su	3-5	60	July 2003	Kranzberger Forst, Freising, Germany	L64	Löw et al. (2006), Matyssek et al. (2006)
	~ 13.4 ± 0.8	m,su	3-5	60	July 2004	"	"	"
	16	m,su		adult		Bornhöveder Wald, Plön, Germany	W	Dilly et al. (2008)
	~ 8.2 ± 1.9	m,su	5	100	summer 2003	Canopy Crane site, Basel, Switzerland	L64	Hoch & Keel (2006)
	~ 19 ± 1.1	m,su	96	100	June 2003	“	L64	Leuzinger et al. (2005)

Species	A_{max} µmol CO_2 m^{-2} s^{-1}	Leaf type	n_M	Age of trees years	Date of measurement	Location	System used	Reference
F. sylvatica	~ 11 ± 1.3	m,su	3-4	100	June 2003	"	L64	Zotz et al. (2005)
(continued)	~ 10.7 ± 1.8	m,su	4	90-110	July 1991	Lüneburger Heide, Germany	W, B3	Terborg (1998), Leuschner et al. (2001)
	~ 9.6 ± 1.3	m,su	3	90-110	July/Aug 1992	"	"	"
	~ 8 ± 1.3	m,su	5	90-110	July 1992	"	"	"
	1.8	m,sh		115	1968	Solling, Germany	W	Schulze et al. (1977)
	7.2	m,sh	4-10	135-140	1986	Solling, Germany	W	Schulte (1992)
	4.2	m,sh	4-10	135-140	1987	"	"	"
	4.1	m,sh	4-10	135-140	1988	"	"	"
	6	m,sh		adult	summer 1998/1999	Bornhöveder Wald, Plön, Germany	W130	Kutsch et al. (2001)
	6.2	m,sh		adult		"	W	Dilly et al. (2008)
	9.5 ± 1.1	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	4.3 ± 0.1 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	~ 7.8 ± 1.2	ju,su	10	5	Aug 1999	Essen, Germany	L64	Wittmann et al (2001)
	18.3 ± 1.8	ju,su	4	2-3	summer 2011	Göttingen, Germany	L64	This study
	14.2 ± 0.6	ju,su	36	7	Aug 2007	Akulla, Sweden	C2	Gardiner et al (2009)
	~ 6.6 ± 0.3	ju,su	10	2	summer 1994	Nancy, France	L62	Valladares et al. (2002)
	~ 9.3 ± 0.8	ju,sh	10	5	Aug 1999	Essen, Germany	L64	Wittmann et al (2001)
	11.8 ± 0.5	ju,sh	36	7	Aug 2007	Akulla, Sweden	C2	Gardiner et al (2009)
	~ 7 ± 0.4	ju,sh	12	4	Aug 1996	western Austria, near Geman border	L64	Kazda et al. (2004)

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
F. sylvatica	~ 7.5 ± 0.5	ju,sh	12	5	Aug 1997	"	"	"
(continued)	~ 9 ± 0.3	ju,sh	12	6	Aug 1998	"	"	"
	~ 7 ± 0.6	ju,sh	12	7	Aug 1999	"	"	"
	~ 8.5 ± 0.4	ju,sh	12	8	Aug 2000	"	"	"
	~ 8 ± 0.5	ju,sh	12	9	Aug 2001	"	"	"
	7.1	ju	84	1	July 1996	north of Copenhagen, Denmark	C1	Paludan-Müller et al. (1999)
	9.5	ju	84	1	Aug 1996	"	"	"
	8.4	ju	84	1	Sep 1996	"	"	"
Fraxinus angustifolia	16.7	m,su	9	16	Aug - Sept 1996	Dyje River, Czech National Forest	L64	Kazda et al. (2000)
Fraxinus	16.3 ± 0.5	m,su	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
excelsior	14.3 ± 2.3	m,su	5	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 15	m,su	6	25	summer 1995	Amance, France	L62	Le Goff et al. (2004)
	12 ± 0.4	m,sh	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	14.3 ± 1.4	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 11	m,sh	6	25	summer 1995	Amance, France	L62	Le Goff et al. (2004)
	~ 5	m,sh	6	25	summer 1995	"	"	"
	17.6 ± 2.6	ju,su	6	2-3	summer 2011	Göttingen, Germany	L64	This study
	5 ± 0.3	ju,sh	10	saplings	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)

Species	**A_{max}**	**Leaf type**	**n_M**	**Age of trees**	**Date of measurement**	**Location**	**System used**	**Reference**
	μmol CO_2 m^{-2} s^{-1}			years				
Populus tremula	~ 12.3 ± 0.6	ju,su	10	4	Aug 1999	Essen, Germany	L64	Wittmann et al (2001)
	13.8 ± 0.8	ju, su	24	8	June - Aug 2008	Göttingen, Germany	L64	Müller (2011)
	12.3 ± 1.0	ju, su	24	8	"	"	"	"
	13.0 ± 0.8	ju, su	24	8	"	"	"	"
	12.5 ± 0.8	ju, su	24	8	"	"	"	"
	12.9 ± 0.7	ju, su	24	8	"	"	"	"
	13.9 ± 0.8	ju, su	24	8	"	"	"	"
	16.4 ± 0.3	ju, su	30	1	June - Aug 2009	Solling, Germany	"	"
	17.1 ± 0.4	ju, su	4	saplings	Aug 2007	Kuopio, Finland	L64	Mäenpää et al. (2011)
	~ 15.8 ± 1.8	ju, su	3-7	8-10	July 1997	Tartu, Estonia	SM, L626	Aasamaa & Söber (2001)
	~ 8.4 ± 0.3	ju,sh	10	4	June - Aug 2008	Göttingen, Germany	L64	Müller (2011)
Quercus cerris	8.1 ± 0.5	m,su	18	85-90	spring/early summer 2003	Bükk Mountains, Hungary	LA	Meszaros et al. (2007)
	17.1	m,su	3	80	June - Aug 1987	Bab, Czechoslovakia	L62	Marek et al. (1989)
	12.6	m,sh	3	80	"	"	"	"
	6.3 ± 0.6	m,sh	18	85-90	spring/early summer 2003	Bükk Mountains, Hungarian	LA	Meszaros et al. (2007)
Quercus petraea	~ 18 ± 0.6	m,su	3-4	100	June 2003	Canopy crane site, Basel, Switzerland	L64	Zotz et al. (2005)
	~ 16.4 ± 1.8	m,su	4	180-200	July 1991	Lüneburger Heide, Germany	W, B3	Terborg (1998), Leuschner et al. (2001)

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Q. petraea	~ 16.1 ± 1.3	m,su	5	180-200	July/Aug 1992	"	"	"
(continued)	~ 16.4 ± 1.8	m,su	4	180-200	July 1992	"	"	"
	8.3 ± 0.4	m,su	18	85-90	spring/early summer 2003	Bükk Mountains, N Hungary	LA	Meszaros et al. (2007)
	~ 15 ± 2.2	m,su	96	100	June 2003	Canopy crane site, Basel, Switzerland	L64	Leuzinger et al. (2005)
	3.3 ± 0.4	m,sh	18	85-90	spring/early summer 2003	Bükk Mountains, N Hungary	LA	Meszaros et al. (2007)
	~ 14.5 ± 0.4	ju,su		1	summer 2004	Madrid, Spain	SM, LC	Rodriguez-Calcerrada et al. (2008)
	~ 5.8 ± 1.0	ju,su	12	4	1996	western Austria, near German border	L64	Kazda et al (2004)
	~ 7.9 ± 0.8	ju,su	12	5	1997	"	"	"
	~ 8.5 ± 0.4	ju,su	12	6	1998	"	"	"
	~ 6 ± 0.5	ju,su	12	7	1999	"	"	"
	~ 9 ± 0.5	ju,su	12	8	2000	"	"	"
	~ 9.5 ± 0.6	ju,su	12	9	2001	"	"	"
	~ 9.5 ± 0.1	ju,sh		1	summer 2004	Madrid, Spain	SM, LC	Rodriguez-Calcerrada et al. (2008)
Quercus pyrenaica	~ 17 ± 0.1	ju,su		1	summer 2004	Madrid, Spain	SM, LC	Rodriguez-Calcerrada et al. (2008)
	~ 8 ± 0.4	ju,sh		1	"	"	"	"

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measurement**	**Location**	**System used**	**Reference**
Quercus robur	~ 16.3 ± 1.6	m,su		150-200	May - Nov 1996	Tartu, Estonia	LA	Aasamaa & Söber (2001)
	~ 14 ± 2	m,su	25	150-200	1999, day 200	Wytham Woods, Oxfordshire, UK	ADC	Morecroft et al. (2008)
	10.9	m,su	9	120	Aug / Sept 1996	Dyje River, Czech National Forest	L64	Kazda et al. (2000)
	~ 19 ± 0.8	m,su	6-9	20	2002, beginn of summer	Po Valley, northern Italy	C1	Grassi & Magnani (2005)
	~ 15.7 ± 0.1	m,su	6-9	20	2002, end of summer	"	"	"
	6.6	m,sh		150-200	May - Nov 1996	Wytham Woods, Oxfordshire, UK	ADC	Morecroft & Robert (1999)
	10.7	m,sh	9	120	Aug / Sept 1996	Dyje River, Czech National Forest	L64	Kazda et al. (2000)
	~ 13.5 ± 0.9	ju,su	10	2	summer 1994	Nancy, France	L62	Valladares et al. (2002)
	~ 16.3 ± 1.6	ju	3-7	8-10	July 1997	Tartu, Estonia	SM, L626	Aasamaa & Söber (2001)
	20.2 ± 1.2	ju	36	6	Aug 2007	Akulla, Sweden	C2	Gardiner et al. (2009)
	10.3 ± 0.8	ju	36	6	"	"	"	"
Salix caprea	~ 18.3 ± 1.7	ju	3-7	8-10	July 1997	Tartu, Estonia	SM, L626	Aasamaa & Söber (2001)
Salix dasyclados	14.7 ± 3.4	ju,su	6	3	Sept 2000	Saare, Estonia	L64	Merilo et al. (2006)
	10.5 ± 9.8	ju,sh	6	3	"	"	"	"

Species	**A_{max}** µmol CO_2 m^{-2} s^{-1}	**Leaf type**	**n_M**	**Age of trees** years	**Date of measure-ment**	**Location**	**System used**	**Reference**
Salix viminalis	11.9 ± 7.9	ju,su	6	3	Sept 2000	Saare, Estonia	L64	Merilo et al. (2006)
	15.8 ± 3.0	ju,su	6	3	“	“	“	“
	9.2 ± 4.2	ju,sh	6	3	"	"	"	"
	9.2 ± 8.2	ju,sh	6	3	"	"	"	"
Tilia cordata	12.2 ± 0.1 c	m,su	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	15.8 ± 2.6	m,su	7	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	~ 13 ± 1.5	m,su	96	100	June 2003	Canopy crane site, Basel, Switzerland	L64	Leuzinger et al. (2005)
	~ 9.5	m,su	1	100	June 2003	"	L64	Zotz et al. (2005)
	21.1	m,su	9	120	Aug/Sept 1996	Dyje River, Czech National Forest	L64	Kazda et al. (2000)
	4.7 ± 0.1 c	m,sh	12	20-40	July 2005	Beskydy Mountains, Czech Republic	L64	Urban et al. (2007)
	8.5 ± 1.9	m,sh	8	80-120	summer 2008/2009	Hainich NP, Germany	L64	This study
	6.5	m,sh	9	120	Aug/Sept 1996	Dyje River, Czech National Forest	L64	Kazda et al. (2000)
	20.4 ± 2.2	ju,su	6	2-3	summer 2011	Göttingen, Germany	L64	This study
	~ 13.4 ± 0.8	ju	3-7	8-10	July 1997	Tartu, Estonia	SM, L626	Aasamaa & Söber (2001)
Tilia platyphyllos	11.5 ± 0.4	m,su	10	80	July to Aug 2001	Hainich NP, Germany	L64	Hölscher (2003)
	5.6 ± 0.3	m,sh	10	80	July to Aug 2002	"	"	"
	5.7 ± 0.4	ju,sh	10	saplings	July to Aug 2003	"	"	"

Table A4: Species means (± SE) of V_{cmax}, J_{max} and A_{max} of sun or shade leaves of mature trees, or of juveniles according to the literature survey and own measurements. V_{cmax} and A_{max} in µmol CO_2 m^{-2} s^{-1}; J_{max} in µmol e^- m^{-2} s^{-1}. The species means were obtained by weighting the means given in the individual studies by the number of observations per study. n_S – number of studies per species. The species' successional status (Ss) is indicated by e for early, m for mid and l for late. The scores assigned to the species for their relative shade tolerance at the juvenile stage (Shade toler.) and the shade intensity below mature trees (Shading intens.) follow Ellenberg & Leuschner (2010) (1 = very low, 5 = very high). – indicates no data.

Species	**Ss**	V_{cmax}			J_{max}			A_{max}			**Shade toler.**	**Shading intens.**
		M	SE	n_S	M	SE	n_S	M	SE	n_S		
SUN												
P. tremula	e	75.0	1.0	1	181.0	4.8	3	-	-	-	-	2
B. pendula	e	-	-	-	-	-	-	9.2	0.1	5	-	2
F. excelsior	e	73.6	9.5	1	155.9	14.0	1	15.5	0.8	3	-	3
F. angustifolia	e	101.8	2.5	2	162.7	5.1	2	16.7	-	1	-	
A. glutinosa	m	-	-	-	-	-	-	15.5	-	1	-	3
Q. cerris	m	-	-	-	-	-	-	9.4	0.5	2	-	
Q. robur	m	107.9	4.0	2	145.8	13.6	2	14.5	1.2	5	-	2
Q. petraea	m	63.0	1.0	1	180.0	6.7	1	14.3	1.9	6	-	3
A. campestre	m							14.5	5.8	2	-	3
A. pseudopl.	m	76.5	3.2	2	175.3	12.7	1	11.1	0.5	5	-	4
C. betulus	m	56.7	3.7	1	115.8	7.0	1	12.7	0.7	6	-	5
T. platyphyllos	m	-	-	-	-	-	-	11.5	0.4	1	-	4
T. cordata	l	59.6	1.4	3	131.1	11.2	2	13.6	1.3	5	-	4
F. sylvatica	l	57.0	5.5	10	128.5	18.9	8	14.9	0.9	17	-	5
SHADE												
P. tremula	e	30.0	4.5	1	60.1	4.1	2	-	-	-	-	2
B. pendula	e	-	-	-	-	-	-	14.4	0.8	5	-	2
F. excelsior	e	56.3	5.5	1	99.7	7.7	1	11.0	0.8	4	-	3
Q. cerris	m	-	-	-	-	-	-	7.2	0.6	2	-	
Q. robur	m	-	-	-	-	-	-	10.3	-	2	-	2
Q. petraea	m	20.0	1.0	1	53.3	-	1	3.3	0.4	1	-	3
A. pseudopl.	m	32.1	3.1	2	141.7	18.9	1	5.9	0.4	3	-	3
C. betulus	m	33.2	5.6	1	63.6	9.3	1	6.3	1.0	3	-	5
T. platyphyllos	m	-	-	-	-	-	-	5.7	0.5	1	-	4
T. cordata	l	35.4	4.3	3	66.7	8.8	5	6.4	0.6	4	-	4
F. sylvatica	l	27.7	2.2	9	62.0	7.1	7	5.7	0.5	8	-	5
JUVENILE												
Salix spp.	e	47.0	6.2	6	-	-	-	12.7	5.6	7	3	-
P. tremula	e	41.1	1.3	1	145.6	5.0	1	13.4	0.7	11	2	-
B. pendula	e	88.3	3.6	3	172.8	10.3	3	12.9	1.2	5	2	-
F. excelsior	e	91.7	4.6	2	161.9	12.1	2	9.7	1.2	2	4	-
Q. pyrenaica	e	-	-	-	-	-	-	12.5	0.3	2	-	-
A. glutinosa	m	-	-	-	-	-	-	11.9	1.1	6	3	-
Q. robur	m	90.5	2.8	1	156.9	7.1	1	15.1	1.0	4	1	-
Q. petraea	m	72.5	5.0	8	153.5	9.4	8	7.9	0.6	8	2	-
A. campestre	m	-	-	-	-	-	-	9.5	-	1	3	-
A. platanoides	m	-	-	-	-	-	-	9.6	0.4	1	-	-
A. pseudoplata.	m	76.7	4.1	2	150.8	10.7	1	7.9	0.6	8	4	-
C. betulus	m	61.6	7.6	1	99.8	14.7	1	9.1	0.5	2	4	-
T. platyphyllos	m	-	-	-	-	-	-	5.7	0.4	1	4	-
T. cordata	l	60.8	2.5	1	109.1	3.9	1	17.2	1.6	2	3	-
F. sylvatica	l	45.7	1.7	11	82.2	3.0	11	9.1	0.6	15	5	-

CHAPTER 5

Synopsis

Are there species-specific differences in the photosynthetic capacity of sun and shade leaves?

This study aimed to characterize the photosynthetic capacity of different species and get a more detailed understanding of their abilities to adapt to different light conditions. We investigated the five broad-leaved tree species *Fraxinus excelsior*, *Tilia cordata*, *Acer pseudoplatanus*, *Carpinus betulus* and *Fagus sylvatica* in the Hainich National Park and differentiated between sun and shade leaves. We showed that the sun leaves of our five species have similar photosynthetic capacities, even if some species have higher light-saturated net photosynthesis rate (A_{max}), maximum carboxylation efficiency (V_{cmax}) or maximum electron transport rate (J_{max}) values than the other species. Hence, the light climate in the uppermost sun layer seems to be more uniform and each species seems to be nearly equally able to deal with that light climate. The only exception seems be to *F. sylvatica* which has relatively low but non-significantly different A_{max} values. Simultaneously, beech sun leaves show a slightly higher, not significant, leaf day respiration rate (R_d) than the other species. The low A_{max} values of the sun leaves support the results of Kutsch et al. (2001) who argued that the sun layer actually consists of two layers. The uppermost sun-1-layer has lower A_{max} values than the sun-2-layer below it. The sun-2-layer has occasionally high light conditions but it is saved from permanent high light conditions by the sun-1-layer (Kutsch et al. 2001). Another possibility is that our beech leaves had lower A_{max} values due to stomatal limitation which might be provoked by drought and/or heat stress.

An interesting finding is that the species differed in their capability to produce shade leaves. The photosynthetic capacity of shade leaves varied significantly between the species, with sycamore maple, ash and beech having higher photosynthetic capacities than the other species. Additionally, we observed considerable variation in morphological traits. The crown shape and the foliage distribution varied strongly between the species (Frech et al. 2003) which resulted in species-specific radiation extinction and light transmission and also species-specific shade adaptations. Hornbeam, lime and beech show morphological but not physiological differences between sun and shade leaves. Specific leaf area (SLA) varied 2-3 fold in these three species whereas SLA was always <200 $cm^2\ g^{-1}$ in maple and ash. The latter two species show therefore a lower low-light acclimation potential. The leaf size were larger in shade than in sun leaves but in ash the shade leaves tended to be smaller. The uniformity of the ash leaves can be seen as further proof for the non-existing shade canopy of this species. Ash leaves had the lowest, and beech the highest, shade adaptation, with hornbeam showing no real shade acclimation in its physiology. We developed six criteria for sun-shade-leaf differentiation:

a) Shade leaves show an SLA over 200 cm² g^{-1} and the sun-shade difference is 2-3 fold in SLA.

b) Typical shade leaves are at least 20 % larger.

c) A_{max} on leaf area basis ($A_{max,a}$) is as high or slightly lower as in shade leaves.

d) A_{max} on leaf mass basis ($A_{max,m}$) is higher in shade leaves.

e) Photosynthetic nitrogen use efficiency (PNUE) is higher in shade leaves.

f) Leaf area based R_d ($R_{d,a}$) of shade leaves is lower.

F. sylvatica nearly fulfilled all criteria, and the other species only partly did so. Only some species showed significant sun/shade leaf differentiation in their photosynthetic capacities. We did compare only sun and shade leaves as in previous studies (Masarovicova & Stefancik 1990, Niinemets et al. 1998, Sack et al. 2006), but there a more differentiated sun-shade leaf chararcterisation was found. In order to understand the continuum of leaves in a canopy, we analysed the leaf photosynthetic capacity in relation to the relative irradiance (RI) in which they grew and examined which plant trait has the greatest impact on the shade adaptation.

Leaf morphology, foliar N and photosynthetic capacity within the canopy

With increasing height of the canopies, we found in the five investigated tree species an increase of relative irradiance (RI) as well as nitrogen per leaf area (N_a) and a decrease of SLA. RI, SLA and N_a are the key determinants of photosynthetic capacity. With increasing RI the SLA and nitrogen per leaf mass (N_m) decreased and N_a increased. N_a was strongly negatively correlated with increasing SLA whereas N_m was only for some species positively correlated. We found a larger intra-canopy plasticity than has been reported in e.g. Sack et al. (2006) or Niinemets et al. (2004). The species ash and sycamore maple have a smaller canopy extension, a lower intra-canopy SLA variation, a lack of shade leaves with SLA >220 cm² g^{-1}, higher N_a

in shade and sun leaves, a lower slope of the RI/SLA relationship and a more or less constant N_m along the canopy gradient. Lime and beech both simultaneously increased SLA, N_m and leaf size under low light, whereas hornbeam only increased SLA. Lime has morphologically the most distinct shade leaves of these species. The small size and the low N content in beech and hornbeam shade leaves made the leaves less costly in terms of N investment and supporting structure. Hornbeam was neither flexible in leaf size nor in N investment per leaf mass, which determines most leaves as shade leaves. Therefore, this species was relatively inflexible with respect to the allocation of photosynthetically relevant compounds to leaf tissue. The species adaptation consisted mainly of alteration of SLA and of N_m or leaf size. $\delta^{13}C$ was more negative in shade leaves of all species. There were no systematic differences between the early- to late-successional species, meaning that limitation on C assimilation by drought-induced partial stomatal closure did not differ between the five species.

Correlating the photosynthetic capacity with RI, SLA and N_a, we found that almost all species correlated with area-related V_{cmax} and J_{max}, whereas only *T. cordata* and *C. betulus* correlated with area-related A_{max} and the remaining three species with mass-related A_{max}. R_d was mostly uncorrelated with RI, SLA or N_a. We conclude that J_{max} was optimized with respect to light availability in light-demanding species whereas V_{cmax} was optimized in shade-tolerant species. V_{cmax} and J_{max} were better predicted by N_a than by SLA or RI. In the literature, a strong relation of A_{max} to N_a is seen (Field & Mooney 1983, Reich et al. 1998), but the N_a influence may disappear when the light gradient is considered.

We conclude that the five temperate broad-leaved tree species differ in their strategy of adaptation of leaf morphology and function to light availability, and we suggest that canopy architecture may play an important role in determining the degree of shade adaptation. The intra-canopy light gradient is also associated with vertical gradients in atmospheric water vapour saturation deficit (VPD), leaf water status and leaf temperature, which influence leaf morphology and function. The canopy architecture is also of great importance for whole-canopy or stand-level perspectives of shade adaptation which may be more straight-forward for the classification of the species. Nonetheless, these studies help to compare tree species because the five species were measured in the same area which excludes possible side effects like differing water availability, soil nutrient status and land use history which can weaken general conclusions of species comparisons.

Photosynthetic capacity of Central European broad-leaved tree species

We compared our study on mature trees with an in-depth study of juveniles of the same five tree species and compiled a literature survey of almost every abundant European broad-leaved tree species to examine general trends in photosynthetic capacity. So far, there has been no other study which compares all three photosynthetic parameters (V_{cmax}, J_{max} and A_{max}), the successional status, the tree age and the sun-shade-leaf-differentiation.

The in-depth study displayed differences in V_{cmax} and J_{max} between the species only for the juvenile trees. We demonstrated that only few species-specific differences were found between the mature sun and juvenile leaves (J_{max} in juveniles was lower in lime trees; A_{max} was higher in maple and beech). Overall, the photosynthetic capacity in juveniles seemed to be similar to mature sun leaves. Our juvenile study grew under high light conditions, which explains the homogeneity of the results. Hölscher (2004) showed differences between juveniles grown in the understory of mature trees and the sun leaves of the same species. The discrepancy can be explained by the different growth irradiances.

With the compilation of the photosynthetic capacity over the European broad-leaved tree species we were able to make general conclusions for the species. For comparisons, we classified the species into successional groups. Within the successional groups we found differences between sun and shade leaves of mature trees and shade and juvenile leaves (V_{cmax} and A_{max} mid-successional species, J_{max} early and late successional species). The values of mature sun and juvenile leaves showed just tendencies for higher juvenile values, which again can be explained in that in most of the studies the juveniles grew under high light. We saw no differences between the successional groups with one exception: A_{max} shade leaves differed significantly between early- and mid-successional tree species. The few existing comparisons and some textbooks show contrasting results (Bazzaz 1979, Koike et al. 2001, Larcher 2001, Lambers et al. 2008, Kutsch et al. 2009) with higher A_{max} values for early-successional tree species. These studies mix data of species with different age or successional status or do not distinguish between sun and shade leaves. The problem of having only two late-successional tree species makes the statistical evaluation a little difficult, but this was due to the fact that we tried to make clear differences between mature sun, shade and juvenile leaves and did not mix the successional groups.

With the data of *F. sylvatica*, we additionally could see long-term changes in the photosynthetic capacity over the last 40 years. Both V_{cmax} and A_{max} values increased over this period of time. Even taking the modification of measuring technique into account (Ceulemans & Saugier 1991), we found the foliar N increase most likely as the reason of the increase.

Finally, we conclude that for up-scaling photosynthetic capacities in global terrestrial biosphere models we would advise not mixing data of juvenile and mature trees as already stated by Larcher (1969). Even for up-scaling to whole canopy or stand-level photosynthesis a detailed description of the species' photosynthetic capacity is of advantage. The intra-canopy light regime and the foliar N content are of high importance for the characterisation of the species. The photosynthesis rate is suitable for extrapolation to stand- or canopy-level carbon gain but it is a poor indicator of the primary productivity of forests (Ceulemans & Saugier 1991). Measuring leaf photosynthesis is of great importance to understand the species characteristics which are necessary as a base for up-scaling for global biosphere models and therefore for the prediction of forest alteration under global change.

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Summary

Forests are important not only as a habitat for animal and plant species, but also for economy, protection of soil, local recreation areas and they provide air-purification. Forests which were earlier almost solely monocultures are now more and more converted into mixed species stands. For this conversion it is important to get a deeper knowledge about the involved species. The photosynthetic capacity of a species is additionally needed for the up-scaling to canopy- or stand-level photosynthesis.

We investigated the photosynthetic capacity of the five broad-leaved tree species *Fraxinus excelsior*, *Acer pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica* and *Tilia cordata* in the Hainich National Park, Thuringia. Additionally, we focussed on the species ability to adapt to different light regimes and compared our findings with a literature compilation of European temperate broad-leaved tree species. We measured light saturated net photosynthesis rate under ambient CO_2 concentrations (A_{max}), maximum carboxylation efficiency (V_{cmax}), maximum electron transport rate (J_{max}) and leaf day respiration rate (R_d) along a light gradient inside the canopies. All investigated tree individuals grew in the immediate vicinity of each other. We included measurements about relative irradiance, N content per leaf area and leaf mass and height of the trees.

The sun leaves of the five investigated species had similar photosynthetic capacities and did not differ significantly, which can be explained by similar light conditions in the uppermost canopy layer. On the contrary, the ability to produce shade leaves differed between the species. Shade leaves were at least 20 % larger and had a specific leaf area (SLA) over 220 $cm^2\ g^{-1}$. The A_{max} rate on leaf area basis was as high or slightly lower as in sun leaves and the A_{max} rate on mass basis tended to be higher in sun leaves. The photosynthetic nitrogen use efficiency was higher in shade leaves, whereas R_d was lower. *F. sylvatica* was fulfilled all the above mentioned criteria and the other species showed only partly a significant sun-shade differentiation.

The species showed different flexibilities to produce shade leaves and their adaptation consisted morphologically mainly on the alteration of SLA. V_{cmax} and J_{max} correlated in almost every species with RI, nitrogen per leaf area (N_a) and SLA

whereas both V_{cmax} and J_{max} were better explained by N_a than by RI or SLA. Additionally, we found that J_{max} was optimized with respect to light availability in light-demanding species whereas V_{cmax} was optimized in shade-tolerant species. Area-related A_{max} correlated with RI, SLA and N_a only in *T. cordata* and *C. betulus* whereas mass-based A_{max} correlated in *F. excelsior*, *A. pseudoplatanus* and *F. sylvatica*. We conclude that the five temperate broad-leaved tree species differ in their strategy to adapt leaf morphology and function to light availability. In a comparison to high-light grown juveniles of the same species we demonstrated that the juvenile leaves had similar photosynthetic capacities like the mature sun leaves which is in debt to the high growing irradiance of the juveniles.

Finally, we compared V_{cmax}, J_{max} and A_{max} over many European broad-leaved tree species. We focussed on a clear separation of juvenile (age over one year) and mature (age over 20 years) trees as well as on the separation of sun and shade leaves and the categorisation of successional status. We found differences between mature sun and shade leaves and mature shade and juvenile leaves. A significant differences between the successional groups could not be detected which is contrary to the several studies and the common text book knowledge. These contrasting results may be explained by the fact that most other studies mix data of juveniles and mature trees or sun and shade leaf values. Additionally, we found an increase in V_{cmax} and A_{max} over the last 40 years in *F. sylvatica*, which can be explained by increasing foliar nitrogen contents.

In conclusion, we would strongly recommend not to mix between juvenile and mature photosynthetic capacity data for photosynthesis up-scaling to global terrestrial biosphere models. Here, a detailed knowledge of the species photosynthetic capacity is of advantage as well as for the forest conversion.

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Curriculum vitae

Nicole Legner, born 01.12.1981 in Aalen, Germany

Education

04/2008 – 03/2012	PhD thesis Department Plant Ecology and Ecosystem Research, University of Göttingen Supervised by Prof. Dr. C. Leuschner, Prof. Dr. F. Thomas, Dr. S. Fleck
10/2007 – 12/2007	Diploma thesis: „Die Rolle der hydropassiven und –aktiven Komponenten der stomatären Luftfeuchtereaktion und deren Interaktion“ Supervised by Prof. Dr. Wolfgang Bilger, Dr. Hartmut Kaiser Department Plant Ecophysiology, University of Kiel
10/2001 – 02/2008	Study of biology at the University of Kiel (diploma) Major: botany Minor: ecology, phytopathology, cell biology
1998 – 2001	Commercial high school in Heidenheim (Wirtschaftsgymnasium), Germany High school degree: Abitur
1992 – 1998	Junior high school Königsbronn (Realschule), Germany

Publications

Kaiser H, Legner N (2007) Localization of mechanisms involved in hydropassive and hydroactive stomatal responses of *Sambucus nigra* to dry air. Plant Physiology 143, 1068 – 1077.

Eidesstattliche Erklärung

Hiermit versichere ich die vorliegende Arbeit mit dem Titel “Spatial variation of photosynthetic capacity of early-, mid-, or late-successional broad-leaved tree species in a temperate mixed forest“ selbstständig und unter ausschließlicher Verwendung der angegebenen Literatur, Verweise und Hilfsmittel erstellt zu haben. Verwendete Quellen wurden als solche gekennzeichnet.

Göttingen, März 2012