DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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IMPORTANCE OF STRUCTURAL FEATURES OF LEAVES AND CANOPY IN DETERMINING SPECIES SHADE-TOLERANCE IN TEMPERATE DECIDUOUS WOODY TAXA

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The dissertation is accepted for the commencement of the degree of *Doctor philosophiae* in ecophysiology of Tartu University on June 7, 1996 by the Doctoral Committee of the Faculty of Biology and Geography of the University of Tartu.

Opponents: Dr. Heino Moldau (Chair of Plant Physiology, Institute of Molecular and Cell Biology of University of Tartu) and Dr. John R. Evans (corresponding opponent, Australian National University, Research School of Biological Sciences, Canberra)

This Thesis will be presented for public criticism at the Institute of Botany and Ecology of University of Tartu (Auditorium 207, Lai 40) on June 26, at 10.15 a.m.

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

Present thesis is based on the following articles, which are referred to in the text by their Roman numerals

I. Niinemets, Ü. and K. Kull. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. Forest Ecology and Management 70: 1–10.

II. Kull, O. and Ü. Niinemets. 1993. Variation in leaf morphometry and nitrogen concentration in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L. Tree Physiology 12: 311–318.

III. Niinemets, Ü. 1995. Distribution of foliar carbon and nitrogen across the canopy of *Fagus sylvatica*: adaptation to a vertical light gradient. Acta Oecologica 16: 525–541.

IV. Niinemets, Ü. 1996. Partitioning of foliar nitrogen influences species shade-tolerance in four temperate deciduous woody taxa. (Submitted)

V. Niinemets, Ü. 1996. Compromises between sapling allometry and shade-tolerance in two temperate deciduous species. (Submitted)

VI. Niinemets, Ü. 1996. Changes in foliage distribution with tree size and relative irradiance: differences between the saplings of *Acer platanoides* and *Quercus robur*. Ecological Research. (In Press)

VII. Niinemets, Ü. 1996. Plant growth-form alters the relationship between foliar morphology and species shade-tolerance ranking in temperate woody taxa. Vegetatio. (In Press)

1. INTRODUCTION

In temperate forest ecosystems, where water, temperature and other stress factors moderately limit productivity, light availability plays a central role in determining plant growth and survival (Küppers 1992). Because of the interspecific differences in the efficiency of light use, which varies in intensity and spectral quality during stand development, irradiance also influences species composition of forest stands (Bazzaz 1979, Bazzaz and Wayne 1994). As succession goes on, light becomes progressively less available and early-successional species, which have inherently limited capacities to adjust their crown and foliage attributes towards effective light capture in understory, are replaced by late-successional species (Bazzaz 1979, Küppers 1989, 1994). However, though late-successional species can tolerate very low light levels in the understory, they use, due to genetically determined physiological and morphological constraints, high irradiances less effectively than early-successional species (Horn 1975, Bazzaz 1979, Bazzaz and Carlson 1982). Of course, there are not just only early- and late-successional species but also something in between, and species separation across gap-understory continuum has encouraged researches to rank woody taxa according to their ability to tolerate shade, i.e. shade-tolerance (Spurr and Barnes 1980, Hicks and Chabot 1985). It appears that the shade-tolerance rankings of woody species, most of which are based on forester's and ecologist's knowledge on species behaviour, and only very few on some quantitative work on species dispersal across understory habitats, have remained remarkably constant during almost a century (Table 1).

It is important to recognise that any stress factor, which decreases plant ability to use available light, will increase the minimum daily light dose that the plant requires to survive under given conditions. Therefore, there is no single minimum light level, which an individual of the particular species tolerates, and 'shade-tolerance' is not an absolute rather than a relative term (Spurr and Barnes 1980). Changes in a number of site factors potentially capable of affecting shade-tolerance, such as nutrient (Tilman 1993) and water availability (Bazzaz and Wayne 1994), air and soil temperature (Bazzaz and Wayne 1994), parallel gradients of irradiance across gap-understory continuum. Furthermore, given the disproportionate increases in the biomass costs for mechanical support with increasing tree size, the proportion of foliage, which serves to capture light and fuel the growth with assimilated carbon, decreases with increasing size (Givnish 1988). This results in shade-tolerance to change during tree ontogeny (Zon and Graves 1911, Givnish 1988, Yevstigneyev 1990). Thus, species dispersal across light gradients is determined by a complex interplay of various edaphic, climatic and ontogenetic factors.

Nevertheless, species ranking on the basis of shade-tolerance is strikingly constant (Table 1), suggesting that the relative light requirements vary considerably less than the absolute ones. Given this constancy and the important role of species response to light gradients in succession, it appears relevant to ask why species have become to function at particular light levels, and what are the morphological and physiological attributes responsible for shade-tolerance. The current study was designed to highlight these issues.

2. OBJECTIVES

There exists already a solid body of knowledge on light-related adjustments in foliar and canopy parameters (see for review e.g. Björkman 1981, Givnish 1988, Bazzaz and Wayne 1994). However, most effort in the research on species shade-tolerance has been directed towards studying photosynthetic parameters of foliage (e.g. Björkman 1981, Bazzaz and Carlson 1982), and the understanding of adaptive changes in structural features of foliage and canopy lags far behind photosynthesis research. Of course, it is extremely important to study photosynthesis, because this is the only source of reduced carbon in green plants. Unfortunately, in ecophysiological studies on carbon assimilation the measured rates are usually expressed on a surface area basis only (e.g. Bazzaz

Table 1. Comparison of various shade-tolerance scorings: Spearmann rank correlation coefficients (number of cases)

A. European species

Shade-tolerance ranking^{*1}	Gayer	Warming	Walter	Ellenberg (1982)	Jahn	Ellenberg (1991)
Gayer (1898)						
Warming (1909)	0.929 (14)					
Walter (1968)	0.821 (10)^{*2}	0.895 (9)				
Ellenberg (1982)	0.791 (17)	0.698 (16)	0.602 (11)^{*3}			
Jahn (1991)	–0.601(16)^{*3}	–0.825 (15)	–0.881 (10)	–0.620 (34)		
Ellenberg (1991)	–0.791 (17)	–0.698 (16)	–0.579 (12)^{*3}	–0.993 (42)	0.619 (41)	
Otto (1994)	0.836 (17)	0.878 (16)	0.662 (11)^{*3}	0.658 (32)	–0.522 (29)^{*2}	–0.683 (33)

^{*1} All rankings increase with increasing species shade-tolerance, except for those of Jahn ('light requirement') and Ellenberg ('light figure'), which are negatively related to shade-tolerance. ^{*2} significant at $p<0.01$. ^{*3} significant at $p<0.05$. All other coefficients are significant at $p<0.001$. The scale of Ellenberg (1991) is derived from light measurements in the habitats of species dispersal, all other scales base on ecologist's and forester's knowledge on species biology.

B. North-American species

Shade-tolerance ranking	Zon and Graves	Baker	Curtis and McIntosh	Graham	Fowells	Minore
Zon and Graves (1911)						
Baker (1949)	0.856 (86)					
Curtis and McIntosh (1951)	0.723 (11)^{*2}	0.587 (20)^{*2}				
Graham (1954)	0.868 (16)	0.910 (20)	0.986 (6)			
Fowells (1965)	0.728 (69)	0.780 (115)	0.424 (16)^{*4}	0.872(19)		
Minore (1979)	0.712 (17)	0.859 (18)	–	–	0.847(17)	
Hicks (1985)	0.841 (8)^{*2}	0.802 (13)	0.894(5)^{*3}	0.949 (4)^{*3}	0.627(12)	–

^{*4}— not significant. Other significance values are as in table 1A. – no pairs were available. Curtis and McIntosh (1951) derived their scale from a study on species occurrence in late-successional forests, Graham (1954) used the correlation between various crown morphological attributes and species ability to endure shade, other scales base on ecologist's and forester's knowledge on species biology.

and Carlson 1982, Evans 1989, Ceulemans and Saugier 1991). Insofar as (rate per area)=(rate per dry mass)×(dry mass per area), the expression of assimilation rates on an area basis often neglects foliar structure (Charles-Edwards and Ludwig 1975, Reich and Walters 1994, Niinemets and Kull 1995, Niinemets 1996). This appears particularly relevant when photosynthesis is studied across light gradients, because leaf dry mass per area (LMA) is linearly related to irradiance (Fig. 1, I–VI). Thus, the differences in photosynthesis rate per unit leaf area between species and light environments may be related to foliage structural parameters rather than to foliar chemistry and photosynthetic potential of leaf cells (Fig. 2). The information depicted on Fig. 2 suggests that changes in leaf structure rather than in physiology play a paramount role in adaptation to irradiance.

Nevertheless, the adaptation to irradiance does involve modifications in foliage chemical composition (Evans 1987, 1988, Terashima and Evans 1988, Ellsworth and Reich 1992, 1993, Niinemets 1996, II, III, IV). Again, the relationships of area and mass based contents of leaf chemicals with irradiance may differ qualitatively (Ellsworth and Reich 1993, Niinemets 1996, II, III, IV).

Given the relevance of the adaptations in both leaf structure and composition for species shade-tolerance, the first priority of this Thesis was to study changes in foliar morphology and chemical composition across the gradients of irradiance (I–IV). After generalising the patterns within and between species I expected this analysis (1) to provide important insight into species dispersal across gap-understory continuum, and (2) to open new perspectives for reconsideration of existing information on the gas-exchange of leaves and thus to further contribute towards (1).

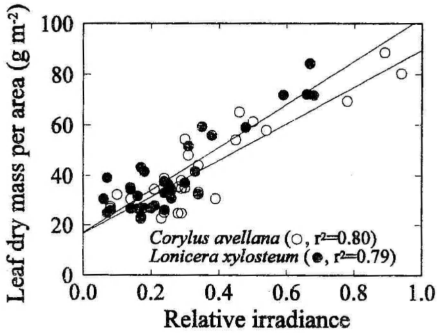

Fig. 1. Relationship between relative irradiance and leaf dry mass per area in two shade-tolerant species (data replotted from the study II).

However, in many cases economics of gas-exchange alone fails to elucidate the different patterns of species occurrence along gradients of irradiance, and either life form (Küppers 1989, 1994), branching patterns (Givnish 1988, Küppers 1989, 1994), differences in foliage distribution (Horn 1971, Ardhana *et al.* 1988) or in plant allometry (Givnish 1988, Kohyama and Hotta 1990, Kohyama and Grubb 1994) may provide an explanation. Though it is generally acknowledged that plant architecture may be altered in response to irradiance (Givnish 1988), most of the aforementioned analyses are static, i.e. they do not consider the adaptive responses of crown architecture to incident irradiance. As the second priority, this Thesis was to contribute towards more extended understanding of adaptive modifications in canopy architecture, biomass allocation and the role of these changes in shade-tolerance (V–VII). Combining both the analyses of foliar structure and composition (I–IV), and biomass allocation to foliage and the distribution of the assimilative surface in space (V–VII) I hoped this Thesis to provide a basic framework of concepts within which to further examine the significance of every single modification in terms of carbon balance — the work that has already begun (Niinemets 1995a, b).

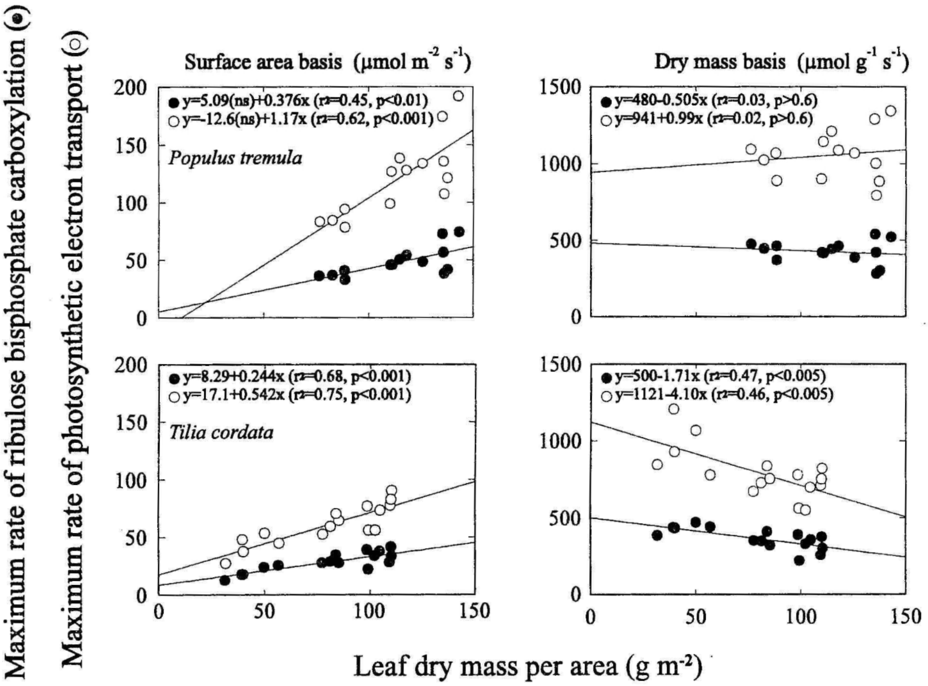

Fig. 2. Dependencies of two key parameters of the biochemical photosynthesis model of Farquhar and von Caemmerer (1982) on leaf dry mass per area in shade-tolerant *Tilia cordata* and in intolerant *Populus tremula* (Niinemets and Kull, in preparation). Both maximum rate of ribulosebisphosphate carboxylation (Vc_{max}) and maximum rate of electron transport (J_{max}) were determined from net photosynthesis *vs.* intercellular CO_2 concentration curves as described in Wullschleger (1993), and further standardised to 25 °C using the temperature dependencies for Vc_{max} and J_{max} reported in Niinemets and Tenhunen (1996). Vc_{max} and J_{max} rather than the net photosynthesis rates at an ambient CO_2 (C_a) are depicted because they are more informative in terms of biochemical limitations of photosynthesis, and they are also independent of stomatal effects. At a C_a=350 ppm, photosynthesis is usually limited by J_{max} at low irradiance and by Vc_{max} at high irradiance.

3. METHOD

It has been acceptable to present data on light-related modifications in leaf and canopy properties without reporting the light levels at which the measurements were carried out, e.g. "shade" leaves *vs.* "sun" leaves, "shade" environment *vs.* "sun" environment. This kind of typological thinking has encouraged one to see divisions where none existed, a problem, which has seriously dogged studies on light-related modifications in foliar and canopy architecture. As light changes continuously, so do foliage and canopy attributes (Fig. 1). Furthermore, it is to expect that more shade-tolerant species would grow under more shady conditions than less tolerant ones. Consequently, the comparisons between "shade" and "sun" parameters between these species groups always involve light as a confounding variable. As a more extended approach, it is widely approved (Bazzaz and Carlson 1982, Walters *et al.* 1993a, Wayne and Bazzaz 1993a, Sipe and Bazzaz 1994) to study the differences in species light response via partitioning the continuous variation in light climate between several light levels. Though useful for separating very distinct species, fixing of a more subtle variability requires *a priori* knowledge on where exactly in light scale to look for the difference.

This is why a different approach is used throughout this study: a continuous index of relative irradiance conditions (RI), varying from 0 (no irradiance penetrating the canopy) to 1 (irradiance above the canopy), is constructed, and the variability in all measured foliar and canopy parameters is related to this index. Estimation of RI is based either on just the proportion of open sky (I,VII) or on the proportion of penetrating diffuse irradiance, calculation of which takes into account cosine of incidence effects (II–VI). Nevertheless, both estimates are highly correlated (I). Diffuse irradiance rather than an index, combining both diffuse and direct irradiances is used, because the temperate woody species show limited potential to use and adapt to direct irradiances with high maximum intensities (Wayne and Bazzaz 1993a, b). Furthermore, foliage sampling along the habitats of various exposure and across the canopy has always been constrained to south aspect of the canopy. Given the constant compass direction of samples, RI provides also an estimate of direct irradiance. RI values may be used to determine long-term integrated light dozes at various canopy locations (Salminen *et al.* 1983, Rich *et al.* 1993, Niinemets, Kull and Sõber in preparation).

Of course, various environmental factors also change with irradiance across natural light gradients (cf. Introduction, Fig. 3A). To clearly separate light effects and the influence of confounding environmental variables on studied foliar and canopy parameters several growth-chamber experiments have been planned (Niinemets 1995b).

Furthermore, it appears that light quality (Messier and Bellefleur 1988, Dale and Causton 1992, St-Jacques and Bellefleur 1993) and day duration (Fig. 3B) change across natural light gradients as well. As light penetrates through the canopy it becomes depleted from blue and red spectral bands, and enriched by green and far-red bands. This appears relevant, because foliage and canopy attributes of woody species may be affected differently by irradiance, which differs in red/far-red ratio (Kwesiga and Grace 1986, Kwesiga *et al.* 1986, Tinoco-Ojanguren and Pearcy 1995), a response that is most likely mediated through the phytochrome pigment system (Casal and Smith 1989). Day length (Fig. 3B) may also be an important external variable, which alters growth (Leibundgut and Heller 1960, Hughes and Evans 1963, Marczynski and Joustra 1993), morphology (Hughes and Evans 1963) and phenology (Borchert 1991) of woody taxa. Nevertheless, RI is a good index of both red/far-red ratio (Dale and Causton 1992) and day length (Fig. 3B). Inasmuch as the changes in spectral quality of light and photoperiod length inherently accompany natural light gradients, they should not be of too much concern in studying successional sequence and shade-tolerance of species in natural conditions. Again, to gain more illuminating insight into the effect of various light parameters on foliage and canopy properties, several laboratory experiments are necessary.

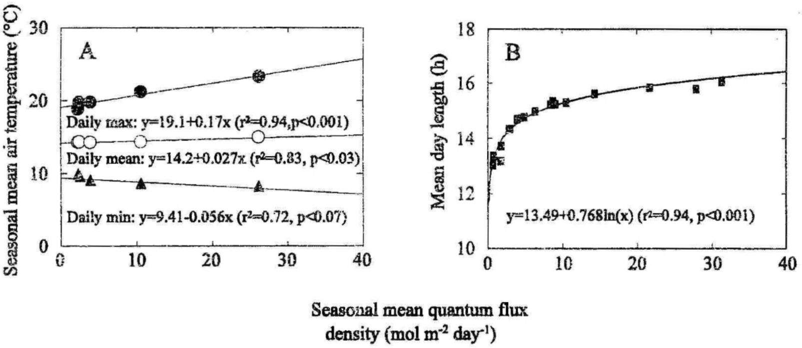

Fig. 3. Correlations of (**A**) mean seasonal (3.06.95–3.10.95) air temperature and (**B**) mean day length with mean seasonal quantum flux density (400–700 nm) across the canopy of a mixed *Populus tremula* and *Tilia cordata* stand in Järvselja (Estonia). Max, mean and min stand for mean seasonal daily maximum, average and minimum air temperature. Day length was defined as the day period with quantum flux densities (Q) >3 μmol m^{-2} s^{-1}. Air temperature was measured with termistors, quantum flux with photon sensors (OPT-21, Burr-Brown. Inc., USA), which were calibrated against a PAR sensor (Li-Cor, Inc., Nebraska, USA). The highest temperature and quantum sensors were situated at *ca* 25 m, the lowest ones at 4 m. Data from Niinemets, Kull and Sõber (in preparation).

This Thesis was not designed to refine the understanding of species successional sequence or to rank species according to shade-tolerance, because this kind of information is already available (Table 1). Rather it serves to explain why species grow under particular irradiances and what morphological and physiological attributes are responsible for the observed behaviour. Since it is most detailed and covers the most species, I choose the scale of Ellenberg (1991) to relate measured foliage and canopy parameters to. Though Ellenberg (1991) argues that his scale is not shade-tolerance or light requirement ranking *per se*, rather than just the habitat separation between species in natural conditions, in fact, none of the shade-tolerance scales listed in Table 1 is based on more information. Having established the qualitative relationships between foliage and canopy properties, and previously estimated shade-tolerance rankings, it may further become useful to turn back and to reconsider the shade-tolerance scorings on the basis of obtained morphological and physiological information.

4. SUMMARY AND DISCUSSION OF THE PAPERS

4.1. Influence of irradiance on foliar structure

4.1.1. Foliar morphology

Foliage and canopy adjustments, which change the quantum interception efficiency on an incident light basis will also influence the minimum light requirement the plant needs to survive. Therefore, as irradiance decreases, the adaptations contributing towards more effective light capture gain in importance. Since leaf dry mass per area (LMA) determines the biomass requirements for the construction of unit foliar surface area, the first hypothesis was that more shade-tolerant species should have lower LMA, and consequently a more extensive foliar display under given irradiance than less tolerant species. Previous work was fully consistent with this hypothesis (Jackson 1967, Abrams and Kubiske 1990). Unfortunately, in former studies light levels other than ambiguous "sun" *vs.* "shade" were not estimated. Given the species separation across gap-understory continuum, shade-tolerant species may have had lower LMA simply because they may have grown under lower irradiances (Fig. 1, cf. Objectives). To clarify the matters, LMA was examined in 85 woody species representing 83% of Estonian native flora (I). It appeared that, indeed, there is an interactive effect between species shade-tolerance and LMA, whereas at a common irradiance shade-tolerant species tend to have lower LMA than intolerant species (I).

A more detailed study with three species (II) showed that the upper boundary of LMA at high irradiance was similar between shade-tolerant and intolerant species. However, intolerant *Betula pendula* had greater biomass requirement for leaf area construction under low irradiance than more tolerant *Corylus avellana* and *Lonicera xylosteum* did (II).

In *C. avellana*, there was also a positive effect of tree size on LMA (II). This phenomenon was related to an enhanced requirement for supporting tissues in leaves due to increasing water limitations with increasing plant size. Greater LMA in taller plants has major implications for species shade-tolerance: insofar as greater support costs inevitably bring about greater LMA and thus decrease the foliar surface which is necessary to capture light, changes in LMA with tree size may provide a mechanistic explanation why shade-tolerance decreases during plant ontogeny (cf. Introduction). Extensive survey of literature (Malkina 1983, Linder 1985, Leuning *et al.* 1991b) as well as further research (Niinemets and Kull 1995, Niinemets 1996, III, V) established a more general positive relationship between LMA and tree size.

Though both study I and II and later also V supported the argument of greater LMA in shade-tolerant species, there was an important discrepancy in the study IV. In this paper the changes in foliar structure across a light gradient were followed in three tree species (*Acer platanoides*, *Populus tremula* and *Quercus robur*) and in a shrub (*Padus avium*). Though the differences in LMA between tree species were in good agreement with the previous results, *P. avium*, which was less-tolerant than *A. platanoides* and more tolerant than two other tree species, had lowest LMA at low irradiance and highest at high irradiance (IV). This observation gave first impulse towards development of a hypothesis of plant life-form effects on LMA *vs.* shade-tolerance relations. I tested this hypothesis in VII (s. 4.2.3).

Given the correlation between temperature and irradiance (Fig. 3A, Bazzaz and Wayne 1994), we also expected leaf form and size to depend on irradiance, and species shade-tolerance rank. In particular, the study I focused on leaf size, which determines leaf temperature for constant radiation load and wind speed (Gates 1980 and references therein). Irradiance had no effect on leaf size, however, shade-intolerant species tended to possess smaller leaves than tolerant species (I). Inasmuch as boundary layer conductance for heat exchange and gaseous exchange of water vapour and CO_2 with atmosphere decreases with increasing leaf size (Gates 1980), shade-tolerant species with larger leaves may be constrained to understory habitats, where energy balance of leaves is more favourable. Again, the relationship between leaf size and shade-tolerance appeared to be sensitive to plant life-form (VII).

For the correlation between leaf size and shade-tolerance, there is also another explanation, which is more directly related to shade-tolerance. Horn (1971) distinguished between two canopy architectural types: 'monolayer' and 'multilayer'. The most effective foliar display for light capture ('monolayer') is formed when all leaves are arranged regularly side by side in a horizontal layer. The alternative to 'monolayer' is 'multilayer', which takes advantage of penumbra effect and has leaves distributed randomly between various layers. 'Monolayer', which casts deep shade and intercepts light effectively is a typical architectural pattern for late-successional species, whereas early-successional ones often have 'multilayer' canopies, which are open to invasion but expose more foliar area than 'monolayers' (Horn 1971). Since the distance between leaf layers to take advantage of penumbra effect is directly proportional to leaf size, small leaves favour 'multilayered' canopies.

4.1.2. Foliage chemical composition

The change of LMA with irradiance (Fig. 1, I–VI) has major implications for estimating foliage photosynthetic production across light gradients (cf. Objectives). If foliar chemical composition would remain constant, a positive proportional relationship between photosynthetic capacity per area and LMA is anticipated. Indeed, LMA and net assimilation rate per leaf area are positively related (Jurik 1986, Oren *et al.* 1986, Gutschick and Wiegel 1988, Ellsworth and Reich 1992, Ducrey 1994). However, the correlation between assimilation rate per leaf dry mass and LMA is either positive (Chazdon and Kaufmann 1993), not significant (Ellsworth and Reich 1992, Chazdon and Kaufmann 1993, Ducrey 1994) or negative (Ducrey 1994, see also Fig. 2), suggesting that foliar chemistry is affected by light conditions.

Since most of foliar nitrogen is invested in photosynthetic apparatus (Field and Mooney 1986, Evans 1989), and nitrogen is also the mineral element, which is required in largest quantities for photosynthetic function (Field and Mooney 1986), a strong positive correlation between foliage nitrogen content and photosynthesis is often found (Field and Mooney 1986, Evans 1989, Reich and Walters 1994, Schulze *et al.* 1994). Furthermore, due to its high requirement for biomass construction, N is also the nutrient, which most universally limits growth (Garnier and Freijsen 1994, Schulze *et al.* 1994). Given the constraints set by N availability, it is of particular importance how nitrogen is distributed in foliage across various light environments, and what is the role of nitrogen in shade-tolerance. These questions were addressed in studies II–IV. Of course, limited supply of many other elements such as phosphorus (Reich and Schoettle 1988, Terry and Rao 1991), magnesium (Dorenstouter *et al.* 1985), iron (Spiller and Terry 1980, Terry and Rao 1991), calcium (Reich *et al.* 1995) etc. may divert photosynthesis from optimum, and accordingly, reducing light use efficiency for an incident irradiance, affect shade-tolerance. There are many forest stands, where these nutrient imbalances may be very important to characterise, but these effects will not be handled here.

As expected, we always encountered strong positive relationships between leaf nitrogen per area (N_a), and LMA and irradiance (II–IV). However, the relationships with leaf nitrogen per dry mass (N_m), which does not confound the variation in LMA ($N_a = N_m \times LMA$), were qualitatively different between the species (II, IV). It appeared that in shade-tolerant species (*C. avellana*, *L. xylosteum* from the study II, *Fagus sylvatica* from III, *A. platanoides* and *P. avium* from IV) N_m increased with decreasing irradiance and LMA, but in intolerant species it either increased with irradiance (*B. pendula* from II) or it was constant across light gradient (*P. tremula* and *Q. robur* from IV). Other data further strengthen the argument that shade-tolerant species have highest nitrogen investment in low, and intolerant species in high irradiance: N_m decreased with increasing canopy height or light availability in shade-tolerant *Abies alba* (Aldinger 1987), *Acer saccharum* (Ellsworth and Reich 1992), *Borojoa patinoi* (Lynch and González 1993), *Picea abies* (Niinemets 1996), but it increased with increasing canopy height or light availability in intolerant *Eucalyptus grandis* (Leuning *et al.* 1991a), *Pinus radiata* (Kelly and Lambert 1972), *Pinus sylvestris* (Heinze and Fiedler 1976), *Pseudotsuga menziesii* (Lavender and Carmichael 1966) and was virtually constant in *Nothofagus solandri* (Hollinger 1989).

Having identified the interspecific differences in N_m distribution patterns, it seemed pertinent to ask why these differences exist, and are they accompanied by changing investment patterns of nitrogen in photosynthetic compounds determining light harvesting (chlorophylls and proteins associated with them) and light use (Calvin cycle enzymes, compounds associated with photophosphorylation and photosynthetic electron transport) in photosynthesis.

Due to the asymptotic nature of leaf absorptance *vs.* chlorophyll relationship, only minor gains in leaf absorptance may be achieved with large investments of foliar nitrogen in light harvesting compounds (Evans and Seemann 1989). However, though expensive in terms of nitrogen, greater light absorptance improves quantum yield of photosynthesis for an incident irradiance. This may be especially crucial for species mostly occurring under low irradiance. Thence I hypothesised that increased nitrogen requirements for light harvesting cause N_m to increase with decreasing irradiance in shade-tolerant species. This hypothesis received preliminary support from the study on nitrogen distribution across the canopy of very shade-tolerant *Fagus sylvatica* (III). First, in this study there was no correlation between N_m and foliage non-structural carbohydrate concentration (ethanol-soluble carbohydrates + starch), which was considered to give an estimate of daily photosynthetic production (Servaites *et al.* 1989, Takahashi *et al.* 1993), suggesting that increased N_m was not invested for the enhancement of dark reactions of photosynthesis. Second, the increase in N_m with decreasing irradiance was paralleled with increasing foliar magnesium concentration. Given the positive relationship between leaf Mg and Chl (Schulze and Küppers 1985), and that *ca* 60% of leaf Mg was invested in chlorophyll in this study, I interpreted these results as an evidence indicating higher investment of resources towards light capture at low irradiance in this species. This explanation was further tempered in light of the study IV, where foliar chlorophyll concentrations were directly measured.

I found that leaf Chl concentrations consistently increased in all four studied species with decreasing irradiance, however, for a given leaf nitrogen content the proportion of foliar nitrogen invested for chlorophyll formation was higher in shade-tolerant species (IV). This result was in full accord with previous research, showing greater nitrogen investment for light capture in shade-tolerant species (Seemann *et al.* 1987, Evans 1989, 1993, Evans and Seemann 1989). Combining the data of the studies II and IV, it appeared that nitrogen parameters were strongly correlated with shade-tolerance: more tolerant species had lower mean N_m, but the extent and velocity of the increase in N_m with decreasing irradiance increased with increasing shade-tolerance (IV).

On the other hand, there was also evidence that leaf photosynthetic production was higher at a common irradiance in less shade-tolerant species (again, carbohydrate analysis served to provide an estimate of the foliage photosynthetic properties). This outcome is consistent with greater photosynthetic capacities reported for intolerant plants (Bazzaz 1979, Björkman 1981, Bazzaz and Carlson 1982, Küppers 1984) and also in good agreement with higher N_m in these species. Collectively, the results of the study IV suggest that the goal, towards which nitrogen partitioning in leaves is optimised, shifts with decreasing shade-tolerance from maximisation of the capacity of light capture in very shade-tolerant species towards maximisation of dark reactions of photosynthesis. Optimisation of both light and dark reactions of photosynthesis at the same time is probably impossible due to genetically determined constraints.

However, lower N_m of shade-tolerant species also signifies that the costs of foliar biomass formation in terms of nitrogen are lower in these taxa: with similar nitrogen investment in leaves, shade-tolerant species may construct more extensive foliar display and capture more light than the intolerant ones. Accordingly, economics of biomass allocation rather than economics of photosynthesis may provide an explanation for different N_m distribution patterns. This point made it necessary to consider the variability in N_m also from a canopy perspective.

4.2. Influence of irradiance on canopy architecture and biomass allocation

4.2.1. Plant growth and allometry

I suggested in the previous chapter that shade-tolerant species may have greater biomass investment in foliage, because foliage construction is less expensive in terms of nitrogen in these species. Furthermore, shade-tolerant species generally have also lower LMA than intolerant ones (4.1.1.). As a result of the hypothesised greater biomass allocation to leaves and lower LMA, shade-tolerant species should be able to form a more extensive foliar display, capture more light and outcompete intolerant species in environments where light is scarce.

In traditional growth analysis (Hunt 1982) relative growth rate (RGR, the rate of dry matter increment per unit total dry mass) is expressed as RGR=LAR ×NAR, where LAR is leaf area ratio (total leaf area per total plant mass) and NAR is net assimilation rate (the rate of dry matter increment per unit leaf area). Given a higher proportion of biomass in foliage (LMR, leaf mass per total plant mass) and a lower LMA, LAR (LMR/LMA) should be greater in shade-tolerant species. However, earlier work with seedlings has brought contradictory evidence: LAR may be larger either in intolerant species (Loach 1970, Rincón and Huante 1993) or in more tolerant species (Loach 1970). Another question is, if the results extracted from the work with seedlings are simply extendible to saplings and further to trees. There are two major concerns: first, as woody plants increase in size and as they age, growth becomes more deterministic, i.e. the number of annual leaf flushes decreases and growth terminates earlier in season as well (Borchert 1991). This would most drastically affect LAR in intolerant species, which tend to have indeterminate growth patterns (Bicknell 1982). Second, as trees grow, the proportion of biomass invested in leaves generally decreases (Whittaker 1962, Walters *et al.* 1993b). For habitat separation between the species along gradients of irradiance it is particularly relevant how rapidly the fractional investment of biomass in foliage decreases with size. This appears to be variable between species (Whittaker 1962, Walters *et al.* 1993b), signifying that interspecific differences in allometry may alter competitive relations during plant ontogeny.

To gain insight into biomass distribution in saplings of the species differing in shade tolerance and the role of allometry in shade-tolerance I studied growth and biomass partitioning in shade-tolerant *A. platanoides* and in intolerant *Q. robur* (V). Further, I expected this paper to provide a linkage for reconsideration of results obtained with seedlings in the context of forest development and succession.

It appeared that *A. platanoides* had greater proportion of biomass in foliage than *Q. robur* (V). As a result of lower LMA, *A. platanoides* had also greater LAR (V). Thus, *A. platanoides* behaved exactly as I speculated previously based on its lower foliar N concentration (IV). In contrast, NAR was significantly larger in *Q. robur*, a result, which is most likely attributable to higher foliar N_m and photosynthetic capacity in this species (IV). However, RGR — the product of LAR and NAR — was not different between the species (V). The same RGR was achieved in a completely different way: *A. platanoides* increased the intercepting foliar area, while *Q. robur* increased the productivity per unit area. Thus, lower NAR may effectively be compensated with enhanced biomass investment in foliar area construction. It is important to recognise that reverse should not necessarily be true — in low irradiances there may not simply be enough light to supply enhanced carbon assimilation capacities with energy. Based on this evidence, I supposed that lower shade-tolerance of the saplings of *Q. robur*, as indicated by lower minimum irradiance at which the saplings were encountered in the understory, was caused by constrained biomass investment for foliage formation in this species. Further analysis showed that biomass allocation to foliage changes during sapling ontogeny. Interestingly, *A. platanoides* kept the proportion of biomass in foliage constant with increasing sapling size, however, LMR decreased with advancing sapling growth in *Q. robur* (V). This is a very important difference in terms of shade-tolerance, implying that saplings of similar height require more light to survive in *Q. robur* than in *A. platanoides*. Of course, greater investment of biomass in leaves *vs.* standing biomass may result in lower volume gain and reduced competitive ability in more open habitats in *A. platanoides*.

Inasmuch as interspecific differences in allometry proved to be a fairly weighty factor in determining species success to survive under low irradiances, growth studies on seedlings may contribute little towards understanding stand-level processes.

4.2.2. Foliage distribution

To outdo the competitors it is not just greater foliar area that counts, but enhanced ability to capture light. Additional investment in foliage is of little use if this results in increased self-shading within the canopy. Definitely, high biomass investment in foliage is a prerequisite of improved light interception by the plant, but this foliage needs to be distributed in space in a way that minimises self-shading. Thus, economics of biomass allocation is closely related to adaptive strategies of canopy architecture.

Since higher LAR effectively balanced lower NAR in *A. platanoides*, and gave similar RGR in both *A. platanoides* and *Q. robur* (V), it follows that higher LAR did not result in increased self-shading rather than in enhanced light interception in *A. platanoides*. In general, shade-tolerant species seem to possess more effective foliar display for light absorption than intolerant species (Horn 1971, Ardhana *et al.* 1988, see also 4.1.1). The questions — how shade-tolerant *A. platanoides* managed to avoid self-shading, and what are the differences in canopy attributes between *A. platanoides* and *Q. robur*? — were addressed in the paper VI. Previous studies on canopy architecture (Horn 1971, Ardhana *et al.* 1988) have stressed genetic aspects, however there is some evidence indicating that canopy architecture is affected by irradiance as well (Steingraeber *et al.* 1979, Canham 1988). In both *A. platanoides* and *Q. robur* LAR increased with decreasing irradiance, suggesting that their canopy structure should also be dependent on irradiance.

Crown architecture of the studied species responded to irradiance in a completely different way: foliage distributions were adjusted with declining irradiance in *A. platanoides* to display more foliar area, however, they were independent of irradiance in *Q. robur* (VI). Furthermore, leaf area and weight per unit stem length were also larger in *Q. robur*, and resulted in elevated light gradients across the canopy in this species. Because increased foliage production inevitably results in greater self-shading within the canopy in *Q. robur*, enhanced investment of biomass in foliage does not necessarily lead to an increased light capture in this species. Thus, low biomass allocation to leaves in *Q. robur* (V) may have resulted from a limited ability to adjust crown architecture towards exposing the extra foliage. These results suggest that branching patterns play a significant role in species dispersal across gap-understory continuum.

4.2.3. Plant life-form effects

Now, having discussed a large number of adaptive modifications in leaf (4.1.1, 4.1.2.) and canopy structure (4.2.2.) as well as in biomass allocation (4.2.1.), it is pertinent to ask what are the most important competitive attributes? The current Thesis demonstrates that there is no single answer. Furthermore, the plant traits responsible for shade-tolerance may vary during species ontogeny. As trees grow taller, their ability to change LMA (II,III,V) and biomass investment in foliage decreases (V). Thus, it is to expect that branching patterns and adaptive modifications in canopy architecture gain and foliar parameters lose in importance with increasing plant age and size. However, this may be different in the case of species, which due to limited potential for height growth are constrained to understory, e.g. shrubs. Küppers argues that branching patterns (Küppers 1985, 1989, 1994) and life-form (Küppers 1989) are stronger competitive attributes than foliar parameters (Küppers 1984), because they determine the volume gain per unit biomass investment the species attains. Canham and Burbank (1994) further demonstrate that differences between early- and late-successional trees in light interception are more closely related to differences in crown depth rather than to light extinction per unit crown depth. Because life-form sets limits to both height growth and to adjustment of crown depths, I hypothesised that foliar parameters should be more important competitive attributes in shrubs than in trees, and tested this hypothesis in paper VII.

Plant life-form significantly altered the relationships between LMA, leaf size and shade-tolerance (4.1.1.): all qualitative tendencies were significant in shrubs, but none was significant in trees (VII). Thus, the relationships between shade-tolerance rank and foliar structure (I), positive for LMA and negative for leaf size, resulted from high plasticity of foliar architecture in shrubs. Study VII suggests that shade-tolerance of trees, which have relatively constant leaf structure, may be most affected by the variability in biomass partitioning and crown geometry. Alteration of leaf form and investment pattern for construction of unit foliar surface area, changing the efficiency of light interception per unit biomass investment in leaves, is a competitive strategy inherent to shrubs.

5. CONCLUDING REMARKS

I have presented and discussed a number of modifications in foliar and canopy architecture, which are likely to alter the light use-efficiency on an incident irradiance basis, and accordingly, affect shade-tolerance. A major conclusion of this Thesis is that there is no one single morphological or physiological trait that would equally well describe separation of all studied species across light gradients. Moreover, various morphological and physiological traits are correlated with each other, further complicating the analysis. Nevertheless, having identified the broad variation patterns of foliar and canopy morphology with irradiance within species, and variation patterns between species, this Thesis provides a good starting point for a more pin-pointed modelling study for selecting the adaptations, which have major impact on plant carbon economy. This kind of study would give a physiological basis for the ranking of species according to the ability to tolerate shade, and as such would strongly enhance our understanding on the role of various species during succession.

I focused particularly on an ontogenetic aspect of shade-tolerance. Apart from an increasing light requirement with increasing plant age and size (Zon and Graves 1911, Givnish 1988, Yevstigneyev 1990), it also appears that during the ontogenetic development from seedling to tree, the importance of various plant traits for efficient light harvesting is not constant. There is a basic tendency of leaf properties to be most important competitive attributes earlier in ontogenesis and in smaller plants, and of canopy architecture and biomass allocation to gain in relevance later in ontogenesis in trees. The discrepancy between laboratory experiments on seedlings and forester's knowledge of species behaviour in forest stands is a major reason, why current models of forest development (Shugart 1984, Urban *et al.* 1991) use highly simplified assumptions on species biology.

Of course, structure is only one aspect of adaptation to irradiance. Since it is often difficult to distinguish between structure and function, this Thesis also serves to provide a basic framework for separating the structural and physiological aspects (e.g. photosynthesis) of leaf function across light gradients.

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PARASVÖÖTME HEITLEHISTE PUITTAIMEDE VARJUTOLERANTSI SÕLTUVUS LEHTEDE JA LEHESTIKU STRUKTUURSETEST PARAMEETRITEST

Kokkuvõte

Käesoleva doktoritöö eesmärgiks oli uurida kohastumusi lehtede ja võra struktuursetes parameetrites, mis määravad parasvöötme heitlehiste puittaimede varjutolerantsi, s.t. võime säilitada elutegevus madalal valguse intensiivsusel. Väga mitmetes varasemates töödes on uuritud puittaimede lehtede ja lehestiku morfoloogilisi tunnuseid ja seostatud neid varjutolerantsiga. Kahjuks on valgusetingimusi sageli mõõdetud või hinnatud väga ebatäpselt (nt. ainult "valgus" ja "vari") — asjaolu, mis võib olla kirjanduses esinevate vastuolude põhjuseks. Erinevalt paljudest eelnevatest uurimustest vaadeldi käesolevas töös varjutolerantsi sõltuvust struktuursetest parameetritest alati nende tunnuste valgussõltuvuse perspektiivi kaudu. Töö esimeses osas uuriti lehtede morfoloogia ja lämmastikusisalduse sõltuvust suhtelisest kasvukoha valgustatusest ja liikidevahelisi erinevusi leheparameetrites. Teine osa tegeles lehe tasemel leitud seoste edasise uurimisega kogu taime kontekstis, samuti oli selles osas oluliseks prioriteediks puude kasvu ja vananemisega seotud varjutolerantsi muutuste selgitamine.

Osutus, et varjuliikidel võrreldes valguseliikidega oli nii madalam lehtede pindtihedus (kuivmass lehepinna kohta) kui ka väiksem lämmastikusisaldus — seega on sama lehestikumassi juures lehepind ning lehelämmastiku sama koguhulga juures lehtede mass suurem varjuliikidel. Samuti ilmnes oluline tendents lehelämmastiku investeerimiseks varjuliikidel eelkõige varjulehtedesse ja valguseliikidel valguselehtedesse.

Uurimused kogu taime tasandil kinnitasid lehtede parameetrite analüüsil püstitatud hüpoteese biomassi jaotumise kohta varju- ja valguseliikidel valguse gradiendis. Tõepoolest, varjuliikidel oli nii suhteline biomassi investeering lehtedesse kui ka kogu lehepind suurem kui valguseliikidel. Samas oli varjuliikide võrastiku arhitektoonika plastilisem kui valguseliikidel, lubades eksponeerida lehti paremini päikesekiirguse neelamiseks. Valguseliikidel kaasnes suurenenud lehepinnaga lehtede suurem omavaheline varjutamine lehestikus.

Tuginedes leitud seostele lehtede morfoloogia, lämmastikusisalduse ja biomassi jaotamise ning valguse kättesaadavuse vahel võib järeldada:

1) Varjuliikide prioriteediks on võimalikult efektiivne valguse neelamine. Selleks investeeritakse ressursse lehes eelistatult valguse neelamise pigmendisüsteemidesse ning taime tasandil eelkõige lehtedesse.

2) Valguseliikidel on prioriteediks efektiivne valguse kasutamine. Lehe tasandil investeeritakse ressursse efektiivsesse süsiniku assimileerimise aparaati, taime tasandil puitunud struktuuridesse, mis võimaldavad edukalt

konkureerida kõrgel valgusel keskkonnaressursside pärast. Loomulikult esinevad kõik üleminekud valguse- ja varjuliikide vahel.

Käesolev doktoritöö rõhutab ühe olulise puittaimede varjutaluvust mõjutava aspektina ka puude suurust ja vanust. Tehtud töö alusel saab järeldada, et puu ontogeneesi käigus muutub erinevate lehtede ja lehestiku parameetrite roll varjutolerantsis. Kui seemikutel ja noortel puudel on olulisimateks varjutolerantsi määravateks tunnusteks lehtede parameetrid, siis puude kasvades suureneb võra arhitektoonika ja biomassi jaotamise olulisus efektiivse valguse neelamise tagamisel.

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Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability

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Abstract

Leaf weight per area (LWA) and leaf size were examined in 85 species of woody plants representing 83% of Estonian native flora.

Average values of 68.6 g m^{-2} for LWA and 6.62 cm^2 for leaf size were estimated for the medium light availability. Mean LWA values can be used to correct for the bias in estimating foliage functional properties in forest stand models and for converting leaf biomass into foliage area. LWA increased with relative light availability (1 minus stand canopy cover) and species light demand, indicating that LWA was higher at the same light availability for more intolerant species. Leaf size is a canopy parameter that should be considered when canopy radiative balance and distribution of solar radiation is of interest. Mean leaf size was not so closely related to light availability as LWA, decreasing with species light demand and increasing with total plant height. Variation in leaf size is discussed in terms of species shade tolerance and height growth.

Keywords: Light availability; Leaf morphology; Leaf size; Interspecific variability; Woody plant; Shade tolerance; Tree size

1. Introduction

Comparative quantitative data sets for plant ecological parameters have gained importance as a condition for community models. However, even the best contemporary databases (e.g. Grime et al., 1988) still consist of a relatively small number of species and lack several simple parameters.

Stand physiological models are frequently based on total foliage area, and many methods to derive foliage area rapidly have been developed; these include remote sensing techniques or ordinary forest inventory methods based on crown size, stem basal area, etc. (e.g. Waring et al., 1977; Vomperskii and Utkin, 1988). However, it is difficult to obtain correct estimates for total foliage, as indirect methods (e.g. sapwood area–leaf area relationships) have been found to be species- and habitat-specific (Long and Smith, 1988). Leaf area estimation via direct biomass harvesting is considered to the most reliable technique (Jurik et al., 1985) and could be used in verifying the indirect methods. However, to convert leaf dry mass into leaf area one should

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know the mean value of leaf dry weight per area (LWA).

However, using total foliage area in stand models presumes that all units of foliage contribute equally to the whole stand carbon and water balance. The dependence of leaf structure on the prevailing light climate is well known (Björkman, 1981) and is often described in terms of sun and shade leaves (Jackson, 1967; Carpenter and Smith, 1981; Abrams and Kubiske, 1990). Leaves in the upper part of the canopy ('sun' type) have higher rates of carbon assimilation and water loss and are thus physiologically more 'active' (Woodman, 1971; Boardman, 1977; Björkman, 1981). Therefore, to characterise foliage functional effectiveness, light gradients within the canopy must be taken into account (Čermák, 1989). Čermák (1989) showed that foliage area weighted by relative irradiance (solar equivalent leaf area) eliminates the bias caused by untransformed foliage areas in stand model predictions.

It appears that LWA represents a morphological variable for assessing the functional activity of the foliage. Several quantitative studies show a linear relationship between LWA and leaf photosynthetic capacity (Linder, 1985; Jurik, 1986; Oren et al., 1986) and light availability (Jurik, 1986; Oren et al., 1986; Čermák, 1989; Kull and Niinemets, 1993). Considering this linear relationship, relative irradiance and thus also solar equivalent leaf area can be calculated using LWA values (Čermák, 1989).

$$I_x = c(\mathrm{LWA}_x - \mathrm{LWA}_{\min}) \qquad (1)$$

where I_x is relative irradiance at height x in the canopy, c is an empirical species-dependent parameter, LWA_x and $\mathrm{LWA}_{\min}$ are LWA at height x in the canopy and the theoretical minimum of LWA (LWA at zero light) respectively. However, LWA can also be influenced by site quality (Jurik, 1986), air temperature, leaf age (Oren et al., 1986), tree dimensions and age (Linder, 1985; Leuning et al., 1991; Kull and Niinemets, 1993). In order to study multispecies canopies it is important to have information on interspecific variability in LWA, and also on LWA and light intensity relationships.

Leaf size is also an important canopy parameter, affecting canopy energy balance and, owing to the penumbra effect, the distribution of solar radiation within the crown (Horn, 1971; Taylor, 1975). Leaf size varies with light conditions: leaves intercepting more solar radiation are usually smaller (Vogel, 1968). Great variability in leaf size exists in the multispecies canopy. Leaf size is reported to increase with increasing tree height (Senn et al., 1992) and to decrease with increasing crown width (King, 1991a,b). Interspecific variability in leaf size may contribute to more complete light utilisation (Horn, 1971; Barkman, 1988; Lei and Lechowicz, 1990) and more favourable energy balance (Parkhurst and Loucks, 1972; Givnish, 1987) thus being an important factor determining species shade tolerance.

Relationships between leaf morphological characteristics and light requirement of species are not satisfactorily documented. In the first approximation, shade intolerant species grow at more open sites and are mainly early successional species. In the same light environments, there exists a tendency of shade intolerant species to possess more 'sun' type leaves than tolerant species. Shade intolerant species seem to have higher LWA (Abrams and Kubiske, 1990; Kull and Niinemets, 1993) and leaf thickness (Jackson, 1967; Goulet and Bellefleur, 1986; Abrams and Kubiske, 1990). Carpenter and Smith (1981) and Lei and Lechowicz (1990), however, found a reverse trend for leaf thickness. Though LWA and leaf thickness are often correlated, they can also vary independently (Witkowski and Lamont, 1991) and therefore the relation between species shade tolerance ranking and leaf structure needs further examination.

The task of the present study was to investigate LWA, leaf size and light availability relationships, and to identify the patterns in interspecific differences in LWA, leaf size, and species light demand.

The other aim of this work was to obtain quantitative leaf characteristics for a majority of the species in a certain area, to be used in calculations of local vegetation structure and dynamics. Several authors have presented estimates for mean LWA and leaf size (Saeki and Nomoto, 1958; Chabot and Hicks, 1982; Abrams and Kubiske, 1990) for temperate zone species. However, usually the species of only one community are considered. Thus, comprehensive data sets covering most of the flora of natural woody species have so far not been available for the temperate zone.

2. Material and methods

Leaves of woody plants were collected from mid-July until early September in 1986–1988. Only fully expanded, mainly undamaged leaves showing no signs of senescence were sampled. In evergreen species current year leaves were collected. Twenty-six sampling sites were located in different natural communities in Estonia (Fig. 1) (there is no phytocoenose, where all sampled species coexist). Some species, primarily the rare ones, collected from site 20 (Fig. 1) grew in artificial communities, i.e. in the Botanical Garden of Tartu University and in parks of Tartu.

Light conditions in the study sites were characterised by visually estimated stand canopy cover (SCC) values. SCC is the relative amount of sky covered by the crowns of overstory trees. An SCC value of 1.0 corresponds to completely closed canopy and an SCC value of 0.0 corresponds to fully open habitat (canopy trees are missing). SCC was determined to the nearest 0.1, thus a relative 11 level light scale was obtained. SCC throughout the study was always estimated by the same person. Subjective under- or overestimation in different stands is largely counteracted by using only the mean values for SCC. As SCC estimates the shading of the overstory, then 1 − SCC characterises relative light availability under the canopy.

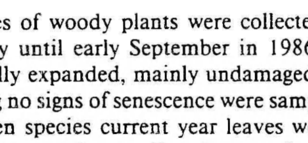

Fig. 1. Location of sample sites in Estonia. 1, Metsküla (Saaremaa); 2, Sõrve; 3, Laelatu, Puhtu; 4, Metsküla (Haapsalu); 5, Penijõe; 6, Rabavere; 7, Kastna; 8, Surju; 9, Kanaküla; 10, Tõstamaa; 11, Suure-Jaani; 12, Pikasilla; 13, Tääksi; 14, Kurgja; 15, Tooma; 16, Rõhu, Haage and Rahinge; 17, Ulila; 18, Luunja; 19, Kärevere, Ilmatsalu and Tähtvere; 20, Tartu; 21, Võõpsu.

In total, 88 taxa (85 species and three *Salix* hybrids) were analysed (Table 1). Seventy-one of the species studied (26 trees, 40 shrubs and five dwarf shrubs; 93%, 83% and 50% of the total number of the respective natural woody species) are native to Estonia and 14 (all shrubs) have been naturalised (reproduce and disperse naturally). Four species (*Andromeda polifolia*, *Juniperus communis*, *Ledum palustre* and *Taxus baccata*) are evergreens; all other species are deciduous. The taxonomical nomenclature is given by Czerepanov (1981).

One to six plants (average 3.3) of each species, mainly at the mature stage of development and under different SCC were chosen. Leaves were collected from distal branches from the south aspect, either from the upper and lower third (mainly on trees) or from the middle of the crown (mainly on shrubs and dwarf shrubs). In the first case, mean leaf parameters (Table 1) were found by averaging the values for sun (upper third) and shade (lower third) leaves. On average, 250 (50–500) leaves per sample location in a plant were analysed. A relatively large number of analysed leaves per sample was necessary in order to obtain reliable estimates for mean leaf size (Tamm and Hannus, 1977).

Leaf area was measured using an electronic-optical areameter (Automatic Areameter AAC-400, Hayashi Denkoh, Tokyo, Japan) or manually on a computer graphic tablet. In evergreens, four to six linear measures of leaf were taken and leaf area was calculated considering the leaf to consist of triangles and quadrangles of various size. Relative error of instrumentation in leaf area estimations did not exceed 5%. Only projected leaf area was used. In species with compound leaves, leaflets were considered to be functional equivalents of simple leaves, and thus

Table 1
Mean (±SE) leaf morphological parameters and characteristics of sample plants in 88 woody taxa

Species^{a}	Life form^{b}	Mean SCC	Mean plant height (m)	LWA ($g\ m^{-2}$)	ΔLWA^{c} (%)	Leaf area per leaf (S) (cm^2)	ΔS^{d} (%)	SCC for ΔLWA and ΔS^{e}
Acer platanoides (3)	T	0.70±0.06	12.7±0.7	48.2±2.8	4.8	53.7±3.4	−33.2	
Alnus glutinosa (21)	T	0.23±0.12	3.30±0.06	77.4±5.6	31.9	8.45±0.4	−32.0	
Alnus incana (16,19,21)	T	0.46±0.13	9.9±3.1	67±10	14.6	18.8±3.7	−4.2	(0.55±0.12)
Amelanchier spicata^{f} (19)	S	0.45±0.25	2.5±0.5	51±12	18.0	8.3±1.0	2.4	
Andromeda polifolia (6)	D	0.0	0.20	131.6		0.6		
Aronia melanocarpa^{f} (21)	S	0.0	1.2	107.5		7.1		
Berberis vulgaris (3)	S	0.40±0.21	1.5±0.5	76±15	4.2	2.79±0.15	18.2	(0.55±0.25)
Betula humilis (17,21)	S	0.36±0.12	1.36±0.11	81±12	20.8	3.6±1.3	25.0	
Betula nana (6)	S	0.20±0.10	0.55±0.15	107.0±0.6		0.41±0.01		
Betula pendula (16,21)	T	0.43±0.18	8.0±1.2	76±14	12.4	6.23±0.22	2.1	
Betula pubescens (16,19,21)	T	0.63±0.18	8.3±2.0	63±11	10.4	8.9±1.7	−1.1	
Cerasus vulgaris^{f} (19)	T	0.8	1.5	26.8±0.8	7.1	11.3±0.6	−15.2	
Chamaedaphne calyculata (15)	D	0.25±0.25	0.55±0.05	101.5±7.2		1.71±0.43		
Corylus avellana (3)	S	0.60±0.15	5.67±0.33	37.0±4.9	23.8	26.0±1.3	−5.1	
Cotoneaster integerrimus (20)	S	0.7	1.9	53.4±1.3	6.7	8.8±2.4	55.4	
Crataegus curvisepala (6,10)	S	0.60±0.07	2.6±1.1	88±10	15.6	2.9±0.5	−88.9	(0.5)
Crataegus monogyna (3,20)	S	0.17±0.12	4.1±2.1	110±14	12.2	4.4±2.4	11.6	(0.25±0.11)
Daphne mezereum (3)	S	0.75±0.05	0.70±0.30	30.9±4.1		5.45±0.45		
Euonymus europaea (20)	S	0.70±0.12	2.2±0.7	51±11	20.3	8.7±1.9	12.9	
Frangula alnus (19,21)	S	0.60±0.15	2.27±0.15	26.1±6.0	27.5	15.6±3.3	18.3	(0.5±0.2)
Fraxinus excelsior (3)	T	0.50±0.12	10.2±2.1	83.3±8.5	−8.4	9.3±0.8	−4.4	
Grossularia reclinata^{f} (19,21)	S	0.80±0.10	0.60±0.10	29.1±0.6		3.91±0.49		
Juniperus communis (13)	S	0.60±0.06	1.83±0.17	94.5±1.5		0.0876±0.006		
Ledum palustre (8,14)	D	0.60±0.10	0.48±0.02	73±13		0.70±0.29		
Lonicera baltica (6)	S	0.45±0.13	1.50±0.14	74.1±6.2		4.1±0.8		
Lonicera xylosteum (3,6)	S	0.63±0.22	1.27±0.15	40.1±7.8	36.1	9.67±0.38	−42.5	(0.9)
Malus domestica^{f} (16)	T	0.63±0.09	1.30±0.06	38.7±3.8	16.4	16.2±4.0	43.3	(0.70±0.07)
Malus sylvestris (6)	T	0.60±0.06	2.1±1.0	51.0±2.6	−14.4	5.1±1.3	28.2	(0.5)
Myrica gale (6)	S	0.23±0.09	1.27±0.12	97.8±4.3		1.34±0.08		
Padus avium (3,16,19)	T	0.47±0.20	8.7±2.8	39±10	5.0	13.4±1.6	−0.8	
Pentaphylloides fruticosa (20)	S	0.5	1.1	49.5±6.1	−29.8	2.56±0.1	10.4	
Physocarpus opulifolius^{f} (19,21)	S	0.55±0.05	2.65±0.35	41±13	30.4	21.5±7.1	25.5	
Populus tremula (19)	T	0.5	16.0	86.7±2.4	7.5	28.1±0.7	7.2	
Prunus spinosa (20)	S	0.50±0.15	3.3±0.6	58.4±5.6	11.8	3.6±1.3	−8.8	
Pyrus pyraster (6)	T	0.47±0.20	5.7±1.20	89±19	10.8	11.9±1.1	0.7	(0.1)
Querqus robur (3)	T	0.57±0.12	17.7±0.9	60.7±2.1	3.2	24.4±4.4	−9.9	
Rhamnus cathartica (4,6,16)	S	0.48±0.18	2.10±0.41	64±16	12.3	6.5±1.8	5.1	(0.75±0.04)
Ribes alpinum (3,16)	S	0.47±0.24	1.37±0.38	63±14	11.2	6.3±1.9	−19.2	(0.70±0.08)
Ribes nigrum (3,4,16)	S	0.53±0.22	1.50±0.25	57±16		30.7±14.6		
Ribes rubrum^{f} (16)	S	0.8	1.5	29.9±2.4	19.9	29.1±0.6	−6.4	
Ribes spicatum (16,19)	S	0.55±0.16	1.30±0.07	26.1±1.9	11.9	27.0±3.2	17.6	
Rosa caesia (3,7)	S	0.40±0.30	1.10±0.10	84±32		3.1±0.6		
Rosa canina (20)	S	0.3	1.2	94.4±4.7	−15.2	2.18±0.18	−22.4	
Rosa ciesielskii (20)	S	0.0	1.7	108.1±0.4	−1.1	2.47±0.04	4.0	
Rosa dumalis (6,20,21)	S	0.35±0.06	1.88±0.24	88.4±8.8	8.4	4.4±0.6	−36.4	(0.30±0.07)
Rosa glauca^{f} (20)	S	0.30±0.06	2.63±0.07	90.2±1.4	17.4	1.95±0.13	−20.8	
Rosa majalis (6,20)	S	0.65±0.06	1.53±0.19	51.5±4.7	1.1	3.5±0.9	47.8	

Species[a]	Life form[b]	Mean SCC	Mean plant height (m)	LWA ($g\ m^{-2}$)	ΔLWA[c] (%)	Leaf area per leaf (S) (cm^2)	ΔS[d] (%)	SCC for ΔLWA and ΔS[e]
Rosa mollis (20)	S	0.63 ± 0.12	1.70 ± 0.25	78 ± 19	0.5	4.63 ± 0.41	5.8	(0.75 ± 0.04)
Rosa rugosa[f] (19.20)	S	0.23 ± 0.09	1.50 ± 0.06	120.1 ± 9.1	6.5	3.7 ± 0.9	10.2	
Rosa spinosissima[f] (20.21)	S	0.60 ± 0.12	1.90 ± 0.25	71.7 ± 5.2	2.2	0.74 ± 0.15	24.4	
Rosa subcanina (3.4)	S	0.30 ± 0.15	1.57 ± 0.23	105.7 ± 8.1		2.5 ± 0.6	46.3	(0.5)
Rubus idaeus (16)	S	0.8	1.7	37.0 ± 2.2	−15.7	3.4 ± 0.4	−34.5	
Salix acutifolia (21)	T	0.5	10.0	56.9 ± 1.6	7.8	4.8 ± 0.4	−23.3	
Salix alba (18.19.20.21)	T	0.45 ± 0.16	13.3 ± 2.1	99 ± 12	−8.1	5.3 ± 0.7	2.0	(0.60 ± 0.05)
Salix alba × fragilis (19.20.21)	T	0.40 ± 0.06	7.5 ± 3.0	77 ± 12	−3.7	6.7 ± 1.5	−88.9	(0.35 ± 0.04)
Salix aurita (3.6.16)	S	0.37 ± 0.18	1.63 ± 0.23	83 ± 12	−15.4	3.1 ± 0.5	18.6	(0.7)
Salix aurita × cinerea (3)	S	0.4	2.0	97 ± 12	30.1	7.6 ± 2.2	57.5	
Salix caprea (3.19)	T	0.80 ± 0.06	12.8 ± 0.6	59.6 ± 5.1	12.1	13.7 ± 0.8	−18.0	
Salix cinerea (3.21)	S	0.20 ± 0.12	1.7 ± 0.6	100.2 ± 6.6	6.7	5.4 ± 1.0	10.0	(0.4)
Salix daphnoides (16.20)	T	0.47 ± 0.19	9.2 ± 2.4	94 ± 13	−8.9	5.9 ± 1.2	30.0	
Salix dasyclados (21)	S	0.37 ± 0.09	4.7 ± 0.7	93.3 ± 3.6	12.4	8.0 ± 2.0	1.2	
Salix dasyclados × phylicifolia (20)	S	0.4	3.3	111.8 ± 6.1	14.4	3.2 ± 0.7	46.3	
Salix fragilis (20)	T	0.1	1.3	113.6		4.7		
Salix lapponum (21)	S	0.37 ± 0.15	1.30 ± 0.06	103.1 ± 3.5	16.7	3.35 ± 0.45	27.1	
Salix myrsinifolia (3.6.21)	S	0.25 ± 0.12	1.6 ± 0.7	75.8 ± 9.1	10.9	3.4 ± 1.1	43.4	
Salix myrtilloides (17)	S	0.40 ± 0.06	0.33 ± 0.03	65.4 ± 4.3		0.66 ± 0.09		
Salix pentandra (8.9)	T	0.43 ± 0.15	3.0 ± 1.0	69.7 ± 7.2	9.0	9.6 ± 2.9	18.1	
Salix phylicifolia (3.8.20)	S	0.28 ± 0.11	1.48 ± 0.45	98.7 ± 7.6	6.6	4.7 ± 1.1	0.0	
Salix purpurea (11)	S	0.1	1.6	105.3		1.3		
Salix rosmarinifolia (3.21)	S	0.30 ± 0.20	1.10 ± 0.10	105 ± 34		0.74 ± 0.06		
Salix starkeana (19.21)	S	0.30 ± 0.21	0.77 ± 0.15	85 ± 11	16.9	1.85 ± 0.34	−88.8	
Salix triandra (20.21)	S	0.37 ± 0.15	3.5 ± 1.3	82.6 ± 5.9	14.2	6.6 ± 1.1	7.3	
Salix viminalis (9.12)	S	0.50 ± 0.06	3.8 ± 0.3	75.6 ± 2.2	21.7	4.6 ± 1.1	19.6	
Sambucus nigra[f] (5)	S	0.5	3.0	55.2		6.0		
Sambucus racemosa[f] (3.16)	S	0.50 ± 0.25	2.43 ± 0.47	48 ± 18	15.2	6.9 ± 1.0	13.8	(0.75 ± 0.04)
Sorbaria sorbifolia[f] (20)	S	0.63 ± 0.09	1.47 ± 0.09	40.6 ± 8.6	−13.8	14.9 ± 0.7	11.4	
Sorbus aria (2)	T	0.45 ± 0.22	1.73 ± 0.27	86 ± 29		37.8 ± 4.5		
Sorbus aucuparia (19)	T	0.30 ± 0.21	5.2 ± 1.9	66 ± 12	37.0	13.1 ± 1.2	3.0	
Sorbus intermedia (1.20)	T	0.42 ± 0.14	7.2 ± 2.3	84 ± 18	18.6	31.8 ± 2.2	8.3	(0.65 ± 0.11)
Swida sanguinea (3.6)	S	0.47 ± 0.12	1.90 ± 0.21	46.8 ± 8.8	14.1	16.6 ± 0.7	20.2	
Syringa vulgaris[f] (3.20.21)	S	0.67 ± 0.09	3.8 ± 1.1	64 ± 17	−9.8	16.5 ± 2.5	−39.1	
Taxus baccata (20)	T	0.80 ± 0.10	1.30 ± 0.10	78.1 ± 4.5	−13.5	0.50 ± 0.03	2.0	
Tilia cordata (3)	T	0.70 ± 0.10	8.0 ± 4.0	25.5 ± 2.3	18.1	26.3 ± 1.9	12.5	
Ulmus glabra (3.20)	T	0.73 ± 0.15	6.6 ± 2.8	38.5 ± 9.8	16.4	20.9 ± 3.9	13.4	
Ulmus laevis (16.20)	T	0.60 ± 0.09	11.2 ± 2.5	52.3 ± 8.1	−24.5	24.3 ± 4.6	1.8	
Vaccinium myrtillus (21)	D	0.8	0.4	40.2		1.4		
Vaccinium uliginosum (19)	D	0.50 ± 0.20	0.75 ± 0.05	57.8 ± 5.9		2.01 ± 0.29		
Viburnum opulus (3)	S	0.50 ± 0.15	3.00 ± 0.29	57 ± 15	4.2	22.2 ± 2.4	24	(0.65 ± 0.04)

[a] Numbers in parentheses refer to the sample site; see Fig. 1 for key.

[b] T, tree; S, shrub; D, dwarf shrub.

[c] $\Delta LWA = [LWA(\text{upper third}) - LWA(\text{lower third})]/LWA(\text{upper third}) \times 100$.

[d] $\Delta S = [S(\text{upper third}) - S(\text{lower third})]/S(\text{upper third}) \times 100$.

[e] Given only if mean SCC and SCC for ΔLWA and ΔS are different.

[f] Naturalised species.

their mean area was calculated. After leaf area determinations the leaves were dried at 90°C for 48 h and weighed to the nearest 0.1 mg. To clearly distinguish between total leaf area of a plant and leaf area per leaf, the latter is referred to as leaf size throughout the paper.

To compare species shade tolerance, the nine-level scale of light demand of Ellenberg et al. (1991) was used. Our species ranked from 4 to 9 (Table 1) on this scale, where the levels refer to the light demand of the plant as a percentage of full skylight: 4, 5–10%; 5, 10–20%; 6, 20–30%; 7, 30–40%; 8, 40–50%; 9, > 50%. These figures of light requirement were derived by Ellenberg et al. (1991) by measuring species sapling dispersal under different quantum flux densities in natural communities.

The difference between leaf parameters from the upper and lower third (sun-shade leaves) weighed by the values for the upper third (*Δ*LWA and *ΔS* for leaf weight per area and leaf size, respectively) was used to describe the changes in leaf structure within the crown (Table 1).

To find mean values for leaf size and LWA for Estonia the variability in mean SCC was minimised: only data for 60 species were used for which mean SCC values within the range of 0.45–0.55 were available. Variation in SCC (0.495 ± 0.034, mean ± SD) for the new sample was negligible, when compared with that of the former sample (0.47 ± 0.19). Linear correlation and regression techniques were used in data processing. LWA and leaf size for sun and shade leaves were compared using Student's *t*-test. All statistical relationships were considered significant at $P<0.05$. Leaf area (S, cm^2) and total plant height (H, m) showed strongly skewed distribution and therefore were transformed before statistical analysis using natural logarithmic transformation (log*S*, log*H*).

3. Results

Mean LWA, *Δ*LWA, leaf size, *ΔS*, SCC and total plant height for all species are presented in Table 1. Significant negative correlation occurs between mean cover and species light demand ($r^2=0.317$, $P<0.001$).

Mean LWA for all species pooled increased significantly with increasing mean $1-\mathrm{SCC}$ ($r^2=0.631$, $P<0.0001$) and species light demand ($r^2=0.306$, $P<0.001$) (Fig. 2). Thus, the less shade-tolerant the species, the higher was LWA at the same canopy cover. There was no correlation between mean LWA and mean plant height. Owing to the great interspecific variability in the absolute values of LWA, mean LWA for the upper and lower third was not significantly different. However, within species there was a tendency for LWA to be higher in leaves from the upper third than from the lower third (*Δ*LWA was greater than zero in 53 out of 67 cases; Table 1).

The log mean leaf size (log*S*) increased with log plant height (log*H*) ($r^2=0.231$, $P<0.001$) and decreased with species light demand ($r^2=0.252$, $P<0.001$) (Fig. 3). There was also a significant trend of log*S* to decrease with $1-\mathrm{SCC}$ ($r^2=0.095$, $P<0.01$). The means of log*S* for sun and shade leaves were not significantly different; however, *S* was greater than zero in 44 out of 68 cases. *Δ*LWA and *ΔS* were independent of SCC, tree height and light demand.

For site comparisons, mean values for 60 species (SCC=0.45–0.55) for LWA of 68.6 ± 2.7 g m^{-2} and mean leaf size of 6.62 cm^2 (antilogarithm of the mean log*S*) were found.

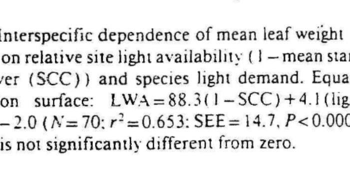

Fig. 2. Interspecific dependence of mean leaf weight (LWA, g m^{-2}) on relative site light availability (1 – mean stand canopy cover (SCC)) and species light demand. Equation of regression surface: $\mathrm{LWA}=88.3(1-\mathrm{SCC})+4.1(\text{light demand})-2.0$ ($N=70$; $r^2=0.653$; SEE = 14.7, $P<0.0001$). Intercept is not significantly different from zero.

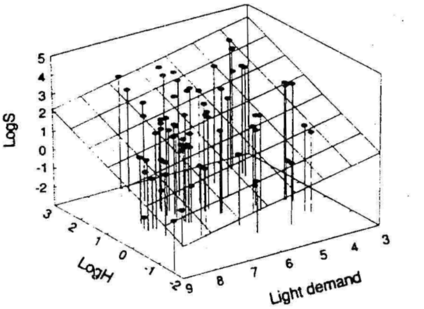

Fig. 3. Effect of species light demand and the logarithm of plant height (log*H*) on mean logarithm of leaf area (log*S*). Equation of regression line: $\log S = -0.36(\text{light demand}) + 0.69 \times \log H + 3.34$ ($N = 70$; $r^2 = 0.536$; SEE = 0.87, $P < 0.0001$). Every point represents a species.

4. Discussion

1 – SCC is a gap-area based estimate of relative light availability. In the case of visual estimation, the total gap area is not weighted with respect to zenith angle and this could result in bias. However, it has been shown that a very strong linear relationship exists between diffuse site factor (relative amount of diffuse solar radiation measured by hemispherical photographic technique) (Anderson, 1964) calculated for weighted gap area (a_d) and for total gap area (a_s) ($r^2 = 0.997$, $P < 0.00001$, $a_s = 0.987 \times a_d$; Ü. Niinemets, unpublished data, 1992).

The result that variation in SCC was a more important factor than species light demand in determining the LWA value (Fig. 2) was surprising. At a light demand value of 5, a LWA change from 18.5 to 106.8 g m^{-2} with the change in SCC from 1 to 0 is expected (Fig. 2). Hutchinson et al. (1986) found also little interspecific variability in the LWA–relative crown height relationship in the canopy of *Acer rubrum*, *Quercus alba* and *Quercus prinus*. Nevertheless, this study also shows that interspecific variability in LWA could not be excluded from the canopy analyses, especially at low SCC values. For instance, at an SCC value of 0, an approximate three-fold change in LWA (from 10.3 to 34.9 g m^{-2}) with the change in species light demand from 3 to 9 is expected; at an SCC value of 5, considerable differences in LWA (from 54.5 to 74.9 g m^{-2} for the same variation in light demand) are still predicted (Fig. 2). Significant correlation between mean SCC and light demand means that shade tolerant species had higher, and intolerant species lower, SCC values (Table 1). Species distribution along the SCC gradient in Table 1 is therefore close to the species dispersal in natural communities and the values of mean LWA and leaf size are thus representative of the conditions of probable species dispersal.

Attempts have been made to estimate species shade tolerance on the basis of LWA values (Jurik, 1986). Shade intolerant species had higher LWA in the understory than tolerant ones (Abrams and Kubiske, 1990). *Acer saccharum* (intolerant) had higher LWA in shade than *Acer pensylvanicum* and *Acer spicatum* (shade intolerant) (Lei and Lechowicz, 1990). *Liriodendron tulipifera* and *Acer rubrum* (intolerant) had greater LWA values than *Cornus florida* (tolerant) in understory (Wallace and Dunn, 1980). Popma and Bongers (1988) reported that gap-dependent species had greater LWA than shade tolerant species. The significant increase in LWA with increasing species light requirement (Fig. 2) in our study is also concordant with this idea.

Usually a three-level shade tolerance scale (tolerant, medium, intolerant) is used in studies of woody plants (e.g. Jackson, 1967; Carpenter and Smith, 1981; Abrams and Kubiske, 1990). The light demand figures of Ellenberg et al. (1991) allow species comparisons to be carried out between herbaceous and woody vegetation as well. The woody species observed in this study were relatively shade intolerant according to this scale, as their light demand was ⩾4. However, the use of these light demand figures relies on the following assumptions: (1) light demand of woody species in central Europe and in Estonia does not differ; (2) light demand does not depend on the developmental stage of woody species. The second assumption, at least, does not seem to correspond to reality as Yevstigneyev (1990) found that shade tolerance decreases dramatically in the ontogeny of different woody species. Leaf thickness and LWA have also been found to increase with tree age or increasing dimensions (Malkina, 1982, 1983; Linder, 1985; Leuning et al., 1991; Kull and Niinemets, 1993). However, Yevstigneyev (1990) did not find any change in species shade tolerance ranking with increasing tree age.

For calculating mean solar equivalent leaf area proposed by Čermák (1989), values for the species-specific parameters c and $\mathrm{LWA_{min}}$ are required (Eq. (1)). Instead of using the theoretical minimum for $\mathrm{LWA_{min}}$ at zero light, LWA values for the leaves growing in deep shade can be used (Čermák, 1989). Thus, after measurement of $\mathrm{LWA_{min}}$, c can be calculated

$$c=\frac{I_m}{\mathrm{LWA}_{I_m}-\mathrm{LWA_{min}}} \qquad (2)$$

where LWA_{I_m} and I_m are mean LWA and corresponding 1 − SCC values (Table 1).

Leaf size seems to be more species-specific (weaker correlation with SCC) than LWA which is significantly light dependent. The decrease in leaf size with increasing species light demand (Fig. 3) seems to be an adaptive feature as effective leaf size (mean width of a leaf or its lobes or leaflets) determines the boundary layer conductance of a leaf (Vogel, 1968; Parkhurst and Loucks, 1972; Taylor, 1975) affecting leaf convective heat exchange, carbon exchange and water loss. Smaller leaves at sunny habitats are expected to have lower leaf temperatures at the same radiation loads, thus avoiding overheating. However, at temperatures below the photosynthetic temperature maximum, higher leaf temperatures can speed up the enzymatic reactions of photosynthesis and thus increase the rates of carbon uptake (Givnish, 1987). This makes it difficult to predict the optimal leaf size for given incident radiation loads. Horn (1971), comparing sun and shade plants, proposed that shade intolerant species may be expected to possess smaller leaves than tolerant ones. Small leaves enable the plant to increase light-saturated leaf area and thus to take advantage of the penumbra effect. However, owing to penumbra, small leaves do not cast deep shade and thus the small-leaved canopy is open to invasion. Moreover, it has been reported that large leaves in shady habitats are advantageous in capturing sunflecks (Horn, 1971).

Additionally, leaf size was found to depend on mean plant height (Fig. 3). Similarly, leaf size increased in *Betula pubescens* ssp. *tortuosa* with increasing tree height (Senn et al., 1992). However, it is not clear if this finding is an artefact of the dataset including partly hybrid species such as *Betula nana* × *B. pubescens*, higher vitality of larger trees or an universal allometric relationship. Leaf size has shown to decrease with increasing crown width in several young woody species, but this tendency was not evident for mature plants (King, 1991a,b). Givnish (1979) proposed that a larger leaf could be beneficial in terms of leaf support, because for the same total foliage area less woody supporting branches are necessary and thus more fixed carbon could be invested into stem growth. This kind of compensatory mechanism may become even more significant with increasing plant size. Whittaker and Woodwell (1967) have reported stem and branch surface to increase more rapidly than leaf area with increasing tree size and proposed that the relation between leaf and wood surface area may limit tree size.

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Variations in leaf morphometry and nitrogen concentration in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L.

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Summary

Relations between leaf dry weight to leaf area (LWA), leaf nitrogen concentration and irradiance inside a natural canopy were studied in *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L. In all species, LWA increased with increasing irradiance. Relative variability in LWA was smaller in *Betula pendula* than in the other two species. In *Corylus avellana*, LWA also depended on total plant height. Foliar nitrogen concentration (on a dry weight basis) increased with increasing irradiance and LWA in *Betula pendula*, but decreased in the other two species. The interspecific variation in response to light availability and in nitrogen partitioning may be caused by different light demands or different life forms (trees versus shrubs), or both, of the species examined, and must be considered in contemporary canopy models.

Keywords: canopy irradiance, leaf area, leaf dry weight, life forms, light availability, LWA, nitrogen partitioning, shade tolerance, SLA.

Introduction

When modelling photosynthesis of the forest canopy it is important to consider the light environment inside the canopy as well as the light-related modifications in structure and function of the individual trees. Qualitative changes in leaf morphology and functioning are well known (e.g., Ludlow 1983, Čermák 1989), but quantitative changes have been less well studied. An understanding of the quantitative relationships in leaf–light modifications is necessary to simulate the dynamics of canopy processes.

To characterize leaf morphology, the ratio of leaf dry weight to leaf area (LWA) is widely used (also known as surface leaf weight (SLW)). The reciprocal of LWA, specific leaf area (SLA), has also often been used. Qualitative modifications in LWA in response to prevailing light conditions are well known, but only a few quantitative investigations have been made (e.g., Drew and Ferrell 1977, Del Rio and Berg 1979, Jurik 1986). Because LWA is usually less in shade-tolerant plants than in shade-intolerant species (Lee et al. 1990), attempts have been made to assess the light demand of a species on the basis of its LWA value (Jurik 1986). However, LWA can also be influenced by site quality (Jurik 1986), air temperature and leaf age (Oren et al. 1986) and tree dimensions and age (Linder 1985). The quantitative relationship between LWA and environmental conditions is of interest because studies have shown close relationships between LWA and the photosynthetic production of leaves (Linder and

Rook 1984, Oren et al. 1986). This relationship arises because both LWA and photosynthesis depend on the prevailing light environment at the leaf. The relationship between LWA and photosynthetic production may be altered by nitrogen availability and by the nitrogen distribution pattern in the canopy because the photosynthetic capacity of leaves depends on their nitrogen content (Field et al. 1983, Linder and Rook 1984, Hirose and Kitajima 1986, Küppers et al. 1988).

At the whole-plant level, the pattern of nitrogen distribution corresponds to the allocation of assimilates among plant organs (Ågren and Ingestad 1987, Levin et al. 1989, van Keulen et al. 1989). The vertical distribution of nitrogen inside an artificial perennial canopy has been studied (Hirose and Werger 1987), but little is known about the distribution of nitrogen in forest canopies, and there are no data sets available where LWA, leaf nitrogen concentration and the light environment of leaves in the forest canopy have been measured simultaneously.

The aim of the present study was to determine whether there are relationships among light environment, leaf nitrogen concentration and LWA, and to examine whether these relationships are species dependent.

Material and methods

The study was undertaken in the nemoral mixed spruce forest at Voore Ecological Station, Estonia in August 1989. The forest is located on a plateau-like crest of a drumlin with brown pseudopodzolic soil. A detailed description of the study site has been given by Frey (1977). Fully expanded leaves were taken mainly from understory individuals of *Betula pendula* Roth., *Corylus avellana* L. and *Lonicera xylosteum* L., with different exposures to light. When possible, samples were taken from several positions in the crown. These species have different light demands. *Betula pendula* is a typical pioneer tree species on fertile sites, which grows up to 35 m high (the height range of the sampled trees was 0.4–8 m), and has a light figure of 4 according to Landolt (1977), which signifies that it is a species occuring chiefly in full light, although sometimes surviving in slight shade. *Corylus avellana* grows to a height of 5 m and is mainly an understory shrub, but it may grow in full sunlight in clearings. Its light figure according to Landolt (1977) is 3, which signifies that it is a species chiefly occuring in shade, but rarely in less than 10% of full sunlight. *Lonicera xylosteum* is an understory shrub, with a maximum height of 2 m, and grows rarely in sunny habitats. Its light figure is also 3 (Landolt 1977), but it seems that in our conditions it may tolerate deeper shade than *C. avellana*.

At every location where sample leaves were collected, irradiance was measured by the hemispherical ("fish-eye") photographic technique (Anderson 1964). From every photograph of the sampling location the relative amounts of canopy gaps were measured with respect to zenith angle, and the diffuse site factor, a_d (relative amount of diffuse solar radiation to horizontal surface), was calculated. No correction for possible differences in direct solar radiation was made. An a_d value of 1 corresponds to full sunlight and an a_d value of 0 corresponds to complete shade.

Four to seven leaves from each sampling location were taken for LWA measurements and three to five additional leaves were collected for nitrogen analysis. The numbers of sampling locations were 26 for *B. pendula*, 27 for *C. avellana* and 33 for *L. xylosteum*. Plant height and sampling height were measured. The area of the leaves was measured manually on a computer graphic tablet. Dry weight was determined after drying the leaves at 85 °C for 48 h. Total nitrogen content was measured by standard Kjeldahl method and nitrogen concentrations were calculated on a mass base (N_m) and on an area base (N_s).

Results

Correlation analysis of the data showed that there were significant correlations between LWA, a_d, N_m and N_s for all of the species (Table 1). Plant height and sampling height (data not shown) were not significantly correlated with LWA, a_d, N_m or N_s, except in *L. xylosteum*, where sampling height was significantly correlated with LWA and N_s.

Table 2 shows mean, maximum and minimum values of LWA and simple linear regression analysis of LWA on relative irradiance for each species. All parameters

Table 1. Correlation coefficients between measured values of leaf weight per area (LWA), relative light (a_d) and leaf nitrogen concentration per dry weight (N_m) and per surface area (N_s).

	N_s	N_m	a_d
B. pendula			
LWA	0.948*	0.516**	0.792*
a_d	0.831*	0.792*	
N_m	0.750*		
C. avellana			
LWA	0.919*	−0.612*	0.893*
a_d	0.850*	−0.427***	
N_m	−0.283		
L. xylosteum			
LWA	0.919*	−0.634*	0.890*
a_d	0.833*	−0.487**	
N_m	−0.293		

* = $P < 0.001$, ** = $P < 0.01$, *** = $P < 0.05$.

Table 2. Simple linear regression analysis of leaf weight per area (LWA) versus relative light (a_d).

Species	LWA ($g\ m^{-2}$)			Parameters of regression equation		
	Mean	Maximum	Minimum	Intercepts ± SE	Slopes ± SE	r^2
B. pendula	56.9	86.1	34.9	39.7* ± 3.4	42.4* ± 6.7	0.628
C. avellana	42.3	88.4	22.7	16.7* ± 3.0	72.7* ± 7.3	0.798
L. xylosteum	39.8	84.1	22.6	16.9* ± 2.5	85.2* ± 7.8	0.792

* = $P < 0.001$.

for *B. pendula*, except the maximum value of LWA, differed significantly from the other species. The regression line for the relationship LWA–a_d for *B. pendula* had a higher intercept and lower slope than the regression lines for *C. avellana* and *L. xylosteum*.

For all three species, multiple regression analysis showed a tendency for LWA to depend not only on irradiance, but also on the height of the sampled tree. But only for *C. avellana* did the two-dimensional analysis yield significant parameters for the regression equation: LWA = $c_0 + c_1 a_d + c_2 H$ (Figure 1), where H is plant height.

Nitrogen concentration expressed per leaf area (N_s) was highly and positively correlated with both a_d and LWA in all species (Table 1). Nitrogen concentration expressed per leaf dry weight (N_m) was also correlated with a_d and LWA. This correlation was positive in the tree *B. pendula*, but negative in the shrubs *C. avellana* and *L. xylosteum* (Figure 2). The plot of N_m versus LWA (Figures 2B, 2D and 2F) can be derived from the plot of N_s versus LWA (Figures 2A, 2C and 2E), because $N_m = N_s/\mathrm{LWA}$. If it is assumed that a linear relationship exists between N_s and LWA:

$$N_s = c_3 + c_4\,\mathrm{LWA}, \tag{1}$$

then

$$N_m = c_4 + c_3/\mathrm{LWA}, \tag{2}$$

that is, the relationship between N_m and LWA represents a hyperbola. Whether this hyperbola (Equation 2) is decreasing or increasing depends on the sign of the intercept value c_3 in Equation 1. Linear regression coefficients for Equation 1 are

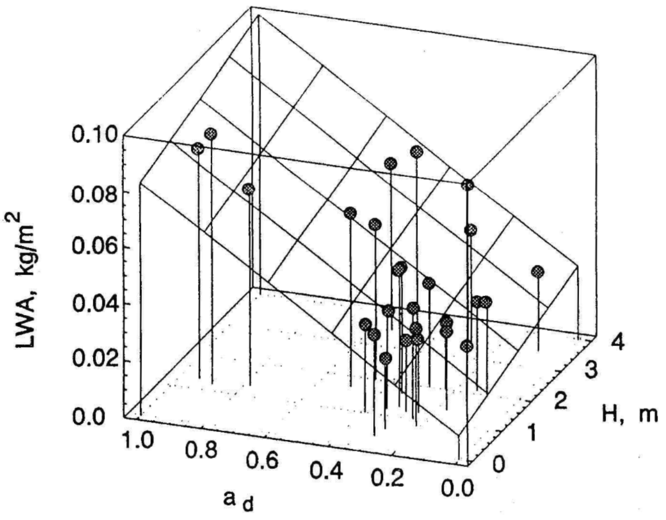

Figure 1. Three dimensional regression of LWA on relative light (a_d) and height of sampled tree (H). Regression equation: LWA = $0.0086 + 0.074a_d + 0.0043H$.

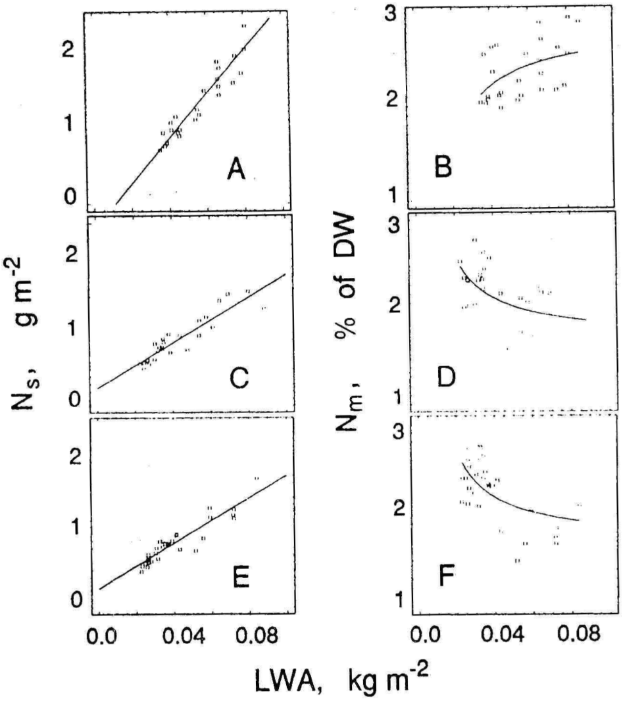

Figure 2. Dependence of leaf nitrogen concentration expressed on a leaf area base (A, C and E) and on a leaf mass base (B, D and F) in *Betula pendula* (A and B), *Corylus avellana* (C and D) and *Lonicera xylosteum* (E and F).

given in Table 3. These coefficients were used to fit hyperbolas to Figures 2B, 2D and 2F. The similarity in the regression coefficients for the shrubs *C. avellana* and *L. xylosteum* is notable (Table 3).

Table 3. Simple linear regression analysis of leaf nitrogen concentration per surface area (N_s, g m^{-2}) versus leaf weight per area (LWA, kg m^{-2}).

Species	Intercept ± SE	Slope ± SE	r^2
B. pendula	−0.33 ± 0.02	30.1 ± 2.1	0.899
C. avellana	0.24 ± 0.06	15.5 ± 1.3	0.844
L. xylosteum	0.25 ± 0.05	15.5 ± 1.2	0.844

Discussion

Leaf weight per area (LWA)

Much of the variation in LWA in the species examined was accounted for by the light environment of the leaves. A comparison of the LWA–a_d relationships in the three species indicated that, although the three species had similar LWA values at full sunlight, *B. pendula*, which is the most shade-intolerant of the three species, differed from the other species in two ways. First, its LWA varied less in response to variations in irradiance, as indicated by the shallow slope of the regression line, than the LWAs of the other two species. Second, *B. pendula* had a higher minimum value of LWA, as indicated by the higher intercept on the regression line, than either *C. avellana* or *L. xylosteum.* Our data support Jurik's conclusion (Jurik 1986) that shade-tolerant species have a lower LWA (Jurik 1986) as a result of higher variability in LWA and lower average irradiance than shade-intolerant species. If it is assumed that the intercept value (Table 2) characterizes the amount of nonphotosynthetic supporting tissue of leaves, because it represents that part of the leaf mass that does not depend on irradiance, then the leaves of the shade-intolerant species, *B. pendula*, had about twice as much supporting tissue as the leaves of the shade-tolerant species *C. avellana* and *L. xylosteum*.

The value of LWA increased with increasing tree height, as indicated by the higher intercept on the LWA axis in Figure 1, although this effect was only statistically significant for *C. avellana*. It seems that leaves of tall trees have relatively more supporting tissue than leaves of small trees. This may be explained by the need to survive water deficits and lower water potentials, which are more severe in the crowns of tall trees. It also means that the carbon requirement for the formation of leaves must be larger in large trees, because it takes more assimilates to produce leaves with the same amount of photosynthetic tissue as in small trees. Our results indicate that the relative variability of LWA decreases in response to variations in irradiance as the amount of supporting tissue increases. An analogous decrease in plasticity of the photosynthetic apparatus of tall trees has been observed in *Picea abies* (Kull and Koppel 1987). Few data have been reported on the dependence of LWA or SLA on tree dimensions. One exception has been noted by Linder (1985), who reported that, in *Eucalyptus* species, average SLA decreased with increasing tree age. If it is assumed that tree age and tree dimensions are related measures, the same conclusion can be drawn from the data in Figure 1.

Distribution of nitrogen

A high correlation between leaf nitrogen concentration expressed on a surface area basis (N_s) and irradiance or leaf weight per area (LWA) has been observed in many species. For example, strong positive correlations between irradiance and N_s have been found in *Solidago altissima* (Hirose and Werger 1987) and *Carex acutiformis* (Hirose et al. 1989), and a high positive correlation between LWA and N_s has been found in *Prunus persica* (DeJong and Doyle 1985). In general, LWA is positively correlated with irradiance. An exception is *Carex acutiformis*, which has erect leaves with a lower LWA in the upper part of the canopy than in the lower part of the canopy (Hirose et al. 1989).

Among species, the relationship between LWA and leaf nitrogen concentration expressed on a dry weight basis (N_m) differs. Nitrogen concentration, N_m, increased with increasing LWA in a dense stand of *Lysimachia vulgaris* (Hirose et al. 1988) but decreased in *Polygonum cuspidatum* (Hirose 1986). Recalculation of data published by DeJong and Doyle (1985) showed that, in *Prunus persica*, N_m is less in leaves with high LWA than in leaves with low LWA, as was the case in *C. avellana* and *L. xylosteum* in our study. A qualitative difference in the N_m–a_d relationships in tree crowns also exists. Mass-concentration of nitrogen is higher in one-year-old shoots of *Picea abies* in the fourth whorl than in shoots in the first whorl (Aldinger 1987). In *Pinus radiata*, N_m decreases from the top of the crown to the base (Kelly and Lambert 1972). As spruce is more shade tolerant than pine, these observations support the conclusion that differences in nitrogen distribution between *B. pendula* and the other two species were caused by the different light demands of these species.

Many physiological processes in plants are closely correlated with nitrogen concentration per dry weight. The most important of these processes are photosynthesis (Linder and Rook 1984, Küppers et al. 1988), growth (Ågren and Ingestad 1987, van Keulen et al. 1989) and allocation of assimilates among plant organs (Ågren and Ingestad 1987, Levin et al. 1989). Consequently, the tree species, *B. pendula*, which has a maximum leaf nitrogen concentration in full sunlight, exhibited maximum photosynthesis and growth in the upper part of the crown, with minimum export of assimilates. In the shrubs, *C. avellana* and *L. xylosteum*, the most active region was located in the lower part of the crown. These findings explain the different life forms of the species studied but not their different light demands.

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Distribution of foliar carbon and nitrogen across the canopy of *Fagus sylvatica*: adaptation to a vertical light gradient

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Abstract

Distribution of foliar carbon and nitrogen was studied across a vertical light gradient in the natural canopy of *Fagus sylvatica*. Leaf dry and fresh weight per area (LWA and LWA$_w$, respectively) increased linearly with diffuse site factor (a_d, relative irradiance). Tree size, independent of a_d, was another determinant of leaf morphology, and both LWA and LWA$_w$ increased with increasing tree dimensions. A positive linear relationship between a_d and the content of total non-structural carbohydrates per leaf dry weight (TNC, the sum of ethanol-soluble carbohydrates and starch) was found, presumably caused by higher photosynthetic production of leaves at greater irradiance. Therefore, to account for confounding variation in TNC with irradiance, it may be necessary in studies on light-related modifications in leaf structure to express the content of leaf constituents on the basis of TNC-free dry weight instead of total dry weight. Total leaf carbon content per dry weight and a_d were not correlated, however, leaf carbon content, corrected for changes in TNC with a_d, increased significantly with relative light availability, suggesting increasing investment of leaf carbon for mechanical support. Leaf water content decreased with a_d, probably due to a less favourable water balance of leaves at higher canopy heights.

Leaf nitrogen content per dry weight (N$_m$) decreased with increasing irradiance. If nitrogen content was expressed on the basis of TNC-free dry weight, the relationship became more scattered, though the qualitative tendency remained. No correlation between leaf nitrogen and TNC, considered as an estimate of daily photosynthetic production, was found, and it was suggested that increasing N$_m$ at decreasing values of a_d was invested for more efficient light harvesting, representing a strategy of nitrogen partitioning inherent to shade-tolerant plants. Because a considerable fraction of leaf magnesium is contained in chlorophyll, decreasing leaf magnesium content, expressed both on total and TNC-free dry weight, with increasing a_d, and a linear relationship between the contents of leaf nitrogen and magnesium, provide additional evidence for the partitioning of foliar nitrogen towards enhanced light capture with decreasing irradiance.

Keywords: Carbon content, irradiance, leaf morphology, magnesium content, nitrogen content, non-structural carbohydrates, nutrient distribution, shade-tolerance, tree dimensions.

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Résumé

La distribution du carbone et de l'azote foliaires a été étudiée au long d'un gradient de lumière vertical dans la canopée naturelle de *Fagus sylvatica*. Les poids sec et frais des feuilles par surface (LWA et LWA_w, respectivement) croissent linéairement avec un facteur de site diffus (a_d, flux radiatif relatif). La taille des arbres, indépendamment de a_d, est un autre déterminant de la morphologie des feuilles, et LWA aussi bien que LWA_w augmentent avec l'accroissement de la taille des arbres. On a trouvé une relation linéaire positive entre a_d et la concentration en hydrates de carbone non-structuraux totaux (TNC, la somme d'hydrates de carbone et d'amidon solubles à l'éthanol), probablement due à une production photosynthétique des feuilles plus élevée à un flux radiatif plus grand. Par conséquent, pour rendre compte de la variation du TNC avec le flux radiatif, il peut être nécessaire, dans les études sur les modifications de la structure des feuilles liées à la lumière, d'exprimer le contenu des constituants de la feuille sur la base d'un poids sec sans TNC plutôt que d'un poids sec total. Le contenu total des feuilles en carbone par poids sec et a_d ne sont pas corrélés; cependant, le contenu des feuilles en carbone, corrigé pour les changements du TNC avec a_d, augmente significativement avec la disponibilité relative de la lumière, ce qui suggère un investissement accru en carbone foliaire dans le tissu de soutien. Le contenu en eau des feuilles décroît avec a_d, en raison probablement d'un bilan hydrique des feuilles moins favorable à des hauteurs de canopée plus élevées.

Le contenu en azote des feuilles par poids sec (N_m) décroît avec l'accroissement du flux radiatif. Si le contenu en azote est exprimé sur la base du poids sec sans TNC, la relation devient moins étroite, bien que la tendance qualitative persiste. On n'a trouvé aucune corrélation entre l'azote foliaire et le TNC, considéré comme une estimation de la production photosynthétique journalière; il est suggéré que N_m, croissant à des valeurs décroissantes de a_d, est investi pour capter la lumière plus efficacement, ce qui représente une stratégie d'allocation de l'azote inhérente aux plantes d'ombre. Étant donné qu'une part considérable du magnésium foliaire est contenue dans la chlorophylle, la baisse du contenu en magnésium des feuilles, exprimé aussi bien sur le poids sec total que sans TNC, avec l'augmentation de a_d, ainsi qu'une relation linéaire entre les contenus en azote et en magnésium des feuilles, apportent une preuve supplémentaire de l'allocation de l'azote foliaire tendant à augmenter l'interception de la lumière lorsque le flux radiatif diminue.

INTRODUCTION

To assess whole canopy carbon gain, expensive time-consuming measurements of spatial distributions of foliage area and photosynthetic properties, of costs for construction and maintenance of leaves as well as of environmental gradients within the canopy are necessary. However, since leaves adapt to long-term differences in light availability (Björkman, 1981; Lichtenthaler, 1981; Lichtenthaler *et al.*, 1981), diverse canopy attributes may be derived from more easily attainable parameters which are linked to inherent vertical light gradients across the canopy. Moreover, leaf structure may even serve as an indicator of relative irradiance within the canopy (Čermák, 1989). Thus, knowledge of quantitative relationships between foliage architecture, composition and light availability may contribute to more advanced indirect estimations of stand carbon balance.

Leaf dry weight per area, LWA, increasing linearly with increasing growth irradiance (Gulmon & Chu, 1981; Jurik, 1986; Oren *et al.*, 1986; Čermák, 1989; Kull & Niinemets, 1993; Niinemets & Kull, 1995), has repeatedly been used to characterise leaf structure quantitatively. Larger LWA in more ample light environments, though manifesting increasing biomass costs for producing unit leaf area, indicates the investment of plant resources preferably where the photosynthetic returns due to greater irradiance are the highest (Gutschick & Wiegel, 1988), and often a strong positive correlation between LWA and leaf photosynthetic capacity, *i.e.* photosynthesis at light saturation, per leaf area ($P^a_{\max}$) exists there (PEARCE *et al.*, 1969; BJÖRKMAN, 1981; JURIK, 1986; OREN *et al.*, 1986). If the chemical composition of leaves, based on leaf dry weight, were constant along a light gradient, a positive proportional relationship between $P^a_{\max}$ and LWA is expected, because $P^a_{\max} = P^m_{\max} \star \mathrm{LWA}$ ($P^m_{\max}$ is the photosynthetic capacity per leaf dry weight). Therefore, any shift in leaf composition is likely to change the fractions of leaf dry matter which are partitioned to assimilative and non-assimilative compounds, and consequently $P^m_{\max}$. In fact, modifications in the stoichiometry of leaf constituents, including carbohydrates (JELMINI & NÖSBERGER, 1978; FJELD, 1992*b*), lignin (KAUSCH & HAAS, 1966), lipids (KAUSCH & HAAS, 1965) and total nitrogen (ELLSWORTH & REICH, 1992; KULL & NIINEMETS, 1993), with respect to prevailing light conditions are documented. The highest diurnal variation of leaf substances, caused by diurnally varying photosynthetic production (SERVAITES *et al.*, 1989) and translocation of leaf carbon (HENDRIX & HUBER, 1986), exhibits the content of non-structural carbohydrates (NSC) (PLHÁK, 1984). In several species NSC increases also with increasing growth irradiance (JELMINI & NÖSBERGER, 1978; FJELD, 1992*a*, *b*). Accordingly, both in short- and long-term, the variation in NSC, implying a differential dilution effect on other leaf compounds, may affect LWA *vs.* light and LWA *vs.* $P^a_{\max}$ relationships.

Taking advantage of frequently occurring positive correlations between N_m (leaf nitrogen content per leaf dry weight) and $P^m_{\max}$ (FIELD & MOONEY, 1986), and N_a (nitrogen content per leaf area) and $P^a_{\max}$ (FIELD & MOONEY, 1986; EVANS, 1989), availability and spatial variability of nitrogen play a key role in a number of model assessments of stand carbon balance (e.g. SINCLAIR, 1991). Furthermore, differences in nitrogen content per area across the canopy closely parallel light-related changes in LWA, leading to a highly significant relationship between N_a and LWA (ELLSWORTH & REICH, 1993; KULL & NIINEMETS, 1993):

$$N_a = C_1 \star \mathrm{LWA} + C_2, \tag{1}$$

where C_1 and C_2 are empirical species specific coefficients. Frequently, a change in LWA with irradiance is the major determinant of the positive relationships between N_a and LWA, since $N_a = N_m \star \mathrm{LWA}$, and even for invariable N_m, N_a increases linearly with LWA and irradiance. However, N_m, equal to:

$$N_m = C_1 + \frac{C_2}{\mathrm{LWA}}, \tag{2}$$

is usually not constant, exhibiting variation patterns qualitatively differing between the species. The intercept of the N_a *vs.* LWA relationship, C_2 (Eq. 1), determines if the hyperbola relating N_m to LWA (Eq. 2) is decreasing or increasing with LWA or if N_m is independent of LWA (KULL & NIINEMETS, 1993). N_m increased with LWA in *Betula pendula* (KULL & NIINEMETS, 1993) but decreased in *Acer saccharum* (ELLSWORTH & REICH, 1992), *Borojoa patinoi* (LYNCH & GONZÁLEZ, 1993), *Corylus avellana* and *Lonicera xylosteum* (KULL & NIINEMETS, 1993). In *Pinus radiata* (KELLY & LAMBERT, 1972) and *Eucalyptus grandis* (LEUNING *et al.*, 1991), N_m decreased from the top towards the crown base. Since all species attaining the highest N_m

values in shade are shade-tolerant, qualitatively different distributions of foliar nitrogen and photosynthetic production within the canopy may be linked to species shade-tolerance.

The aim of this paper was to study the variation in the contents of leaf carbon and nitrogen in the shade-tolerant species *Fagus sylvatica* L., expected to have a decreasing N_m with increasing irradiance. As both C_1 and C_2 are likely to be influenced by a differential effect of NSC on LWA, being larger at higher irradiances and less in lower irradiances, the variabilities in leaf carbon and nitrogen were studied simultaneously, and the alterations of N_m and LWA by NSC were quantified. To achieve a better understanding of the partitioning of leaf carbon and nitrogen between different compartments within the leaf, variation in leaf calcium, mainly present in cell walls (Demarty *et al.*, 1984) and considered to give an estimate of the carbon in cell walls, and in magnesium, often correlated with leaf chlorophyll content (Schulze & Küppers, 1985; Wedler, 1991) and assumed to measure nitrogen investment in light-harvesting proteins and chlorophyll, were also included in the analysis.

MATERIALS AND METHODS

Site description and leaf sampling

The study was accomplished in a small (0.02 ha) naturally regenerated patch of *Fagus sylvatica* in a forest dominated by *Picea abies* (L.) karst. at Oberwarmensteinach (49°59′ N, 11°47′ E; elevation ca. 760 m above sea level), Fichtelgebirge, Germany in the middle of September 1991. The stand is located on a plateau-like crest of a hill with podzolic and brown pseudopodzolic soils formed on phyllite. Spruce trees surrounding the beech site were about 100 years old, the maximal age of beech trees reached 45 years. A detailed description of the research area is given by Hantschel (1987) and Oren *et al.* (1988).

Leaves at terminal branch positions in the canopy were taken from the south aspect of seven variously-exposed beech trees. Total height of sampled trees ranged from 3.6 to 15.2 m and age from 15 to 42 years (at 1.3 m). To ensure sampling along a vertical light gradient, leaves were collected at different canopy heights (two to four locations per tree). Five to nine leaves per sample location were analysed and means for all leaves per sampling location calculated. All leaf samples were taken within one afternoon hour (between 15.00 and 16.00 p.m.) on the 23rd September, immediately placed on ice, brought to the laboratory and stored at – 18 °C until use. At the sampling date the beech trees possessed no marks of foliar senescence, and a control experiment showed that leaf structural parameters and leaf chemical composition were stable, rapid senescing of leaves starting about two weeks later. Four increment cores at 1.3 m (south, north, west, east) were taken and tree age was estimated. Proportions of sap- and heartwood were determined immediately by differential translucence method (Münster-Swendsen, 1987).

Variation in the relative light availability between the sampling locations was characterised by a hemispherical photographic technique (Anderson, 1964) as modified by Nilson and Ross (1979). Several photographs per sampling location were taken, from every photograph the relative area of canopy gaps was measured with respect to zenith angle and the diffuse site factor a_d (relative amount of penetrating diffuse solar radiation) was calculated. The value of a_d always lies within the range of 0.1. A value equal to 1.0 corresponds to the diffuse irradiance above the stand, while a_d of 0.0 to complete shade with no penetrating canopy gaps. a_d gives comparable estimates to other light sensors, especially with respect to long-term light climate (Salminen *et al.*, 1983). No correction for direct solar radiation was made, because the compass direction of the sampling locations was always constant.

Leaf structural and chemical composition

Leaf area was estimated with a video areameter (DIAS, Delta-T Devices, Cambridge, England) and leaves were weighed after oven-drying at 70 °C for 48 h. Ca and Mg contents were determined by inductively coupled plasma emission spectroscopy (INTEGRA XMP, GBC Scientific Instruments, Melbourne, Australia) after the digestion of fine-ground leaves in 65% HNO_3. Total leaf carbon and nitrogen were estimated with a C/N analyser (Model 1500, Carlo Erba, Italy). The content of non-structural carbohydrates was determined colorimetrically by anthrone reaction (Yemm & Willis, 1954; Hansen & Möller, 1975) using glucose as standard. After the extraction of ethanol-soluble fraction with 70% ethanol at 65 °C for 30 min., the residue was treated with 1% HCl at 100 °C for 30 min. to hydrolyse starch. Extinction values for starch were multiplied by a factor 0.897 (weight ratio of starch to glucose at constant carbon content) to correct for weight increase during the hydrolysation. Total non-structural carbohydrate content (TNC) was found as the sum of the contents of ethanol-soluble carbohydrates (ESC) and starch (SC). Additional details concerning the extraction assay are given in Oren *et al.* (1988).

Analysis of leaf parameters

Leaf dry weight per area can be expressed as a product of several variables (Dijkstra, 1990):

$$\text{LWA} = \text{LWA}_w \star \text{D}_w \star \sum_{i=1}^{i=n} \text{M}_m, \tag{3}$$

where LWA_w is fresh weight per leaf area, D_w is the proportion of dry matter in fresh weight, M_m is a proportional amount of a leaf compound and n is the number of compounds separated for the analysis. Accordingly, leaf TNC-free dry weight per area, LWA_c, is given by:

$$\text{LWA}_c = \text{LWA} \star (1 - \text{TNC}) \tag{4}$$

where TNC is expressed as a proportion of dry matter. Similarly, leaf calcium, magnesium and nitrogen contents on the basis of a TNC-free dry weight (Ca_{mc}, Mg_{mc} and N_{mc}, respectively) are equal to:

$$\text{M}_{mc} = \frac{\text{M}_m}{1 - \text{TNC}} = \frac{\text{LWA}}{\text{LWA}_c} \text{M}_m, \tag{5}$$

where M_{mc} is the content of a compound on a TNC-free dry weight basis. Exclusively, residual carbon content (RCC, carbon content without TNC) is given by:

$$\text{RCC} = \frac{\text{LWA}}{\text{LWA}_c} (\text{TCC} - \text{NCC}), \tag{6}$$

where TCC is total carbon content and NCC is leaf carbon in TNC.

Linear correlation, and linear and non-linear regression techniques were used for analysing the data. r^2_s for the non-linear regressions refer to the proportion of explained variance. All relationships were considered significant at $p < 0.05$ (Wilkinson, 1990). Since light-related variation in leaf compounds, if expressed on a leaf area basis, contains also the confounding variation in LWA (*cf.* above), the expressions based on a leaf dry weight or on a TNC-free dry weight are more appropriate for comparisons. Therefore, despite of the highly significant correlations ($r^2 > 0.70$) always existing between a_d, LWA and LWA_c, and leaf area based variables, they were largely neglected in the present analysis.

RESULTS

Leaf morphology

Leaf morphological parameters, LWA_w ($r^2 = 0.48$, $p < 0.001$), LWA ($r^2 = 0.76$, $p < 0.001$, fig. 1) and LWA_c ($r^2 = 0.71$, $p < 0.001$), increased all significantly with increasing relative irradiance. Trees with greater proportion of sapwood in stem basal area at 1.3 m had higher values of LWA_w ($r^2 = 0.23$, $p < 0.05$). Furthermore, LWA_w, LWA and LWA_c increased with increasing tree size, which was characterised by total height (TTH), diameter and circumference at 1.3 m, whereas correlation with TTH ($r^2 = 0.21$, $p < 0.05$ for LWA_w; $r^2 = 0.23$, $p < 0.05$ for LWA and LWA_c) (fig. 1) was always slightly more significant than with diameter or circumference. a_d and tree dimensions were not significantly related ($p > 0.3$). Though there was a positive correlation between TTH and tree age ($r^2 = 0.79$, $p < 0.001$), morphological variables were not significantly correlated with tree age. Correlation coefficients between LWA_w, LWA and LWA_c were always higher than 0.86 (all significant at $p < 0.001$).

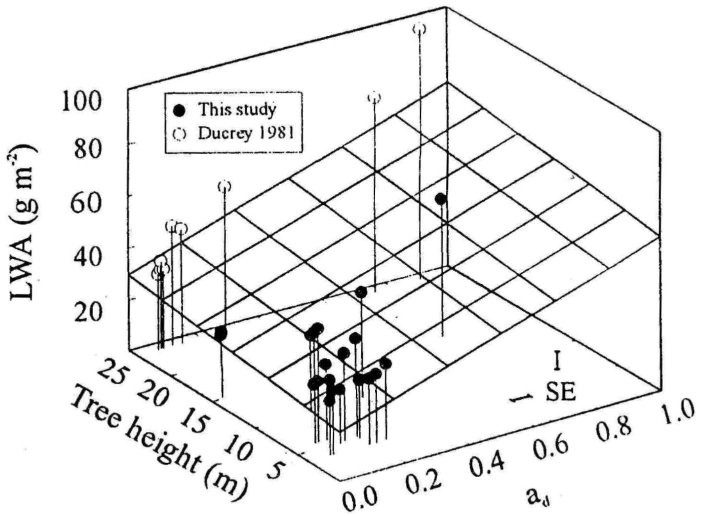

FIG. 1. – Dependence of leaf weight per area (LWA, g m^{-2}) on total tree height (TTH, m) and diffuse site factor (a_d, relative irradiance) in *Fagus sylvatica*. For comparison, the data of DUCREY (1981) for a large *F. sylvatica* tree are also given. Dots: current study, circles: DUCREY, 1981. Equation for the regression plane (only data of current study): $\mathrm{LWA} = 18.5 + 41.6 \star a_d + 0.45 \star \mathrm{TTH}$ ($N = 20$, $r^2 = 0.78$, $p < 0.001$; TTH is significant at $p < 0.07$). Error bars give the maximal standard error of the mean (SE) for both LWA and a_d.

Leaf carbon skeleton

Leaves with greater values of LWA had higher contents of dry matter (fig. 2A) and TNC (fig. 2B). Similarly, D_w and TNC increased with relative irradiance ($r^2 = 0.24$, $p < 0.05$ and $r^2 = 0.53$, $p < 0.001$, respectively). Since starch content varied little with LWA (fig. 2B) and was independent of a_d ($p > 0.2$), most of the increase in TNC with LWA and a_d can be attributed to an increase in the content of ethanol-soluble carbohydrates (data not shown). Ranges of starch and ESC, found in the current study, were similar to the values of Balsberg Påhlsson (1989) for *F. sylvatica.* Total leaf carbon content (TCC) per unit non-structural carbon (leaf carbon in TNC, NCC) decreased with LWA (fig. 2C) and a_d ($r^2 = 0.38$, $p < 0.01$). The decrease resulted from higher NCC at greater values of LWA (fig. 2B) and a_d, and from a constant TCC with LWA (fig. 2D) and a_d ($r^2 = 0.04$, $p > 0.4$). However, leaf carbon expressed on a TNC-free dry weight basis (RCC, Eq. 5) increased significantly with LWA_c (fig. 2D), LWA ($r^2 = 0.34$, $p < 0.01$) and a_d ($r^2 = 0.24$, $p < 0.05$). Increasing RCC did not outweigh the increase in NCC with a_d and LWA (fig. 2B) and thus RCC/NCC similarly to TCC/NCC decreased with LWA_c (fig. 2C), LWA ($r^2 = 0.56$, $p < 0.001$) and a_d ($r^2 = 0.37$, $p < 0.01$).

Though the tree dimensions altered LWA and LWA_c (fig. 1), they did not affect significantly any parameters of leaf carbon distribution along the light gradient.

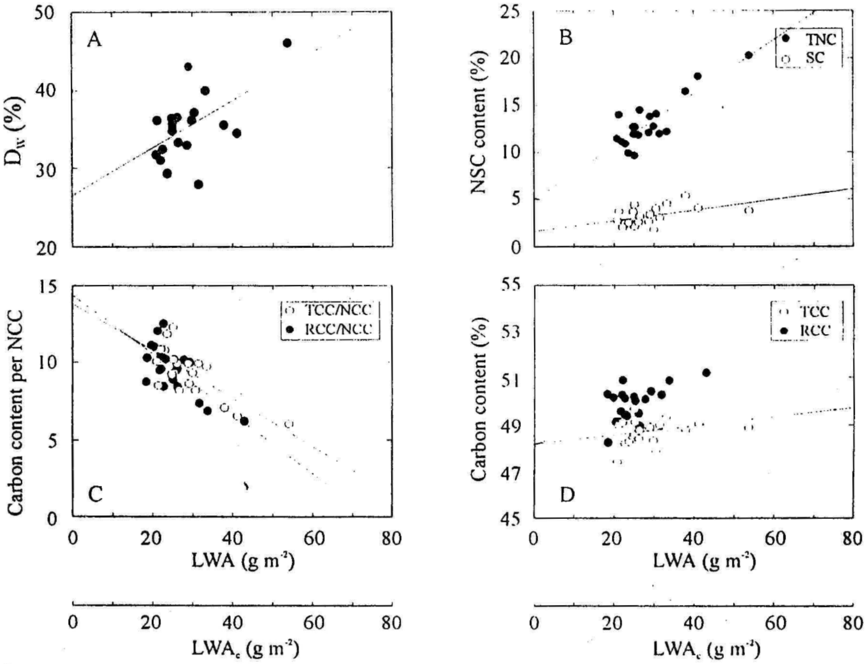

Fig. 2. – Partitioning of leaf carbon and dry matter with respect to total (LWA, g m^{-2}) and non-structural carbohydrate free leaf dry weight per area (LWA_c, g m^{-2}). **A**. Content of leaf dry matter (D_w, %) *vs.* LWA. $\mathrm{D}_w = 26.5 + 0.31 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.32$, $p < 0.01$). **B**. Non-structural carbohydrate content (NSC, %) *vs.* LWA. TNC (dots) is the sum of starch (SC, circles) and ethanol-soluble carbohydrates. $\mathrm{TNC} = 4.9 + 0.28 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.72$, $p < 0.001$); $\mathrm{SC} = 1.6 + 0.056 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.22$, $p < 0.05$). **C**. Total (TCC, %) and residual (RCC, %) carbon per non-structural carbon (NCC, carbon content in TNC, %) (TCC/NCC and RCC/NCC, respectively) *vs.* LWA and LWA_c, respectively. $\mathrm{TCC/NCC} = 13.8\text{-}0.15 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.56$, $p < 0.001$); $\mathrm{RCC/NCC} = 14.4\text{-}0.19 \star \mathrm{LWA}_c$ ($N = 20$, $r^2 = 0.50$, $p < 0.001$). RCC is leaf carbon concentration in TNC-free dry matter. **D**. TCC *vs.* LWA and RCC *vs.* LWA_c. $\mathrm{TCC} = 48.2 + 0.019 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.08$, $p > 0.2$); $\mathrm{RCC} = 48.3 + 0.054 \star \mathrm{LWA}$ ($N = 20$, $r^2 = 0.34$, $p < 0.01$).

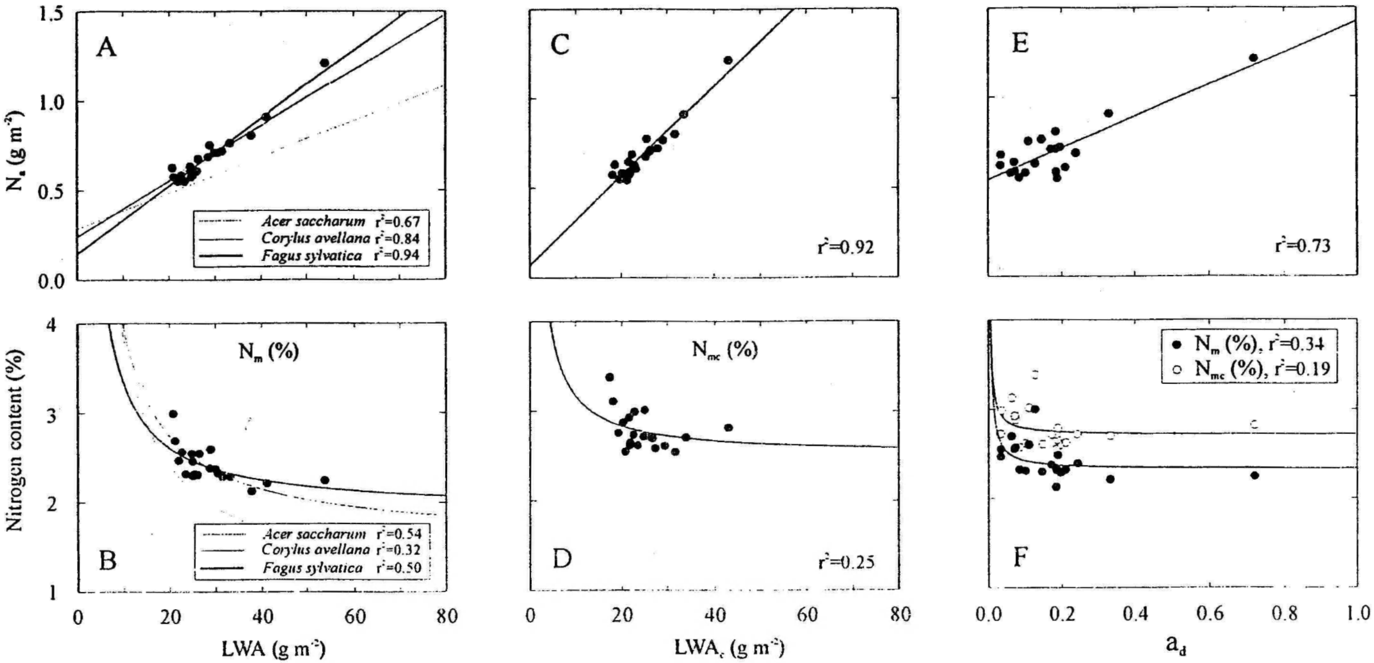

FIG. 3.– Patterns of leaf nitrogen partitioning with respect to LWA, LWA$_c$ and relative irradiance in the shade-tolerant species *Acer saccharum* (punctuated line, recalculated after ELLSWORTH & REICH, 1992), *Corylus avellana* (thin line, recalculated after KULL & NIINEMETS, 1993) and *Fagus sylvatica* ($N = 20$, dots and circles, thick line, current study). **A**. Nitrogen content per leaf area (N$_a$, g m^{-2}) *vs.* LWA (g m^{-2}). *Acer saccharum:* $N_a = 0.284 + 0.0100 * LWA$, *Corylus avellana:* $N_a = 0.240 + 0.0155 * LWA$, and *Fagus sylvatica:* $N_a = 0.144 + 0.0189 * LWA$ ($p < 0.001$). **B**. Nitrogen content per leaf dry weight (N$_m$) *vs.* LWA. *Acer saccharum:* $N_m = 28.4/LWA + 1.0$, *Corylus avellana:* $N_m = 24.0/LWA + 1.55$ and *Fagus sylvatica:* $N_m = 14.4/LWA + 1.89$. Though the non-linear regressions gave slightly higher proportions of determined variance (r^2), all coefficients for the fitted curves were derived from the N$_a$ *vs.* LWA relationships (Eq. 1, 2). r^2-s for the hyperbolic relationships refer to the explained variance of the linear regressions between N$_m$(modelled) and N$_m$(measured). **C**. N$_a$ *vs.* LWA$_c$. $N_a = 0.067 + 0.0250 * LWA_c$ ($p < 0.001$, intercept is not significantly different from zero). **D**. Nitrogen content per TNC-free dry weight (N$_{mc}$) *vs.* LWA$_c$. $N_{mc} = 6.7/LWA_c + 2.5$. Hyperbola was fitted to the data according to the N$_a$ *vs.* LWA$_c$ relationship (Eq. 1, 2). **E**. N$_a$ *vs.* relative irradiance (a_d). $N_a = 0.54 + 0.88 * a_d$ ($p < 0.001$). **F**. N$_m$ and N$_{mc}$ *vs.* a_d. Curves were fitted to the data by a non-linear regression. $N_m = 2.32 + 0.010/a_d$. $N_{mc} = 2.71 + 0.0080/a_d$.

Distribution of leaf nitrogen, magnesium and calcium

Leaf nitrogen content per area (N_a) was linearly related to LWA, LWA$_c$ and a_d (fig. 3A, C, E). The intercept of N_a *vs.* LWA relationship was greater than zero ($p < 0.001$), and accordingly the hyperbola describing the dependence of N_m on LWA was decreasing (Eq. 2, fig. 3B), indicating higher nitrogen investment in foliage at lower light availabilities (fig. 3F). Shade-tolerant species *Acer saccharum* (data of Ellsworth & Reich, 1992) and *Corylus avellana* (data of Kull & Niinemets, 1993) had similar patterns of variation of N_m *vs.* LWA (fig. 3B). Subtraction of NSC from total leaf dry weight decreased the proportion of explained variance in N_{mc} *vs.* LWA$_c$, and N_{mc} *vs.* a_d (fig. 3D, F). Though the intercept of N_a *vs.* LWA$_c$ (fig. 3C) was not significantly different from zero, a tendency of N_{mc} to be higher at lower values of LWA$_c$ (fig. 3D) was still considerable.

Due to the strong positive correlations of TNC with LWA (fig. 2B) and a_d (*cf.* above), and relatively less variable N_m and N_{mc} (fig. 3), the ratios TNC/N_m and TNC/N_{mc} (fig. 4) increased with increasing both LWA$_c$ ($r^2 = 0.79$, $p < 0.001$ and $r^2 = 0.78$, $p < 0.001$, respectively) and a_d ($r^2 = 0.59$, $p < 0.001$ and $r^2 = 0.55$, $p < 0.001$, respectively). Starch content per N_m and N_{mc}, however, was positively correlated with only LWA$_c$ ($r^2 = 0.31, p < 0.01$ and $r^2 = 0.25, p < 0.05$, respectively), but not with a_d ($p > 0.2$, fig. 4). No correlations of N_m and N_{mc} with TNC and SC were significant ($p > 0.2$).

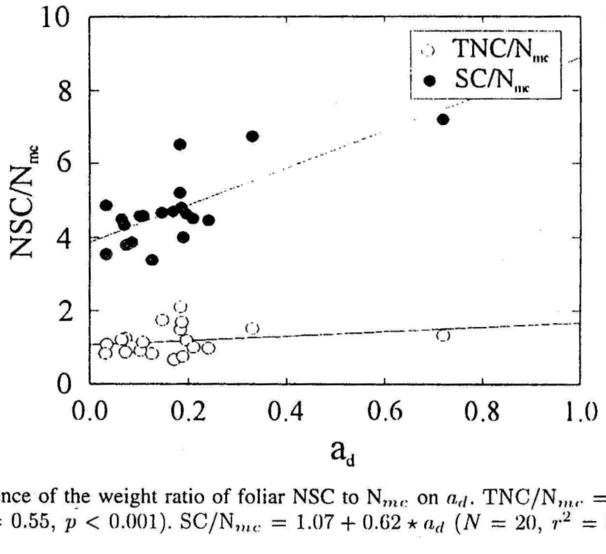

Fig. 4. – Dependence of the weight ratio of foliar NSC to N_{mc} on a_d. TNC/N_{mc} = $3.87 + 5.02 \star a_d$ ($N = 20$, $r^2 = 0.55$, $p < 0.001$). SC/N_{mc} = $1.07 + 0.62 \star a_d$ ($N = 20$, $r^2 = 0.06$, $p > 0.3$).

Leaf Mg content per TNC-free dry matter (Mg_{mc}) and molar ratio of leaf magnesium to nitrogen (Mg/N) decreased with increasing LWA$_c$ (fig. 5A) and a_d ($r^2 = 0.44$, $p < 0.001$ and $r^2 = 0.49$, $p < 0.001$, respectively). A positive relationship between Mg_{mc} and N_{mc} ($r^2 = 0.33$, $p < 0.01$) was also found. Magnesium requirement for leaf chlorophyll formation, calculated from chlorophyll $(a + b)$ *vs.* LWA relationship based on literature data, declined non-linearly with LWA, similarly to Mg_{mc} *vs.* LWA$_c$ (fig. 5A, B).

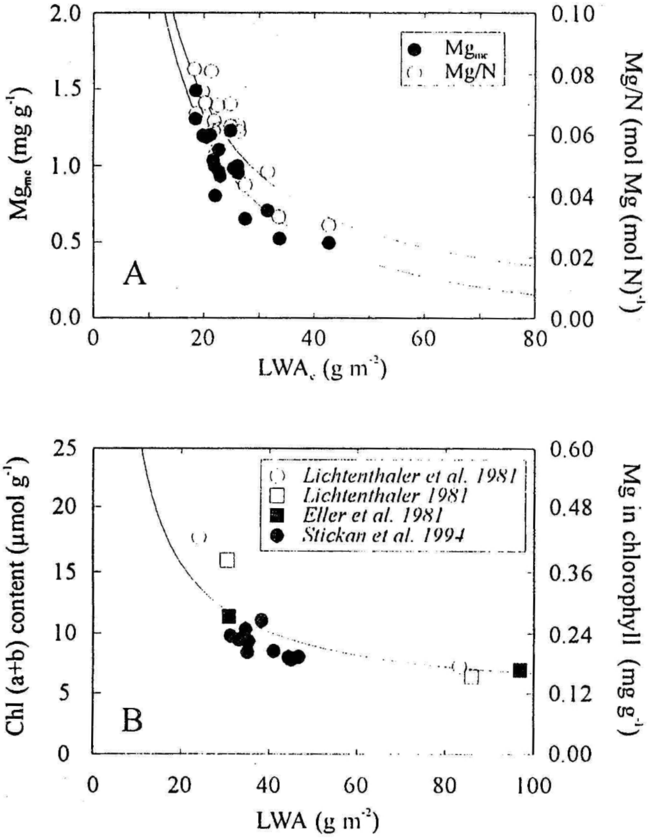

FIG. 5. – Relationships between leaf Mg and chlorophyll *vs.* LWA. **A**. Content of leaf Mg per TNC-free dry weight (Mg_{mc}, mg g^{-1}, dots) and molar ratio of Mg to nitrogen (Mg/N, circles) *vs.* leaf TNC-free dry weight per area (LWA_c). Curves were fitted to the data by a non-linear regression. $Mg_{mc} = 28.3/LWA_c - 0.200$ ($N = 19$, $r^2 = 0.77$), $Mg/N = 0.848/LWA - 0.00037$ ($N = 19$, $r^2 = 0.71$). **B**. Contents of leaf chlorophyll $(a+b)$ (μmol g^{-1}) and magnesium associated with chlorophyll (mg g^{-1}) per leaf dry weight *vs.* LWA. $Chl(a+b) = 226.4/LWA + 4.4$ ($N = 18$, $r^2 = 0.65$). Mg requirement for chlorophyll formation was calculated assuming a molar ratio of $chl(a + b)$ to Mg of one. Data for leaf chlorophyll content were compiled from various studies (ELLER *et al.*, 1981; LICHTENTHALER, 1981; LICHTENTHALER *et.al.*, 1981; STICKAN *et al.*, 1994).

Ca_{mc} was not significantly correlated with either LWA_c or with a_d ($p > 0.4$) and decreased with increasing RCC ($r^2 = 0.31$, $p < 0.01$). If compared to the data of FLÜCKIGER *et al.* (1986), the range of the nutrient contents on the basis of total leaf dry weight was equal to or higher than the optimum for Ca_m (5.4..11.5 mg g^{-1} and N_m (2.55..3.38%) and less than the optimum (1.5..3 mg g^{-1}) in the case of Mg_m (0.4..1.28).

Since TNC varied only between 10-20% (fig. 2B), the relationships did not differ qualitatively if the element contents were expressed on the basis of total dry weight instead of TNC-free dry weight. Tree dimensions and age did not influence the variation in the contents of leaf nitrogen, calcium and magnesium.

DISCUSSION

Leaf morphology and carbon content

Since higher light availabilities result in greater evaporative demands, and thus probably in more severe desiccation stresses, decreasing leaf water content with increasing irradiance and LWA in *F. sylvatica* (fig. 2A) may be a direct consequence of enhanced radiation loads. Leaf water content decreased with increasing LWA also in several Australian subtropical forest species (STEWART *et al.*, 1990), recalculation of the data of HUZULÁK and ELIÁŠ (1975) for *Acer campestre* and *Carpinus betulus* gives also a positive linear relationship between LWA and D_w. In stems of *Picea sitchensis*, large, if compared to the gravitational component of water potential of 0.1 bar m^{-1}, vertical gradients of water potential up to 2 bar m^{-1} have been found (HELLKVIST *et al.*, 1974). Increasing LWA_w with increasing proportion of stem wood in sapwood may hint at the constraints which are set by the water conductance of stems on leaf structure. Moreover, the positive relationship between D_w and LWA (and accordingly negative between water content and LWA) implies that the differences in LWA_w between the leaves from open and shaded habitats are relatively smaller than in LWA, because water content of less-illuminated leaves is higher. Since carbon costs for leaf mechanical support are likely to scale with leaf fresh weight rather than with dry weight per area, variability in the requirement for leaf structural carbon should also be smaller than that expected on the basis of LWA values only. The leaves grown under higher irradiances contained more lignin per leaf dry weight in *F. sylvatica* (KAUSCH & HAAS, 1966) and in *Salix aquatica* (WARING *et al.*, 1985), and less cell wall polysaccharides in *F. sylvatica* (KAUSCH & HAAS, 1965, 1966) than the ones grown under lower irradiances. Inasmuch as carbohydrates contain less carbon than lignin does, carbon requirement for leaf construction was expected to increase with light availability. This was indeed the case when leaf carbon content without the carbon in TNC was considered (fig. 2D). Increased lignification of cell walls at open habitats may be advantageous, because it facilitates the toleration of low leaf water potentials, being more severe there. Since most of the calcium in plant tissues is bound in cell wall polysaccharides (DEMARTY *et al.*, 1984), negative correlation between RCC and Ca_{mc} may indicate an increased proportion of cell walls in less illuminated leaves, as also found previously (KAUSCH & HAAS, 1965, 1966). Higher content of structural polysaccharides in shaded leaves may be necessary to meet the higher supporting requirements due to increasing water loads at decreasing irradiance (fig. 2A, *cf.* above).

An increase of LWA with tree dimensions (fig. 1) agrees with the observed relationships in other woody taxa (HAGER & STERBA, 1985; LINDER, 1985; STEELE *et al.*, 1989; LEUNING *et al.*, 1991; KULL & NIINEMETS, 1993; NIINEMETS & KULL, 1995). In *Picea abies*, LWA as the product of leaf density and thickness (WITKOWSKI & LAMONT, 1991), increased with TTH due to increasing needle density, and with irradiance due to increasing needle thickness (NIINEMETS & KULL, 1995). As an adaptation to lower water potentials, being more severe in crowns of tall trees, higher proportion of leaf carbon may be invested for leaf support in taller trees, resulting in increased leaf density. In *F. sylvatica*, however, the increase of LWA with tree dimensions is likely to be attributable to the changes in leaf thickness rather than to leaf density, because no correlations between tree dimensions and the proportions of total and structural leaf carbon were found. Older trees of *Quercus* *robur* had higher leaf thickness and thickness of palisade parenchyma (Malkina, 1983) than younger trees; in *Picea sitchensis*, LWA and needle dimensions (Steele *et al.*, 1989), in *P. schrenkiana*, size of mesophyll cells and cell number (Baidavletova, 1984) increased with tree age. In *F. sylvatica*, nevertheless, LWA did not depend on tree age. Moreover, though the effect of tree size on LWA was significant, the variation in the relative irradiance across the canopy was the major determinant of LWA (fig. 1), and accordingly LWA may be used as an estimate of long-term relative light conditions (Čermák, 1989). Furthermore, since all relationships of leaf chemical constituents gave slightly higher proportions of determined variance with LWA than with a_d, and no relationship was significantly altered by TTH, LWA may be considered as an even better assessment of long-term relative irradiance than a_d.

Similar response of leaf NSC to growth irradiance (fig. 2B) has been documented for a number of species (Jelmini & Nösberger, 1978; Frey & Nösberger, 1980; Fjeld, 1992*a*, *b*; Graper & Healy, 1992). Also the pool of storage polysaccharides such as starch behaves similarly, though changing relatively less than the pool of oligo- and monosaccharides (~ ESC) (Fjeld, 1992*a*, *b*; Graper & Healy, 1992, fig. 2B). Diurnal variability in NSC, closely following light course during the day (Servaites *et al.*, 1989), can be explained by photosynthesis *vs.* light response curve, whenever carbon export remains nearly the same (Servaites *et al.*, 1989) or changes considerably less with irradiance than does carbon accumulation (Hendrix & Huber, 1986). Accordingly, increased TNC at the top of the canopy may be explained by higher absolute irradiances and consequently higher photosynthetic carbon fixation there. Large diurnal variability in leaf N_m (Kausch & Overdieck, 1974), LWA (Kausch & Overdieck, 1974), contents of K, Ca and Mg (Overdieck, 1976) in *F. sylvatica* is largely explainable by diurnal changes in NSC (Chatterton *et al.*, 1972; Plhák, 1984), concentrating or diluting other leaf substances. Thus, if the spatial and temporal variation in TNC due to the intrinsic light gradient within the canopy is not taken into account, artificial results in studies on leaf composition and structure may be obtained.

Distribution of leaf nitrogen and magnesium

Balsberg Påhlsson (1989) observed a tendency of upper canopy leaves of *F. sylvatica* to contain less Mg and nitrogen per leaf dry weight than lower canopy leaves. In the current study N_m decreased hyperbolically with LWA (fig. 3B) and relative irradiance (fig. 3F), being close to N_m *vs.* LWA curves found for shade-tolerant *Acer saccharum* (Ellsworth & Reich, 1992), *Corylus avellana* and *Lonicera xylosteum* (Kull & Niinemets, 1993). When the effect of TNC on LWA and N_m was subtracted, N_{mc} was virtually constant over a wide range of LWA_c (fig. 3D), still increasing at lower values of LWA_c. Since almost 3/4 of leaf nitrogen in C_3 plants is associated with the photosynthetic apparatus (Evans, 1989), higher N_m in shade may be related to enhanced photosynthetic production per dry weight there. However, in *Acer saccharum*, P^m_{max} (photosynthetic capacity per leaf dry weight) was not significantly correlated with N_m (Ellsworth & Reich, 1992) and N_m was not correlated with TNC in *F. sylvatica*. Furthermore, TNC/N_m and TNC/N_{mc}, which may give first estimates of photosynthetic nitrogen use efficiency, provided TNC is linked to daily photosynthetic carbon production (Takahashi *et al.*, 1993), increased with increasing relative irradiance (fig. 4). Since P^m_{max} is according to the definition the rate of leaf photosynthesis at saturating irradiance and ambient CO_2, where carboxylation capacity limits leaf photosynthesis (Farquhar *et al.*, 1980), but photosynthesis is mostly constrained by insufficient irradiance in the lower canopy, increased leaf nitrogen may be contained in photosynthetic structures improving the efficiency of light interception, and thus may have no direct influence on photosynthesis at high irradiances where $P^{m}_{\max}$ is measured. In the shade plant *Alocasia macrorrhiza* (Seemann *et al.*, 1987; Evans, 1989), the proportion of leaf nitrogen invested for light harvesting, *i.e.* in chlorophyll and proteins associated with it, increased tremendously with decreasing irradiance. It increased considerably less in the sun plants *Spinacia oleracea* (Evans, 1989) and *Phaseolus vulgaris* (Seemann *et al.*, 1987). Enhanced light capture is expensive in terms of leaf nitrogen, and due to a non-linear asymptotic relationship between leaf chlorophyll content and absorptance, only minor gains in terms of intercepted light with large investments of leaf nitrogen for light harvesting can be obtained (Evans & Seemann, 1989). Therefore, in shade species, hyperbolically increasing N_m with decreasing irradiance may be associated with increasingly higher resource allocation for light interception. Though much of the decrease in N_m with decreasing a_d was attributable to a change in TNC (fig. 3), consideration of N_{mc} even as a constant across the irradiance gradient contrasts to the decreasing N_m with decreasing irradiance in sun species (*cf.* Introduction). Furthermore, a quasi-linear increase of N_{mc} with Mg_{mc}, and an increase of Mg_{mc} with decreasing irradiance and LWA_c (fig. 5A) may be interpreted as an evidence of enhanced investment of leaf nitrogen for light capture with decreasing irradiance, for a positive relationship, which saturates at higher values of leaf magnesium, exists between leaf chlorophyll and magnesium contents, (Schulze & Küppers, 1985; Wedler, 1991). Chlorophyll $(a + b)$ *vs.* LWA curve, constructed from the data of various sources (fig. 5B), illustrates the increase in the magnesium demand for chlorophyll construction with decreasing LWA, and consequently with decreasing light availability. Assuming a similar leaf chlorophyll *vs.* LWA relationship for the leaves of the present study, about 35% of leaf Mg was used for the formation of leaf chlorophyll at all irradiances. According to Dorenstouter *et al.* (1985), at an optimal Mg-nutrition about 20% of leaf Mg is contained in chlorophyll, whereas with decreasing Mg availability as much as 60% of leaf Mg may be used for chlorophyll formation. After Flückiger *et al.* (1986), the Mg contents observed in *F. sylvatica* were less than optimal. However, since the requirement for Mg at different parts of the canopy was different, the deficiency was partitioned equally among the leaves. *Quercus prinus, Q. alba, Acer rubrum* and *Fagus grandifolia* have been shown to possess an adaptive ability to modify largely the nutrient use efficiency and to maintain the productivity in spite of decreased nutrient availability (Boerner, 1984). The magnesium distribution pattern observed in *F. sylvatica* is likely to improve whole-canopy magnesium use efficiency, signifying that in studies on plant nutrition, spatial variability in the requirement for different leaf nutrients must be taken into account.

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IV

Niinemets, Ü. 1996. Partitioning of foliar nitrogen influences species shade-tolerance in four temperate deciduous woody taxa. (Submitted)

PARTITIONING OF FOLIAR NITROGEN INFLUENCES SPECIES SHADE-TOLERANCE IN FOUR TEMPERATE DECIDUOUS WOODY TAXA

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Summary

1. Distribution of leaf chlorophyll (Chl), nitrogen and non-structural carbohydrates (NSC, ethanol-soluble sugars and starch) in leaves along a natural light gradient was studied in four deciduous woody species: *Acer platanoides*, *Padus avium*, *Populus tremula* and *Quercus robur* (from most shade-tolerant to intolerant).

2. NSC per leaf dry mass was positively related to relative irradiance (RI), whereas the slope of this relationship was highest for intolerant species, which have intrinsically higher photosynthetic capacities. To account for the changes in NSC with irradiance, which result in covariation or in masking of the variation in leaf Chl and N content per leaf dry mass (Chl$_m$ and N_m, respectively), and in leaf dry mass per leaf area (LMA), the variabilities in Chl and N per NSC-free dry mass and leaf NSC-free dry mass per area were also examined. However, the conclusions were robust and were not significantly biased by using the parameters expressed either on a total or on a NSC-free dry mass.

3. LMA increased linearly with increasing RI in all species, and it may therefore be considered as a species-specific estimate of long-term light conditions.

4. Decreasing irradiance enhanced chlorophyll synthesis, and consistently resulted in highest Chl$_m$ in low-light environments. This was different for chlorophyll content per leaf area, which was correlated (negatively) with RI in only *A. platanoides*. Though N_m and Chl$_m$ were positively related in all species, higher slope of Chl$_m$ vs. N_m in more tolerant species suggests that at a common nitrogen content these species had higher proportion of foliar nitrogen invested in light harvesting apparatus.

5. Leaf nitrogen content per leaf area (N_a) increased linearly with LMA ($N_a = a \times \text{LMA} + b$, where a and b are empirical species-dependent coefficients) in all species, and with RI in all, except for *A. platanoides*. Because $N_m = b/\text{LMA} + a$, the intercepts and slopes of N_a vs. LMA relations control the variation patterns of N_m with LMA and relative irradiance: the slope provides an estimate of mean N_m and the intercept determines if N_m decreases or increases with LMA.

6. The slopes and intercepts of N_a vs. LMA relationships were negatively correlated. Moreover, it appeared that the slope decreased and the intercept increased with increasing species shade-tolerance. Thus, average N_m increases and maximum concentrations of leaf nitrogen shift towards more open habitats with decreasing shade-tolerance. Distribution of foliar nitrogen in this way is likely to contribute towards greater photosynthetic potentials at higher irradiances. Inversely, more tolerant species have greater concentrations of foliar nitrogen at low irradiance — an investment pattern, which provides resources to enhance the capacity of light harvesting in light-limited conditions.

7. The analysis was further extended by including a number of other species from several independent studies. Examination of both sets of data resulted in identical conclusions. Based on this evidence I conclude that the variability in leaf nitrogen concentration in correlation with irradiance plays a central role in species shade-tolerance.

Key-words: *Acer platanoides*, chlorophyll, irradiance, leaf morphology, light harvesting, *Padus avium*, *Populus tremula*, *Quercus robur*.

Introduction

Changes in foliage structural and physiological properties, which improve the efficiency of light interception, gain in importance as light available to fuel photosynthesis becomes progressively deficient with increasing canopy depth. Therefore, plant performance is optimised if the foliage morphology and physiology are adjusted towards long-term light conditions across the canopy (Tooming 1967; Björkman 1981; Givnish 1988; Gutschick & Wiegel 1988). Acclimation to growth irradiance plays even a more significant part in forest understory, where light is the most universally limiting resource for all leaves (Bazzaz & Wayne 1994; Pearcy & Sims 1994).

Nitrogen availability and species-specific distribution patterns of foliar nitrogen in correlation with irradiance may particularly crucially alter plant potential to tolerate low irradiances, because nitrogen scales with thylakoid proteins and leaf chlorophylls (Evans 1989,1993a). While the content of leaf nitrogen per leaf area (N_a) is positively related to relative irradiance (Walters & Field 1987; Lemaire *et al.* 1991; Kull & Niinemets 1993; Niinemets 1995,1996b), the relationships between nitrogen content per leaf dry mass (N_m) and relative irradiance differ qualitatively among deciduous species: N_m increases with increasing irradiance or decreasing canopy depth in *Betula pendula* (Kull & Niinemets 1993) and *Eucalyptus grandis* (Leuning, Cromer & Rance 1991), but decreases in *Acer saccharum, Borojoa patinoi* (Lynch & González 1993), *Corylus avellana* (Kull & Niinemets 1993), *Fagus sylvatica* (Niinemets 1995) and *Lonicera xylosteum* (Kull & Niinemets 1993). Diverse responses of N_a and N_m with respect to irradiance can be explained by introducing an important structural parameter, leaf dry mass per area (LMA), which enables to switch between the mass and area based estimates (N_a=N_m×LMA), and which is positively related to growth irradiance (Gulmon & Chu 1981; Kull & Niinemets 1993; Wayne & Bazzaz 1993; Niinemets 1995,1996a,b). Consequently, even if N_m is invariable or decreases, N_a may increase with increasing irradiance due to the multiplicative effects of light on leaf anatomy (Ellsworth & Reich 1993; Kull & Niinemets 1993; Niinemets 1995,1996b). Unfortunately, most research on the influences of light on nitrogen partitioning has been conducted with N_a, which confounds the variation in both N_m and LMA, and therefore, may not serve as an estimate of nitrogen investments for foliage construction.

Generally, shade-tolerant species have proportionally higher nitrogen investment in compounds responsible for light capture, but intolerant species in CO_2-carboxylating enzymes (Seemann *et al.* 1987; Evans 1989). Given the saturating nature of leaf absorptance vs. chlorophyll relationship (Evans & Seemann 1989) and the low affinity of the major Calvin's cycle enzyme ribulosebisphosphate carboxylase/oxygenase to its substrate CO_2 (Badger & Collatz 1977), both efficient quantum capture and high carboxylation capacity are expensive in terms of leaf nitrogen. Therefore, a single species is probably not able to optimise both of them, and a trade-off may go on between the capacities for light harvesting and CO_2-assimilation. Insofar as higher light harvesting and carboxylating capacities are advantageous only at low and high irradiance, respectively, interspecific differences in nitrogen partitioning may provide a mechanistic basis for species separation along light gradients. Inasmuch as all listed taxa, where N_m responded positively to decreased irradiance, are relatively shade-tolerant, and all other species relatively intolerant, different patterns of N_m distribution across natural light gradients seem to be tightly linked to species potential to endure shade.

With this paper I ask: (1) what is the role of interspecific variability in foliar nitrogen distribution in shade-tolerance? (2) is it possible to determine species' shade-tolerance on the basis of how foliar nitrogen is partitioned between the leaves and within the leaf across the gradients of irradiance? To gain insight into these issues I studied modifications in leaf nitrogen concentration and in foliar morphology in correlation with changes in relative irradiance in four temperate deciduous woody species of differing known response to shade. To further reinforce the argument, the analysis was extended by introducing a number of other species from several independent studies, where species performance in terms of foliar structure and nitrogen economy has been followed over a wide gradient of relative irradiances along the gap-understory continuum.

Materials and methods

Experimental site and plant sampling

The study was conducted in the understory of a forest dominated by about 100-yr-old trees of *Picea abies* (L.) Karst. on gleyic and gleyed pseudopodzolic soils at Tôrvandi (58° 20' N, 26° 42' E; elevation 60–65 m above sea level), Estonia in the middle of August 1993. In addition to *P. abies*, trees of *Betula pendula* Roth., *Pinus sylvestris* L., *Populus tremula* L. and *Salix caprea* L. were found in the overstory, whereas understory was dominated by *P. tremula*, *Padus avium* Miller, *Salix myrsinifolia* Sal. and *Vaccinium myrtillus* L. Saplings of four deciduous woody species, of which *Acer platanoides* L., *P. tremula* and *Quercus robur* L. are trees, *P. avium* is a shrub to small tree, were sampled. Studied saplings of *P. tremula* and *P. avium*, though growing solitarily, were mostly of sprout origin, *A. platanoides* and *Q. robur* were exclusively of seed origin. According to Ellenberg *et al.* (1991), *A. platanoides* is the most, *Q. robur* the least shade-tolerant of the analysed species (Table 1). Mean age, estimated by counting the growth rings at the ground, was not significantly different between *Q. robur* and *A. platanoides* (Table 1). Though the plants at more open habitats were usually larger at a common age, mean height of sampled saplings differed little between the species (Table 1). All studied species at these latitudes usually have determinate growth, producing annually only one flush of leaves. Few plants of *P. tremula* and *Q. robur*, which had flushed twice, were discarded from the analysis. Fully expanded, undamaged leaves were sampled from the uppermost 10 cm crown layer only. Sampling was restricted to midday hours between 12.00 and 13.00 in cloudy days. Five to nine leaves per sample were analysed and means calculated.

Table 1. Characteristics of sample plants

Species (number of trees)	Ellenberg's light figure[1]	Age (years)		Height (m)		Leaf size (cm^2)
	(% range)	Range	Mean (±SE)[2]	Range	Mean (±SE)	Mean (±SE)
Acer platanoides (22)	4 (5–10)	4–21	10.2±0.9a	0.30–2.00	1.04±0.11ab	62.1±6.1a
Padus avium (28)	5 (10–20)			0.50–1.80	1.28±0.09b	32.3±2.1b
Populus tremula (26)	6 (20–30)			0.54–1.60	1.08±0.06ab	38.3±4.2b
Quercus robur (27)	7 (30–40)	3–15	9.1±0.6a	0.30–1.53	0.93±0.06a	34.0±2.4b

[1] European woody species range according to light figures, which have originally been obtained from the observations of species dispersal across gap-understory gradient, from 3 (most shade-tolerant) to 9 (most intolerant) (Ellenberg *et al.* 1991). Species %-range, respective to different light figures, was compiled based on the explanations in Ellenberg *et al.* (1991, p. 67).

[2] Parameters with the same letter are not significantly different (Bonferroni test, P>0.05).

Several hemispheric photographs were made at the location of sampled leaves and the differences in relative irradiance between the samples were quantified after Anderson (1964) as modified by Nilson and Ross (1979). From every photograph the area of canopy gaps was measured with respect to zenith angle, corrected for cosine of incidence effects and diffuse site factor (RI, relative amount of penetrating diffuse solar irradiance) was calculated for uniformly overcast sky conditions. RI ranges from 0 to 1: a value equal to 1.0 corresponds to the diffuse irradiance above the stand, and that of 0.0 to completely closed overstory canopy with no penetrating gaps. Experimental comparisons confirm that RI gives good estimates to other light sensors in long-term (Salminen *et al.* 1983).

Analysis of leaf chemical and morphological parameters

Leaf contours were traced manually with a computer digitizer (QD-1212, QTronix Corp., Taiwan) and leaf area was calculated by self-developed software. Leaves were weighed after oven-drying at 70 °C for at least 48 h. Leaf nitrogen concentration (N_m) was estimated by standard Kjeldahl method. The content of non-structural carbohydrates (NSC) was determined colorimetrically by anthrone reaction (Yemm & Willis 1954) as described previously (Niinemets 1995,1996b). Total non-structural carbohydrate content (TNC) was found as the sum of ethanol-soluble carbohydrates (ESC) and starch. Leaf chlorophyll content was estimated in the solution of 96% ethanol with spectrophotometer SF-16 (Lomo, Leningrad, Russia) from the extinctions at 665 and 649 nm minus the extinction at 750 nm (Wintermans & de Mots 1965; Wintermans 1969). Leaves were extracted in the presence of some magnesium carbonate to avoid the conversion of chlorophylls to pheophytins.

Because diurnal variability in irradiance strongly affects leaf photosynthesis (Servaites *et al.* 1989), but considerably less carbon translocation from the leaves (Hendrix & Huber 1986), concentration of foliar non-structural carbohydrates exhibits the highest daily fluctuation of leaf substances (Plhák 1984). This variability significantly influences LMA (Chatterton, Lee & Hungerford 1972) and the concentration of other leaf substances (Servaites *et al.* 1989). Moreover, cumulative photosynthetic production and the content of NSC are also related (Takahashi, Tsuchihashi & Nakaseko 1993), resulting in an increasing pool size of non-structural carbon with increasing relative irradiance (Niinemets 1995,1996b). Consequently, in many cases the conclusions should be much safer if they base on the leaf parameters calculated on a NSC-free dry mass. This procedure follows Niinemets (1995,1996b): LMA was multiplied, and N_m and leaf chlorophyll concentration (Chl_m) were divided by 1-TNC (TNC is expressed here as the proportion of leaf dry mass) to get leaf NSC-free dry mass per area (LMA^c), and the concentrations of nitrogen (N_m^c) and chlorophyll (Chl_m^c) in NSC-free dry mass.

Linear correlation, linear and non-linear regression techniques were used for analysing the data. Differences between the species were tested by one-way ANOVA. Bonferroni test was used to separate the treatment means. All relationships were considered significant at $P<0.05$ (Wilkinson 1990).

Results

Leaf morphology. Non-structural carbohydrates

The leaves were of similar size in *P. avium*, *P. tremula* and *Q. robur*, but significantly larger in *A. platanoides* ($P<0.001$, Table 1). In all species, both LMA and LMA^c increased significantly with increasing relative irradiance (RI) (Fig. 1). LMA vs. RI relationship had generally linear character, slightly curving only in *P. tremula*. The dependence of LMA^c on RI was linear for all species. The slopes of LMA and LMA^c vs. RI relations were lowest in *A. platanoides*, intermediate in *P. tremula* and *Q. robur*, and highest in *P. avium*. Subtraction of non-structural carbohydrate content from total leaf dry mass always resulted in lower slopes of LMA^c vs. RI than of LMA vs. RI relationships, because there was a tendency of the concentration of total non-structural carbohydrates (TNC, ethanol-soluble carbohydrates plus starch) to increase with LMA in all species ($P<0.05$ for *A. platanoides* and $P<0.001$ for other species) and with RI in all, except for *A. platanoides* (Fig. 2). Inasmuch as starch content was positively related to RI only in *P. avium* ($r^2=0.19$, $P<0.05$), the correlation between RI and TNC, and between LMA and TNC was largely attributable to an increase in ethanol soluble carbohydrates (mostly oligo- and monosaccharides) with RI and LMA (Fig. 2). Mean starch content was also not significantly different between species ($P>0.1$). Due to the constancy of starch concentration, the slopes of ESC vs. RI and TNC vs. RI relations were similar within species (Fig. 2). However, the slopes differed between the species: according to the slope of ESC vs. RI relationship the species ranked as *A. platanoides*<*P. avium*<*Q. robur*<*P. tremula*.

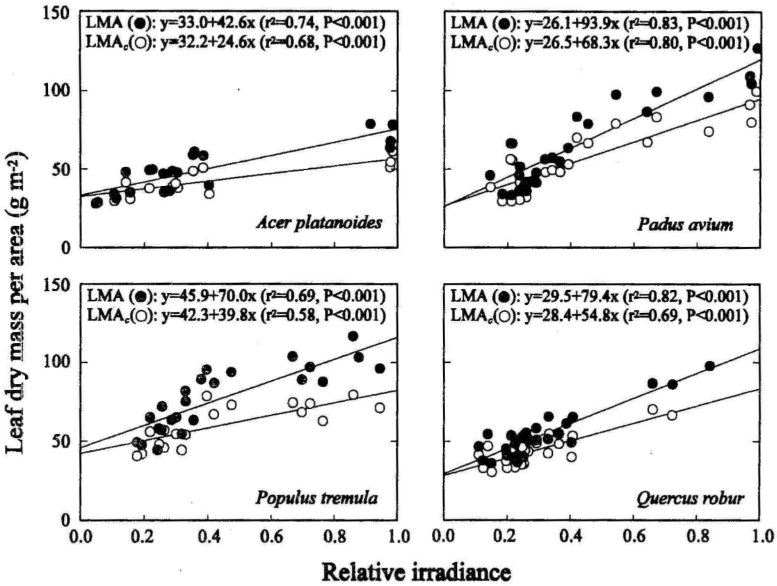

Fig. 1. Dependence of total leaf dry mass per area (LMA, g m^{-2}) and non-structural carbohydrate free dry mass per area (LMA^c g m^{-2}) on relative irradiance.

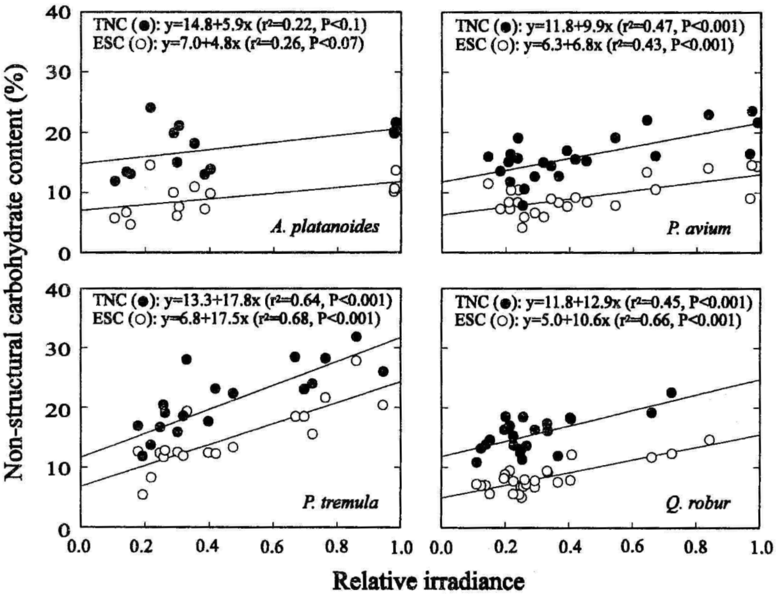

Fig. 2. Pool size of leaf non-structural carbohydrates (%) in dependence on irradiance. ESC — ethanol soluble carbohydrates, TNC — ESC plus starch.

Partitioning of leaf chlorophyll and nitrogen

N_a was positively related to LMA in all species (Fig. 3), but the correlation with LMA^c (Table 2) and RI (r^2=0.15, P>0.07) was not significant for *A. platanoides*. In *P. avium*, *P. tremula* and *Q robur*, N_a was slightly less significantly correlated with RI (r^2-s ranged from 0.48–0.73, P<0.001) than with LMA (Fig. 3) and LMA^c (Table 2). In *A. platanoides* and *P. avium*, N_m decreased with, but in *P. tremula* and *Q. robur*, it was independent of LMA (Fig. 3), LMA^c and RI (data not shown). N_m^c (N_m per NSC-free dry mass) behaved similarly to N_m. However, there were two exceptions: N_m^c increased with RI in *P. tremula* ($P<0.05$) and was not significantly related to RI in *P. avium* ($P<0.1$).

Table 2. Relationships between leaf nitrogen content per leaf area (N_a, mmol m^{-2}) and leaf non-structural carbohydrate (NSC, ethanol-soluble carbohydrates plus starch) free dry mass per area (LMA^c, g m^{-2}).

Species	N_a vs. LMA^c					
	Intercept	P	Slope	P	r^2	*n*
A. platanoides	45.3	0.01	0.59	0.1	0.24	13
P. avium	16.6	0.08	1.47	0.001	0.81	24
P. tremula	−10.5	0.52	2.42	0.001	0.83	20
Q. robur	0.8	0.99	2.03	0.001	0.66	22

Leaf chlorophyll content per leaf area (Chl$_a$) was independent of irradiance in all species ($P>0.2$), except for *A. platanoides*, where it was negatively correlated with RI ($r^2=0.26$, $P<0.02$ respectively). However, chlorophyll content per dry mass (Chl$_m$, Chl$_a$/LMA) increased with decreasing RI (Fig. 4) and LMA ($r^2=0.38$–0.75, $P<0.001$) in all species. Similar correlations occurred also with Chl$_m^c$ (for RI: $r^2=0.23$–0.41, $P<0.05$; for LMA^c: $r^2=0.27$–0.58, $P<0.02$). Relationships of Chl$_m$ vs. RI (Fig. 4) and Chl$_m$ vs. LMA (data not shown) were not linear, and therefore the modelled curves of Chl$_m$ vs. RI, which took into account the hyperbolic dependence on leaf absorptance on leaf chlorophyll content and the changes in leaf anatomy (s. Appendix), resulted in higher proportion of determined variance than the linear approximations (e.g. for Chl$_m$ vs. RI relations the r^2-range was 0.33–0.77 for the modelled vs. 0.29–0.43 for the linear fit).

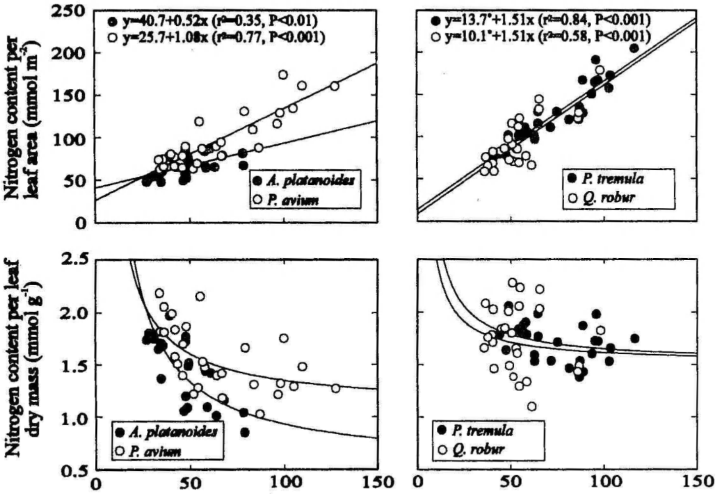

Fig. 3. Relationships between leaf area- and dry mass-based nitrogen content (N_a, mmol m^{-2} and N_m, mmol g^{-1}, respectively), and LMA (only total dry mass based variables). Hyperbolas for the N_m vs. LMA dependencies were fitted to the data using the parameters of linear N_a vs. LMA regressions ($N_a = a + b \times \text{LMA}$, $N_m = a/\text{LMA} + b$). Intercepts denoted by * are not significantly different from zero ($P>0.2$).

Table 3. Dependence of leaf chlorophyll (a+b) content per total (Chl_m, µmol g^{-1}) and per NSC-free dry mass ($\mathrm{Chl}_m{}^c$, µmol g^{-1}) on leaf nitrogen content per total (N_m, mmol g^{-1}) and per NSC-free dry mass ($N_m{}^c$, mmol g^{-1}), respectively.

Species	Chl_m (µmol g^{-1}) vs. N_m (mmol g^{-1})						$\mathrm{Chl}_m{}^c$ (µmol g^{-1}) vs. $N_m{}^c$ (mmol g^{-1})					
	Intercept	P	Slope	P	r^2	*n*	Intercept	P	Slope	P	r^2	*n*
A. platanoides	−11.3	0.001	15.3	0.001	0.78	22	−19.5	0.001	18.4	0.001	0.84	13
P. avium	−1.3	0.002	13.1	0.001	0.62	26	−14.2	0.01	13.3	0.001	0.53	24
P. tremula	−6.0	0.15	8.5	0.001	0.35	26	7.8	0.21	1.4	0.56	0.02	20
Q. robur	−7.6	0.03	10.0	0.001	0.57	24	−7.7	0.17	9.4	0.002	0.42	22

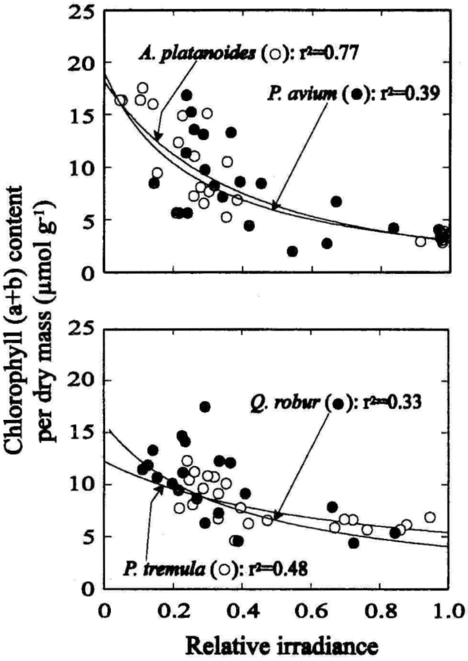

Fig. 4. Effect of relative irradiance on leaf chlorophyll (a+b) content per total leaf dry mass (Chl_m, µmol g^{-1}). The dependencies of LMA and calculated leaf absorptance on irradiance were used to fit the curves to the data (s. Eq. A3 in Appendix). Curve fitting to Eq. A3 with a single non-linear regression procedure yielded similar coefficients as the parameters of the linear regressions between LMA, leaf absorptance and irradiance and did not change the shape and position of the modelled curves considerably.

Chl_a increased with N_a only in *Q. robur* (r^2=0.26, P<0.02), but Chl_m was significantly related to N_m in all species (Table 3). However, the correlation between the quantities expressed on a NSC-free dry mass was not significant for *P. tremula* (Table 3). Further it appeared that Chl_m increased faster with decreasing irradiance than N_m did, causing the ratio of leaf nitrogen to chlorophyll (N/Chl) to be positively related to RI in all species (Fig. 5). Insofar as both N_m at high irradiance and the intercept of N/Chl vs. RI relationship, which provides an estimate of leaf nitrogen not associated with chlorophyll at low irradiance, were the least for shade-tolerant *A. platanoides* and *P. avium* (Figs. 3 and 5), the fraction of leaf nitrogen associated with leaf chlorophyll is likely to be higher in shade-tolerant than in intolerant species. Taking 50 mol N/mol Chl for the nitrogen cost of thylakoids (Evans 1989), the proportion of leaf *N* invested in light harvesting behaved similarly to Chl_m, increasing hyperbolically with decreasing irradiance (data not shown). Though the qualitative tendency was identical for all species, the range of variation was higher in more shade-tolerant *A. platanoides* (*ca* 10–50%) and *P. avium* (*ca* 10–60%) than in less tolerant *P. tremula* (*ca* 15–35%) and *Q. robur* (*ca* 15–40%). Chl a/b ratio was relatively insensitive to irradiance (Fig. 5), declining significantly with decreasing RI only in *P. avium* and *P. tremula*, and with LMA in *P. avium* (r^2=0.20, P<0.03) and *Q. robur* (r^2=0.19, P<0.05).

Implications for shade-tolerance

The intercept of N_a vs. leaf dry mass per area relationship was not statistically different from zero in *P. tremula* and *Q. robur* (Fig. 3, Table 2). Nevertheless, a gradual decline in the intercept values from *A. platanoides* to *Q. robur*, i.e., from the most shade-tolerant to most intolerant species (Table 1) was accompanied by decreasing steepeness of the N_m vs. LMA relations (Fig. 3). This gave a significant negative correlation between the intercept of N_a vs. LMA and Ellenberg's light figure (LF, s. Table 1 for explanation) (r^2=0.94, P<0.03). Though LF was not significantly related to the slope of N_a vs. LMA in the studied species (r^2=0.87, P<0.07), a good negative correlation was present between the slope and the intercept values (r^2=0.98, P<0.001). This correlation was even improved when the confounding variability in NSC was accounted for (r^2=0.999, P<0.001 for the correlation between the intercept and slope of N_a vs. LMA^c). When further data for deciduous *Acer saccharum* (Ellsworth & Reich 1992), *Betula pendula*, *Corylus avellana* and *Lonicera xylosteum* (Kull & Niinemets 1993) and evergreen *Picea abies* (Niinemets 1996b) were pooled with those of the current study, both the slope (Fig. 6A) and intercept (r^2=0.47, P<0.05) were significantly related to LF. The intercept and slope were also significantly correlated for the lumped set of data (Fig. 6B). The evergreen conifer *P. abies* had lower nitrogen concentrations than the deciduous species (data not shown), and the exclusion of this species from the analysis improved the correlations somewhat (e.g. for the relationship between the slope of N_a vs. LMA and LF r^2=0.67 with and r^2=0.75 without *P. abies*).

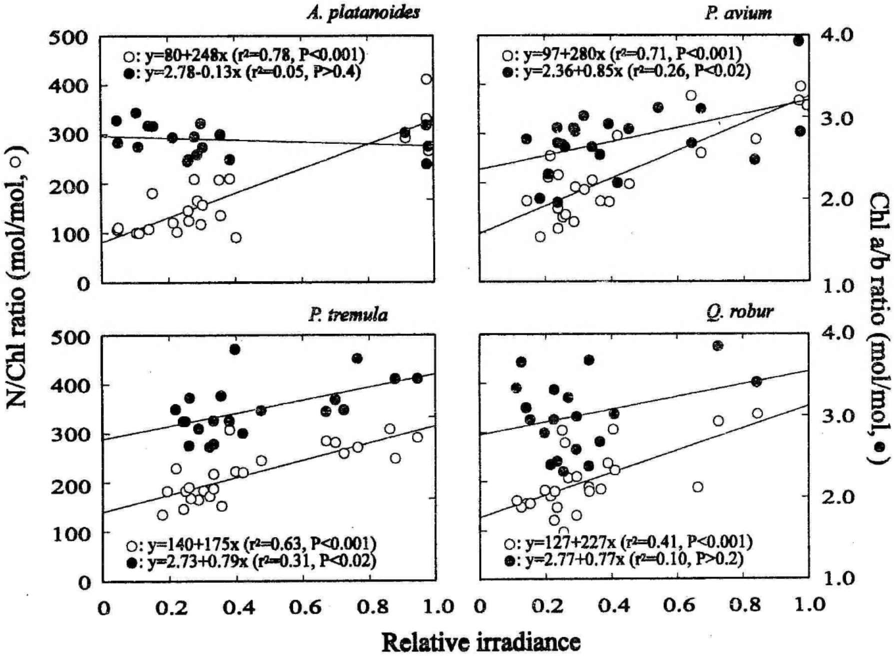

Fig. 5. Influence of relative irradiance on the molar ratios of leaf nitrogen to chlorophyll (a+b) (N/Chl) and chlorophylls a to b (Chl a/b).

To get further insight into the interrelationships between nitrogen partitioning among the leaves (Fig. 6) and within the leaf, I examined the parameters of statistical relationships of leaf chlorophyll vs. nitrogen and irradiance for the dependence on the parameters of N_a vs. LMA relationship. It appeared that the proportional investment of leaf nitrogen in chlorophyll (slope of Chl_m vs. N_m and the intercept of N/Chl vs. RI) was related to the slope of N_a vs. LMA^c (Fig. 7) or to the slope of N_a vs. LMA (data not shown).

Discussion

Leaf morphology

Since LMA and RI are linearly related (Fig. 1 and the references in the introduction section), LMA, which integrates the physiological effects of different light quantities, qualities (Kwesiga, Grace & Sandford 1986) and peak intensities (Wayne & Bazzaz 1993) on leaf structure, may be an even better estimate of long-term light climate than RI. However, species differ remarkably in

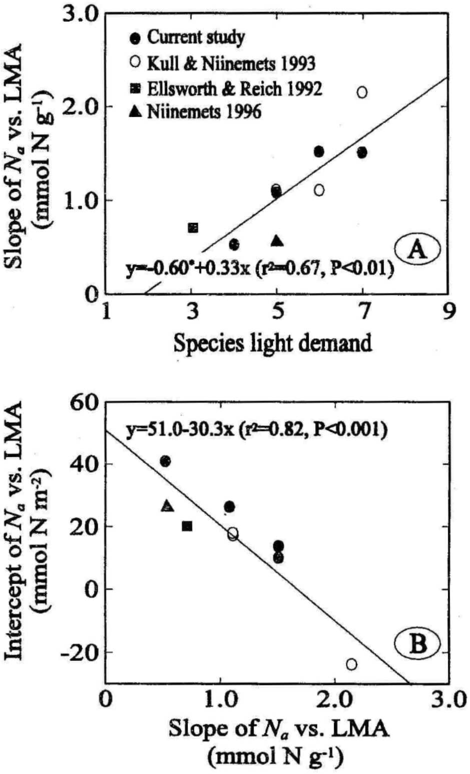

Fig. 6. Nitrogen partitioning in correlation with leaf dry mass per area vs. species light requirement. **A.** Dependence of the slope of the N_a vs. LMA relationship (mmol N g^{-1}) on species light demand value (* — intercept is not significantly different from zero). In addition to the studied species *Betula pendula*, *Corylus avellana* and *Lonicera xylosteum* from Kull & Niinemets (1993); *Acer saccharum* from Ellsworth & Reich (1992) and *Picea abies* from Niinemets (1996b) are also plotted. For the European species, the light demand values were obtained from Ellenberg (1991, see also Table 1). Given that *A. saccharum* is one of the most shade-tolerant North-American woody species (Baker 1949), and that the light demand scale spans from 3 to 9 for the European woody taxa (Ellenberg *et al.* 1991), it was assigned a light demand value of 3. **B.** Correlation between the intercept (mmol N m^{-2}) and the slope of the N_a vs. leaf dry mass per area relationship. Data presentation as in panel A.

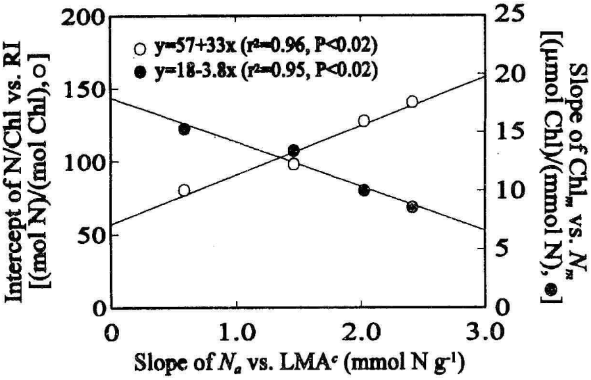

Fig. 7. Nitrogen partitioning in correlation with leaf dry mass per area vs. nitrogen partitioning within the leaf: relationships between the intercept of N/Chl molar ratio vs. RI [(mol N)/(mol Chl)]), slope of Chl_m vs. N_m [(µmol Chl)/(mmol N)] and slope of N_a vs. LMA.

the tuning of leaf morphology with respect to the prevailing irradiance. In general, at a common irradiance shade-tolerant species have lower LMA than intolerant ones (Niinemets & Kull 1994), but there exists a large interspecific variability in morphological flexibility with respect to light conditions. On the basis of LMA vs. RI relationships, shade-tolerant species may have greater (Goulet & Bellefleur 1986; Kull & Niinemets 1993 and *P. avium* in this study) or lower (Loach 1967; Fetcher, Strain & Oberbauer 1983; Walters & Field 1987; Ducrey 1992 and *A. platanoides* in this study), on the basis of leaf thickness vs. RI, greater (Goulet & Bellefleur 1986; Chazdon & Kaufmann 1993), similar (Carpenter & Smith 1981) or lower (Jackson 1967; Fetcher, Strain & Oberbauer 1983; Ashton & Berlyn 1994) plasticity than intolerant species. In the current study, lowest morphological plasticity in *A. platanoides* may be explained by the large leaf size in this species (Table 1): because the costs for leaf support scale positively with leaf size (Givnish 1979), a trade-off goes on between light-mediated anatomical adjustment in leaf thickness and rapidly increasing carbon demand for leaf support. Nevertheless, the current study and the aforementioned evidence from many independent works seem to support the argument that the considerations of species plasticity based on leaf anatomy and morphology alone do not lead to generalisations and patterns which would hold for a large number of taxa.

Non-structural carbohydrates

Because photosynthesis strongly depends on irradiance, but carbon translocation is nearly constant (Servaites *et al.* 1989) or only slightly light-dependent (Hendrix & Huber 1986), the concentration of leaf non-structural carbohydrates closely follows diurnal course of light (Servaites *et al.* 1989). Accordingly, higher daily cumulative photosynthesis at greater irradiances is likely to provide an explanation for the positive relationships between ESC and TNC with RI (Fig. 2, Niinemets 1995,1996b). Of course, species potentials in terms of photosynthetic capacity are also likely to affect the non-structural carbohydrate vs. irradiance relations (Takahashi, Tsuchihashi & Nakaseko 1993).

Photosynthetic capacity per leaf area (P^a_{max}, light-saturated net photosynthesis rate at an ambient CO_2 concentration of 350 ppm) for leaves grown at a RI of 0.9 is 9.0 for *P. tremula* (Tselniker 1979), 7.3 for *Q. robur* (Malkina 1983) and 5.1 µmol m^{-2} s^{-1} for *A. platanoides* (Tselniker 1979). Calculation of P^m_{max} (photosynthetic capacity per leaf dry mass, P^a_{max}/LMA) from the LMA values at RI=0.9 (Fig. 1) gives a species ranking, which is the same as according to the slope values of ESC vs. RI relationships. This calculation shows that the confounding effect of ESC on diverse leaf chemical and morphological parameters is variable at a common irradiance between the species due to different P^m_{max} values. To exclude the light- and species-related variation in ESC, expression of leaf parameters on a NSC-free dry mass may serve as an useful alternative to total dry mass. Yet the subtraction of NSC from total dry mass is open to criticism, since (1) a part of leaf ESC such as leaf glycosides, which also give colour reaction with anthrone (Yemm & Willis 1954), may not directly be associated with daily photosynthetic carbon metabolism as becomes evident from the non-zero intercept values of ESC vs. RI relations (Fig. 2), and (2) NSC-pool is not metabolically inactive, e.g. accumulation of NSC may suppress further photosynthesis (Azcón-Bieto 1983). Nevertheless, in the current study the conclusions were robust and were only slightly biased by using the parameters per total dry mass rather than per NSC-free dry mass.

Partitioning of leaf chlorophyll and nitrogen: significance for light harvesting

An increase in the proportional investment of leaf nitrogen in thylakoids, improving light use-efficiency for an incident irradiance, is a major response of leaf nitrogen partitioning within the leaf to decreased growth irradiance (Evans 1989,1993a). There is a wide consensus that this increase is even more significant for species of greater shade-tolerance (Seemann *et al.* 1987; Evans 1989,1993a). These, previously established patterns, were also observed in the current study. While N_m varied about two-fold with RI and LMA (Fig. 3), the differences in Chl_m were up to five-fold (Fig. 4), resulting in a positive relationship between N/Chl and RI (Fig. 5), and in a negative one between the nitrogen investment in light harvesting and RI. Of course, calculation of nitrogen cost of thylakoids using a constant conversion factor of 50 mol N/mol Chl (Evans 1989) over the whole range of RI is a simplification, and may have resulted in biased estimates, because light-related modifications in thylakoid composition influence the nitrogen requirement for thylakoid formation as well (Evans & Seemann 1989). Adaptation to low irradiance involves an increase in light harvesting complexes of photosystem II (LHC II) (Leong & Anderson 1984; Anderson & Osmond 1987), which are less costlier in terms of nitrogen per unit of chlorophyll than e.g. the protein complexes of photosystems I and II (Evans & Seemann 1989). Given that LHC II proportionally increases with decreasing Chl a/b ratio (Anderson & Osmond 1987; Evans 1988), and that Chl a/b ratio was only slightly related to RI in the current study (Fig. 5) the qualitative relationships between nitrogen investment for light harvesting and irradiance are not likely altered by ignoring the effects of light on thylakoid composition.

Because the relationship between Chl_a and leaf absorptance is asymptotic (Gabrielsen 1948; Evans & Seemann 1989; Agustí *et al.* 1994, s. also Appendix), enhanced quantum capture is expensive in units of nitrogen, and large investments of leaf nitrogen in light harvesting compounds result in only moderately improved returns in terms of intercepted light (Evans & Seemann 1989). This is probably why N_m increases with decreasing irradiance (Fig. 3). The explanation of higher N_m at low irradiance in shade-tolerant species by disproportionately increasing requirements for light harvesting chemicals is further supported by more responsive N_m in more tolerant species (Fig. 3, Table 2), which have also greater fraction of foliar resources in light intercepting compounds (cf. above).

Dependence of light absorptance of plant tissues in the region of PAR (400–700 nm, A_l) on their chlorophyll content has a fundamental character (Agustí *et al.* 1994), which is similar to all plant taxonomic groups. Light-limitation imposed on photosynthesis may considerably be relieved by high leaf chlorophyll concentrations, which improve A_l and the quantum yield for an incident light flux (e.g. Gabrielsen 1948). However, this is different at greater irradiances, where high chlorophyll content causes also mutual shading between the photosynthesising cells in a leaf to increase, and as such reduces $P^a{}_{\max}$ (Leverenz 1987). Therefore, for optimum photosynthetic performance, leaf absorptance should be high under low irradiance and low under high irradiance (Laisk 1982). However, the data which support this hypothesis are contradictory. St-Jacques *et al.* (1991) and Langenheim *et al.* (1984) for a number of seedlings of temperate and tropical woody species, respectively, found higher A_l values in the understory environment, but A_l was independent of growth irradiance in *Pisum sativum* (Evans 1987), and decreased with decreasing irradiance in *Nothofagus solandri* (Hollinger 1989) and *Fagus sylvatica* (Eller, Glättli & Flach 1981). Leaf transmittance, which is negatively related to A_l (Osborne & Raven 1986) was independent of growth irradiance in seedlings of five temperate species (Tselniker 1975). Because A_l is a function of Chl_a (Eq. A1; Evans 1993b; Agustí *et al.* 1994), the inconsistency in the reactions of A_l to light availability should be paralleled with similar variability in Chl_a vs. irradiance relationships. This is indeed the case: with decreasing irradiance Chl_a increases in *A. platanoides* (this study), *A. saccharum* (Ellsworth & Reich 1992), *Fagus grandifolia* (Loach 1967), *Leea coccinia* (Sarracino, Merritt & Chin 1992) and in a number of tropical woody species (Langenheim *et al.* 1984), decreases in *Betula pendula* (Öquist, Brunes & Hällgren 1982), *Canarina canariensis* (Morales, Jimenez & Caballero 1991), *Eucalyptus fastigata* (Cameron 1970), *Fagus sylvatica* (Eller, Glättli & Flach 1981; Lichtenthaler *et al.* 1981) or is virtually constant in *Borojoa patinoi* (Lynch & González 1993), *P. avium*, *P. tremula* (this study) and *Populus tremuloides* (Loach 1967). Given the large variability in Chl_a, it is particularly striking that Chl_m constantly increases with decreasing growth irradiance (Fig. 4, Loach 1967; Eller, Glättli & Flach 1981; Lichtenthaler *et al.* 1981; Wilhelm & Wild 1984; Morales, Jimenez & Caballero 1991; Dale & Causton 1992; Lynch & González 1993). According to Wilhelm & Wild (1984) and the current study (Fig. 4; Appendix) this response is non-linear.

Leaf anatomy is a relevant factor affecting leaf absorptance (Osborne & Raven 1986), because it determines Chl_m, which is necessary to attain the same absorptance ($\mathrm{Chl}_a = \mathrm{Chl}_m \times \mathrm{LMA}$, see also Eqs. A1–A3). Accordingly, for a common A_l the requirement of leaf resources in light harvesting is dependent on the morphological plasticity of a species. As the current study (in terms of Chl_a) and previous research (cf. above) elucidate, A_l and growth irradiance are not necessarily correlated. Nevertheless, leaf absorptance per mass rather than per area provides a measure of how sufficiently photosynthesising cells are supplied with light. Inasmuch as a highly significant correlation occurs between Chl_m and leaf absorbance per dry mass (Agustí *et al.* 1994), adaptation to low irradiance seems to involve modifications in leaf chemistry towards optimising absorptance per mass rather than per area (Fig. 4).

Implications for species shade-tolerance

Photosynthetic plasticity — the slope of the change in either $P^m_{\max}$ or $P^a_{\max}$ with growth irradiance — is consistently lower in shade-tolerant than in intolerant species (Bazzaz & Carlson 1982; Kwesiga, Grace & Sandford 1986; Chazdon & Kaufmann 1993; Ashton & Berlyn 1994; Ducrey 1994). This difference is associated with proportionally lower investment of foliar nitrogen in carboxylating enzymes in shade species (Seemann *et al.* 1987). However, photosynthesis at saturating irradiance poorly reflects photosynthetic behaviour of the species under limiting irradiance, where inverse patterns become evident (Koike 1988; Ducrey 1994). In low-light conditions, where foliar morphology and physiology (cf. refs. above) are modified towards efficient use of light, it may clearly not be essential to maximise the rate of light-saturated photosynthesis for a given N_m. There is evidence that the partitioning pattern of foliar nitrogen changes continuously during succession and that interspecific variability in nitrogen distribution may be a relevant feature determining species composition: early successional species have higher nitrogen use-efficiency ($P^m_{\max}/N_m$) and greater slopes of N_m vs. $P^m_{\max}$ relationships than late successional species do (Reich *et al.* 1994). As succession goes on, efficiency of light use gains in importance and species that are not able (intolerant species) to adjust their physiology and morphology towards improved light interception are replaced by those that are (shade-tolerant ones).

Since the slope and intercept of the N_a vs. LMA relationship determine how N_m is distributed along a light gradient, significant correlations between these parameters and species light requirement (Fig. 6) indicate that the distribution pattern of N_m may play a central role in species shade-tolerance. Given that the slopes of N_a vs. LMA (N_a vs. LMA^c) are statistically more reliable than the intercepts (Fig. 3, Table 2), and closely related to intercepts (Fig. 6B), they may serve as simple predictors of species shade-tolerance. Furthermore, the highly significant correlation between the slope of N_a vs. LMA and the proportional investment of leaf nitrogen for light harvesting (Fig. 7) further strengthens the predictive value of N_a vs. LMA relationships.

Negative correlation between the intercept and slope of N_a vs. LMA relations (Fig. 6B) manifests that the higher is N_m at low light the lower is N_m at high light. Though the nitrogen requirements for light harvesting decrease with increasing irradiance, efficient use of high irradiances calls for increasing nitrogen investment in carboxylating enzymes and proteins responsible for photosynthetic electron transport. Due to decreased nitrogen concentrations at high irradiance (Fig. 3), the latter demands are not likely to be adequately met in shade-tolerant species. Conservative nitrogen investment pattern in light harvesting vs. carbon reduction capacities is probably the reason why shade-tolerant species are of intrinsically low photosynthetic plasticity.

Conifers display also compatible performance to deciduous species: N_m increases with decreasing irradiance in shade-tolerant *Abies alba* (Aldinger 1987) and *Picea abies* (Aldinger 1987; Niinemets 1996b, Fig. 6), but shows the opposite trend in intolerant *Pinus radiata* (Kelly & Lambert 1972), *Pinus sylvestris* (Heinze & Fiedler 1976) and *Pseudotsuga menziesii* (Lavender & Carmichael 1966). However, *P. abies* had lower slope of N_a vs. LMA relationship than the deciduous species (Fig. 6). This discrepancy is probably related to lower foliar nitrogen concentrations and physiological activity in conifers vs. deciduous species (Reich, Walters & Ellsworth 1992; Reich *et al.* 1995).

From a canopy perspective, decreasing N_m with increasing irradiance in shade plants (*A. platanoides* and *P. avium*) results in less costly leaves in terms of nitrogen, and allows to construct larger foliar surface area with the same investment of plant nitrogen in leaf production. This should lead to a more extensive foliar display for light capture and finally to significant improvement of light interception per plant. Indeed, previous research has demonstrated that at a common irradiance the saplings of similar size of *A. platanoides* have greater proportion of plant biomass in foliage and also greater foliar surface area than those of *Q. robur* (Niinemets 1996a).

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Appendix. Modelling of leaf chlorophyll vs. relative irradiance curves

To better understand the significance of light-related variability in leaf chlorophyll concentration per dry mass (Chl_m) I express it in terms of light-related changes in leaf absorptance. An estimate of leaf absorptance, A_l, was calculated according to the empirical equation of Evans (1993b) as:

$$A_l = \frac{\mathrm{Chl}_a}{\mathrm{Chl}_a + 76}, \qquad \text{eqn A1}$$

where Chl_a is leaf chlorophyll (a+b) content per leaf area (µmol m^{-2}). Eq. A1 holds for leaves without significantly hairy and waxy leaf surfaces, and has been derived for a broad range of species with an Ulbricht integrating sphere (Evans 1993b). Chl_m vs. relative irradiance curve was modelled on the basis of two assumptions: (1) LMA is a linear function of RI (see introduction section, Fig. 1); (2) A_l is dependent on RI (e.g. Eller, Glättli & Flach 1981; Hollinger 1989; Ellsworth & Reich 1992). Substituting $\mathrm{Chl}_a=\mathrm{Chl}_m \times \mathrm{LMA}$ in Eq. A1 and expressing Chl_m we obtain:

$$\mathrm{Chl}_m = \frac{A_l \times 76}{\mathrm{LMA} \times (1 - A_l)}. \qquad \text{eqn A2}$$

Revealing LMA in the form of $\mathrm{LMA}=C_1 \times \mathrm{RI}+C_2$, assuming that $A_l=C_3 \times \mathrm{RI}+C_4$, and substituting LMA and A_l in Eq. A2 we achieve a hyperbolic dependence between only Chl_m and RI:

$$\mathrm{Chl}_m = \frac{(C_3 \times \mathrm{RI} + C_4) \times 76}{(C_1 \times \mathrm{RI} + C_2) \times (1 - C_3 \times \mathrm{RI} - C_4)}, \qquad \text{eqn A3}$$

where C_1, C_2, C_3 and C_4 are empirical species specific coefficients which may be obtained from linear regressions between LMA vs. RI and A_l vs. RI or by a non-linear fit to the Eq. A3. The relationship between A_l and RI is more hypothetical than the well-known dependence of LMA on RI. In the current study, calculated leaf absorptance (Eq. A1) was negatively related to irradiance only in *A. platanoides* ($r^2=0.50$, $P<0.001$), but in addition to this species ($r^2=0.24$, $P<0.02$) A_l decreased with LMA also in *P. avium* ($r^2=0.14$, $P<0.06$). Nevertheless, when the slope of hypothesised A_l vs. RI relation (C_3) is not significantly different from zero, C_4 becomes equal to mean leaf absorptance.

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Niinemets, Ü. 1996. Compromises between sapling allometry and shade-tolerance in two temperate deciduous species. (Submitted)

Compromises between sapling allometry and shade-tolerance in two temperate deciduous species

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Abstract

Growth and biomass partitioning across a natural light gradient were examined in saplings (0.3–2.6 m in height) of relatively shade-tolerant *Acer platanoides* and relatively intolerant *Quercus robur* for dependence on relative irradiance, calculated from hemispherical photographs (RI), and on total tree height (*H*). *H* and RI were independent of each other. All allometric relationships between *H* and the parameters of plant biomass and dimensions were positively affected by RI, signifying that at a common *H*, saplings increased horizontal relative to vertical growth in environments with greater irradiance. Mass ratios of plant compartments were also dependent on incident irradiance. Root mass ratio (coarse plus fine roots per total plant biomass) increased with increasing irradiance in both species, and was not different between the species. However, *Q. robur* had a larger stem mass ratio, while *A. platanoides* had a greater leaf mass ratio (LMR). Leaf mass per area (LMA) was lower in *A. platanoides*. As a result of these interspecific differences in fractional allocation of sapling biomass in foliage and biomass requirement for construction of leaf surface area, leaf area ratio (LAR=LMR/LMA) was larger in *A. platanoides*. Relative growth rate of standing biomass (RGR) was significantly correlated with RI in both species, and was not different between the species. In contrast, net assimilation rate per unit leaf area (NAR_a) was larger in *Q. robur*. Thus, in these species similar RGR ($NAR_a \times LAR$) was achieved in a completely different way: *A. platanoides* increased the intercepting foliar area, while *Q. robur* increased the productivity per unit area. Biomass allocation between different compartments was also dependent on sapling size. With increasing *H*, *A. platanoides* maintained a constant proportion of biomass in foliage, but the relative amount of foliage decreased in *Q. robur*. Therefore, due to a decreasing investment of resources in foliage construction with advancing sapling ontogeny, saplings of similar height require more light to survive in *Q. robur* than in *A. platanoides*. Greater investment of biomass in leaves vs. standing biomass may result in lower volume gain and reduced competitive ability in more open habitats in *A. platanoides*. These results suggest that the interspecific differences in allometry significantly alter species competitive relations during sapling development across gap-understory continuum.

Key Words: *Acer platanoides*, dry matter partitioning, gap-understory gradient, growth rates, irradiance, *Quercus robur*

Introduction

Ecophysiology of growth and survival of woody taxa in environments differing in relative irradiance has drawn considerable attention in studies on species shade-tolerance (King 1991, 1994, Kitajima 1994). It appears that the survival of seedlings under low irradiance is dependent on traits which increase their resilience to herbivores and pathogens (Kitajima 1994). Because these traits require high investment of plant resources in non-productive structures, shade-tolerance of seedlings is negatively correlated with growth rate in both high and low irradiance (Kitajima 1994). However, most research on growth of woody taxa across light gradients has been constrained to seedling stage of development, and only in very few cases the growth of above-ground parts of saplings has been followed (Chan and Walstad 1987, King 1991, 1994, Oberbauer *et al.* 1993). Since the probability of plant survival increases with increasing plant age (e.g. Hett and Loucks 1971), it is not necessarily clear to what extent the factors determining shade-tolerance for the seedling and sapling stage are the same. It is further questionable if the results obtained on seedlings can be extended to saplings and even to trees. As a plant gets larger, both standing biomass and storage pools increase, possibly making it less prone to accidental damage or attack by herbivores and pathogens. Yet there is evidence of decreasing plasticity with increasing tree size: larger trees have less foliar area per unit biomass investment in leaves (Kull and Niinemets 1993, Niinemets 1995, 1996b, Niinemets and Kull 1995), greater water limitations in stems and accordingly lower stomatal conductances (Yoder *et al.* 1994), greater proportion of supporting and lower of assimilative structures in foliage (Niinemets 1996b), and lower respiratory and photosynthetic activities of plant structures (Walters *et al.* 1993b) than small trees do. Due to disproportionately increasing biomass requirements for mechanical stability, various allometric constraints also gain in importance as plants increase in size (Whittaker 1962, Ledig *et al.* 1970, Chalmers and van den Ende 1975, Walters *et al.* 1993b).

In woody species, irradiance positively influences both height and diameter growth (Greis and Kellomäki 1981), causing the productivity to increase quasi-linearly with increasing light interception (Jarvis and Leverenz 1983, Chan and Walstad 1987). Though the net carbon gain of both early- and late-successional species is similarly affected by elevated light levels (King 1991, Oberbauer *et al.* 1993), the growth of intolerant species is more responsive to irradiance and surpasses the growth of both seedlings (Kitajima 1994) and saplings (King 1991, Oberbauer *et al.* 1993) of shade-tolerators. To gain insight into the determinants of superior growth, in many cases it appears useful to distinguish between biochemical potentials, which alter productivity per unit foliar area, and allocation patterns, which change foliar area per plant (Lambers and Dijkstra 1987, Poorter 1990). However, these components of growth rate do not separate seedlings of shade-tolerators from those of intolerant species, in which either higher foliar area (Rincón and Huante 1993) or assimilation rate (King 1994), in others both (Walters *et al.* 1993a) may play a dominant role in yielding greater growth. On the other hand, it is well established that the biomass allocation patterns are not constant during plant ontogeny (cf. above); moreover, positive relationship between growth rate and irradiance implies that the changes in irradiance inevitably bring about differences in size, which, in turn, are likely to modify biomass distribution and growth. As trees grow, the proportion of biomass invested in leaves generally decreases (Whittaker 1962, Walters *et al.* 1993b). For habitat separation between species along gradients of irradiance it is particularly relevant how rapidly the fractional investment of biomass in foliage decreases with size. This varies between species (Whittaker 1962, Walters *et al.* 1993b), signifying that interspecific differences in allometry may influence competitive relations during plant ontogeny. Moreover, several environmental variables covary with irradiance across natural light gradients (Bazzaz and Wayne 1994), e.g. water (Bazzaz and Wayne 1994) and nitrogen (Tilman 1993) availabilities may decrease with increasing irradiance. As both water and nutrient accessibilities influence the proportion of plant biomass in roots (Brouwer 1983), apart from a size-related drift in biomass allocation with irradiance, other environmental factors, which become modified across light gradients, may also influence dry matter partitioning.

To get a more detailed understanding of ontogenetic changes in plant allometry and associated alterations in species ability to tolerate shade, I studied sapling growth and biomass partitioning in dependence on both relative irradiance and tree size in two deciduous temperate woody species differing in shade-tolerance. According to Ellenberg *et al.* (1991) *Acer platanoides* L., occurring at minimum relative irradiances (proportion of open sky) as low as 0.05–0.1, is more tolerant than *Quercus robur* L. with a minimum relative irradiance range of 0.3–0.4. In this paper, I address the following questions: (1) How do sapling allometry and growth change across a natural gradient of irradiance? (2) Are the relationships between irradiance, and sapling allometry and growth different between the species? Can these relationships provide an explanation for interspecific differences in shade-tolerance? Having answered to (1) and (2) I focused on: (3) Do allometric changes in dry matter partitioning during ontogeny alter species competitive strength and ability to tolerate shade?

Materials and methods

Experimental site and sapling harvesting

The study site was located in a mixed forest dominated by about 100-yr-old trees of *Picea abies* (L.) Karst. on gleyic and gleyed pseudopodzolic soils at Tôrvandi (58° 20' N, 26° 42' E; elevation 60–65 m above sea level), Estonia. Various thinning histories of different stand regions assured that a considerable range of light availabilities in the understory was available. Also, there were several old (>5 yr) clearcuttings that provided the habitats with the highest relative irradiances. To find the most shaded saplings, extensive searches in the understory were carried out. 22 saplings for *Acer platanoides* and 27 for *Quercus robur*, all of seed origin, were carefully excavated from the soil during two weeks (5–19) in August 1993 across a gradient of incident irradiance. Excavated saplings were placed in plastic bags, and immediately transported to the laboratory for further study. To standardise the conditions for the analysis of chemical composition of foliage and twigs, plant sampling was restricted to midday hours 12.00–13.00 on cloudy days. At our latitudes these species usually have determinate growth and flush annually only once, few plants of *Q. robur* growing under medium irradiances, which had a small number of lammas shoots, were discarded from the analysis.

Several hemispheric photos were taken directly above the crown of every sapling, and the differences between the saplings in relative irradiance (RI) were quantified by a hemispheric photographic method (Anderson 1964) as modified by Nilson and Ross (1979). Correcting measured gap fractions for cosine of incidence effects, relative amount of penetrating diffuse solar radiation was calculated from the photographs. RI ranges from zero to one, whereas a value equal to 1.0 gives the diffuse irradiance above the stand, RI is 0.0 with no penetrating canopy gaps. The calculations of RI were done for uniformly overcast sky conditions, since in long term the influence of different sky brightness distributions on RI is generally less than 5% (Nilson and Ross 1979).

All means for the measured biomass parameters and abbreviations used throughout the study are given in table 1. Because total tree height (H) or natural logarithm of H (LnH) were independent of RI in both *A. platanoides* and in *Q. robur* ($P>0.05$), LnH was included in the statistical models as the second orthogonal variable. None of the means of the allometric parameters were significantly different between the species ($P>0.05$, t-test, Table 1), however the ranges were always larger for *A. platanoides*, e.g. for H (0.30–2.63) m in *A. platanoides* vs. (0.30–1.53) m in *Q. robur*.

Table 1. Explanation of symbols and mean values of all measured allometric parameters in *Acer platanoides* (n=22) and *Quercus robur* (n=27).

Character	Explanation	Mean±SE[*]	
		A. platanoides	*Q. robur*
H	Total tree height (m)	1.04±0.12	0.99±0.06
A	Tree age (yr)	10.2±0.9	9.3±0.6
D_b	Stem diameter at the base (m)	$(1.19\pm0.16)\cdot10^{-2}$	$(1.00\pm0.10)\cdot10^{-2}$
D_m	Mean stem diameter (m)	$(8.34\pm0.87)\cdot10^{-3}$	$(7.19\pm0.60)\cdot10^{-3}$
L	Leaf area (m^2)	0.46±0.11	0.244±0.040
M_l	Leaf mass (kg)	$(2.27\pm0.69)\cdot10^{-2}$	$(1.31\pm0.29)\cdot10^{-2}$
M_s	Stem mass (kg)	$(6.4\pm1.9)\cdot10^{-2}$	$(5.3\pm1.2)\cdot10^{-2}$
V_s	Stem volume (m^3)	$(8.9\pm2.6)\cdot10^{-5}$	$(5.5\pm1.2)\cdot10^{-5}$
M_{sh}	Shoot mass (M_l+M_s) (kg)	$(8.6\pm2.6)\cdot10^{-2}$	$(6.6\pm1.5)\cdot10^{-2}$
M_r	Root mass (kg)	$(7.2\pm2.4)\cdot10^{-2}$	$(5.4\pm1.8)\cdot10^{-2}$
V_r	Root volume (m^3)	$(8.9\pm2.6)\cdot10^{-5}$	$(6.0\pm1.9)\cdot10^{-5}$
M_t	Total plant mass ($M_{sh}+M_r$) (kg)	0.158±0.050	0.121±0.032
V_t	Total volume (V_s+V_r) (m^3)	$(1.83\pm0.57)\cdot10^{-4}$	$(0.98\pm0.24)\cdot10^{-4}$

[*] None of the means were significantly different ($P>0.05$). Means were compared by t-test, all variables, except for A, were transformed before comparisons using natural logarithmic transformation.

Analysis of biomass and sapling growth

Starting from the top of the sapling canopy, phyllosphere layers of 0.1 m were harvested. From every layer a random sample of leaves, consisting at minimum of five, and of all, if there were less than five leaves, was taken for leaf area estimations. Foliar area was measured with a computer digitizer (QD-1212, QTronix, Taiwan). Dry mass of all plant organs was determined after oven-drying at 70 °C to a constant mass. Foliar area in a layer was calculated as the ratio of dry mass of the leaves to leaf dry mass per area (LMA) of the sample leaves in the layer. Leaf area of the layers was further summed up to yield total leaf area per sapling.

Volumes of previously dried (70 °C) whole root systems (coarse and fine roots) and stems with branches were estimated by a water displacement method (Burdett 1979). I preferred the volume of dry rather than fresh organs, because there is evidence that water content of more shaded stems is higher than that of less shaded ones (Ingestad and McDonald 1989). This would have resulted in differential shrinkage of wood (Skaar 1988), and thus in light-related changes in organ density (volume per weight) even if wood anatomy was constant. Though the stem diameter at stem base (mean of two measurements in perpendicular directions) was always larger for fresh than for dry stem, both variables were strongly correlated (r^2=0.78, P<0.001 for *A. platanoides* and r^2=0.93, P<0.001 for *Q. robur*). Thus, the volumes of dry plant material also serve as the estimates of the fresh volumes in natural conditions. Assuming that the cross-section of the stem is circular, mean stem diameter, D_m, was calculated as:

$$D_m = 2\sqrt{\frac{M_s}{\Pi \times \mathrm{WD}_s \times H}}, \tag{1}$$

where M_s is stem dry mass (log and branches) and WD_s is stem density (V_s/M_s).

Sapling age was estimated by counting the tree rings at the base. The annual stem basal area increment was calculated from the measurements of stem cross-section area increment at various stem heights (one to four) as (Whittaker and Woodwell 1968):

$$\Delta\mathrm{BA} = \frac{1}{k}\left(\sum_{i=1}^{i=k}\frac{r_A^2 - (r_A - r_{A-1})^2}{r_A^2}\right), \tag{2}$$

where r_A is current (at age A) stem radius, r_{A-1} is stem radius for sapling age A–1 and k is the number of examined stem heights. Four to six radii in various directions were measured at every height and mean values for both r_A and r_{A-1} used in equation 2. Analogously, stem growth increment could be calculated for plant age A–1 and A–2. Proportions of pith and bark in stem basal area were found by the same technique. Root growth was assumed to be proportional to the actual root/stem mass ratio, and thus annual growth of standing biomass computed as:

$$\Delta\mathrm{M} = \Delta\mathrm{BA}\left(M_s + M_r\frac{M_r}{M_s}\right). \tag{3}$$

Inasmuch as dry matter partitioning may be altered by both changing irradiance (cf. Introduction) and plant size, assuming a constant biomass partitioning over the plant life-time may be incorrect. However, in most-cases the saplings had been established after the changes in light regime in the stand. To get further insight into the temporal variability of growth and environment, several correlations between various estimates of growth rate were calculated. It appeared that (1) current-year stem basal area increment and mean basal area increment of the three former years were strongly correlated (r^2=0.47, P<0.001 for *A. platanoides* and r^2=0.75, P<0.001 for *Q. robur*), (2) as were $\mathrm{Ln}(M_s+M_r)/A$ — an estimate of relative growth rate over the plant life-time (assuming that seed mass at A=0 did not vary appreciably between the studied saplings within the species) — and Ln(ΔM) (r^2=0.47, P<0.001 for *A. platanoides* and r^2=0.32, P<0.001 for *Q. robur*). Correlations (1) and (2) hint at relatively similar growth environments during the sapling life-span, and accordingly, support the use of Eq. 3 for calculation of ΔM. Biomass investment in current-year twigs was also estimated separately, and because it was proportional to stem growth (Fig. 1A) no correction factors were used in equation 3. Since bark makes up only a small fraction of total biomass (data not shown) its growth was ignored. Furthermore, bark growth scaled also with stem growth (Fig. 1B).

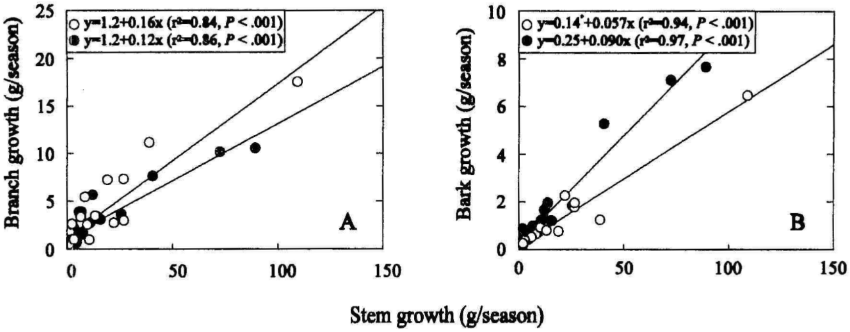

Fig. 1. Correlations of annual stem growth with current-year twig (**A**) and bark growth (**B**) in *Acer platanoides* (O, n=22) and in *Quercus robur* (●, n=27). Twig growth was measured separately. An estimate of bark growth was calculated, assuming similar density of wood and bark, and a constant bark basal area increment over plant life-span ($M_s \times RB_b / A$, where M_s is dry mass of stem, RB_b the proportion of basal area in bark and A is sapling age. Intercepts with * do not differ significantly from zero.

To be consistent with traditional growth analysis, relative growth rate (Hunt 1982) of standing biomass (kg $kg^{-1}season^{-1}$) was calculated as: $RGR = Ln(M_r + M_s) - Ln(M_r + M_s - \Delta M)$. RGR, determined this way, was considered to be a more appropriate estimate than the one including also annual leaf production, because the foliage is lost at the end of the growing season. Nevertheless, all relationships were qualitatively identical by using either RGR for standing or for total biomass.

The length of growing season at these latitudes typically extends to *ca.* 4–4.5 months. Because it was not possible to harvest all saplings at once, "season length" differed between the saplings. Flushing patterns may also depend on habitat exposure (McGee 1986), and therefore the time of growth outset is also not clearly defined. To clarify the significance of the different durations of growth on the annual carbon balance, several calculations with an arbitrarily chosen starting point were carried through. These calculations indicated that the difference in annual production between the foremost and latest harvests might be as large as 15%. However, because sampling date, and RI and sapling size were independent of each other ($P > 0.05$ for both species), the conclusions based on growth rates, standardised for a common season length, should not be qualitatively different from those based on untransformed values.

Net assimilation rate per foliar area (NAR_a), i.e. the production of standing biomass per unit leaf area per season, was calculated as RGR per leaf area ratio (LAR, foliar area per total plant mass), and per foliar dry mass (NAR_m) as RGR per leaf mass ratio (LMR, leaf mass per total plant mass). Proportional investment of total annual production for leaf growth, leaf allocation (LA, $M_f/(M_f + \Delta M)$) (King 1991), was also calculated.

Determination of non-structural carbohydrates

The contents of ethanol-soluble carbohydrates (ESC) and starch were determined in the current-year twigs colorimetrically by anthrone reaction (Yemm and Willis 1954) using glucose as standard. After the extraction of ethanol-soluble fraction with 70% ethanol at 65 °C for 30 min, the residue was treated with 1% HCl at 100 °C for 30 min to hydrolyse starch. Additional details concerning the assay are given in Oren *et al.* (1988).

Data analysis

In seedlings and in herbaceous plants several traits, e.g. RGR and NAR depend linearly on logarithm of relative irradiance rather than on untransformed RI (Blackman and Wilson 1951). Furthermore, a rectangular hyperbola may provide a more mechanistic function for fitting growth vs. long-term irradiance curves (McDonald *et al.* 1992). However, with increasing canopy foliar area the irradiance, which is necessary to saturate growth, increases and therefore, the growth response of mature trees to irradiance is quasi-linear (Jarvis and Leverenz 1983). The studied saplings had already an extensive canopy, and various transformations of relative irradiance improved the explained variance only by several percent, and in some cases resulted in non-random residual variances. Therefore, RI was always left untransformed, and for simplicity's sake, linear correlation and linear regression techniques were used throughout the study. This did not alter the qualitative conclusions, however, it resulted occasionally in physiologically unrealistic predictions (e.g. larger than zero biomass increment at zero light). To linearise the relationship and/or improve normality (Lilliefors' test), it was necessary to transform the metric and mass variables using natural logarithmic transformation (Ln). Interspecific differences in the parameter means were examined with t-test, and in statistical relationships with ANCOVA. All statistical dependencies were considered significant at $P<0.05$ (Mandel 1991).

Results

Sapling allometry and biomass partitioning

All allometric relationships (Table 2) were positively affected by relative irradiance in both species. At a common total height the saplings were larger, having thicker stems and more biomass in each compartment, in environments with greater light availability. Though the allometric dependencies were qualitatively similar in *A. platanoides* and *Q. robur*, the explained variance was always slightly higher in *A. platanoides* (Table 2).

Table 2. Effects of relative irradiance above the canopy (RI) and total tree height (H, m) on sapling allometry. All symbols are explained in Table 1.

Dependent variable	*A. platanoides*				*Q. robur*			
	Intercept	Slopes		r^2	Intercept	Slopes		r^2
		LnH	RI			LnH	RI	
Ln(D_b)	–4.53	0.742	0.772	0.90	–4.53	0.700	0.984	0.74
Ln(D_m)	–5.09	0.598	0.634	0.85	–5.26	0.716	0.916^*	0.68
Ln(L)	–1.64	2.18	0.991	0.95	–2.02	1.78	1.35^*	0.80
Ln(M_l)	–5.13	2.22	1.81	0.96	–5.39	1.83	2.31	0.86
Ln(M_s)	–3.98	2.32	1.41	0.95	–4.10	2.29	2.33	0.84
Ln(V_s)	–10.4	2.23	1.28	0.93	–10.8	2.43	1.83^*	0.83
Ln(M_{sh})	–3.70	2.29	1.53	0.96	–3.85	2.18	2.31	0.85
Ln(M_r)	–4.29	1.86	2.32	0.91	–4.50	2.28	3.16	0.83
Ln(V_r)	–10.9	1.88	2.31	0.92	–11.5	1.27^*	3.57	0.68
Ln(M_t)	–3.26	2.11	1.88	0.94	–3.34	2.17	2.49	0.83
Ln(V_t)	–9.98	2.07	1.81	0.94	–10.2	1.72	2.12^*	0.70

* significant at $P<0.01$. All other coefficients are significant at $P<0.001$.

The saplings of these species had completely different root systems, which may have exploited different soil horizons. The roots of *A. platanoides*, bifurcating frequently, were mostly found in the upper soil layers (never deeper than 0.4 m), whereas the saplings of *Q. robur* always possessed an emergent taproot, reaching up to 1.5 m in the largest saplings, with few lateral branches. Despite the contrasting root systems, biomass partitioning across the light gradient differed little between the species. In both *A. platanoides* and *Q. robur* the biomass of roots relative to total, stem and shoot (stem + leaves) biomass increased (Fig. 2) with increasing irradiance. Given the constant fraction of biomass in leaves (leaf mass ratio, LMR) and greater proportion of roots with increasing irradiance (Fig. 2), stem mass ratio (M_s/M_t) in *A. platanoides* (Fig. 2), and shoot mass ratio (M_{sh}/M_t) in both species were negatively affected by RI (Fig. 2). The ratio of root to foliar biomass separated the species: it was independent of irradiance in *A. platanoides* (P>0.4), but increased with irradiance in *Q. robur* (r^2=0.29, P<0.01).

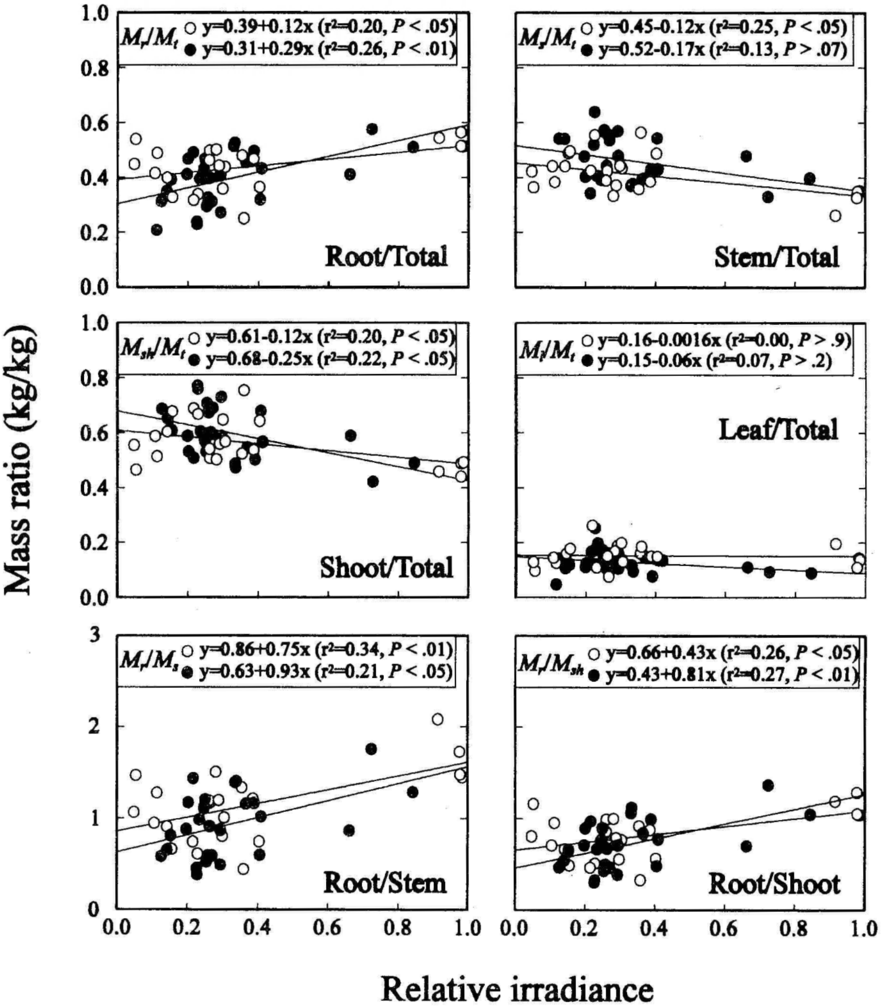

Fig. 2. Dry mass ratios of biomass compartments in relation to relative irradiance. The abbreviations are explained in table 1. Data presentation as in Fig. 1.

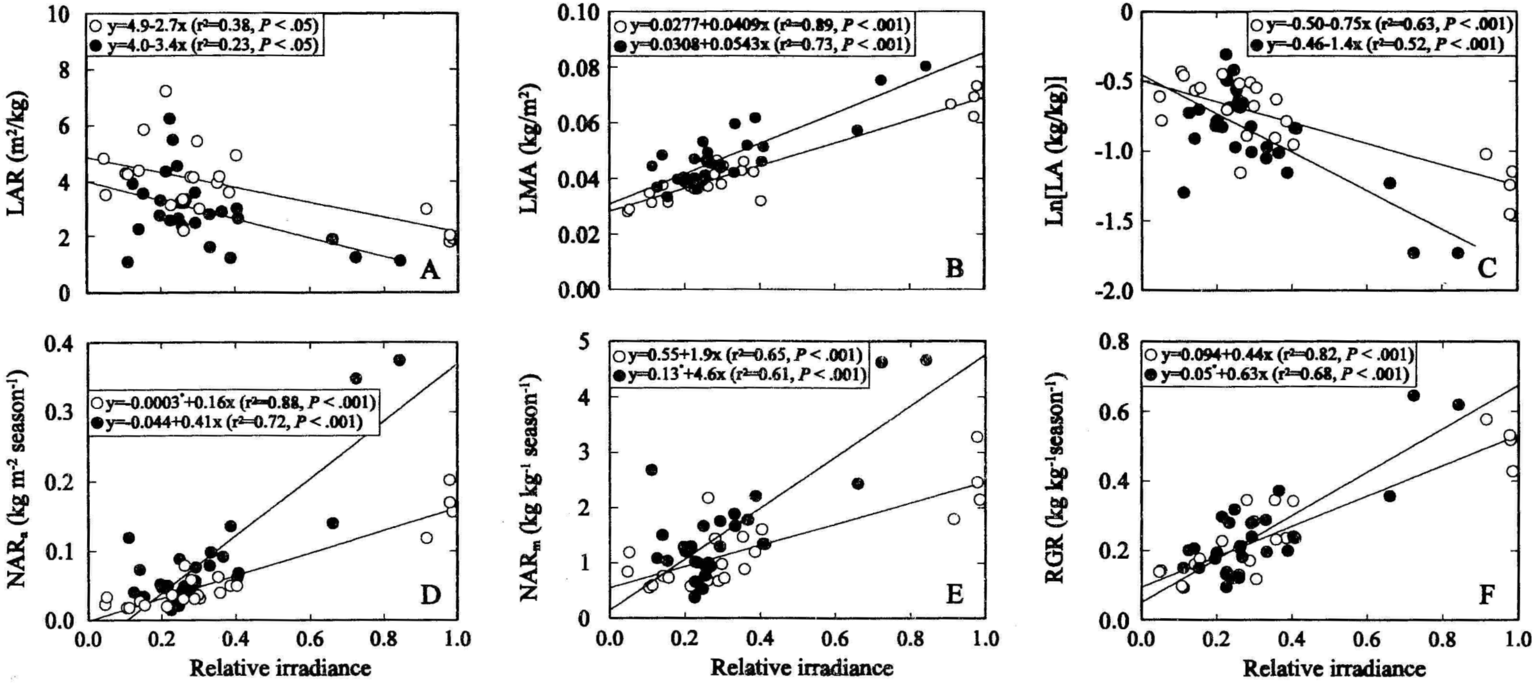

Fig. 3. Effects of relative irradiance on (**A**) leaf area ratio (LAR, L/M_l), (**B**) leaf dry mass per area (LMA, M_l/L), (**C**) leaf allocation ($M_l/(M_l+\Delta M)$), (**D** and **E**) net assimilation rates of standing biomass per foliar area and mass (NAR_a and NAR_m, respectively), and on (**F**) relative growth rate of standing biomass (RGR). Data presentation as in Fig. 1. See Eq. 3 and Table 1 for the explanation of symbols.

Contrary to LMR (Fig. 2), leaf area ratio (LAR, L/M_t) decreased significantly with increasing irradiance in both species (Fig. 3A). This is attributable to a positive relationship between leaf mass per area (LMA) and irradiance (Fig. 3B), because LAR=LMR/LMA. Furthermore, leaf allocation, i.e. the proportional investment of annual production in foliage, was significantly larger in lower irradiances (Fig. 3C).

Table 3. Influence of relative irradiance (RI) and total tree height (H, m) on sapling biomass partitioning and wood density of stem (WD_s). All symbols are explained in Table 1. Only regressions where LnH was significant are depicted, data concerning other biomass ratios are plotted in Fig. 2.

Variable (Species*)	Intercept	*P*	Slopes				r^2
			Ln*H*	*P*	RI	*P*	
M_r/M_t (Ac)	0.358	0.001	−0.103	0.001	0.193	0.001	0.54
M_s/M_t (Ac)	0.483	0.001	0.0897	0.001	−0.183	0.001	0.60
M_{sh}/M_t (Ac)	0.642	0.001	0.103	0.001	−0.193	0.001	0.54
M_l/M_t (Qu)	0.134	0.001	−0.060	0.01	−0.022	ns.	0.32
M_r/M_s (Ac)	0.705	0.001	−0.453	0.001	1.07	0.001	0.64
M_r/M_{sh} (Ac)	0.548	0.001	−0.317	0.001	0.650	0.001	0.60
M_r/M_l (Ac)	2.43	0.001	−1.23	0.05	1.52	ns.	0.26
L/M_t (Qu)	3.56	0.001	−1.62	0.01	−2.34	ns.	0.42
WD_s (Ac)	634	0.001	71	0.005	89	0.05	0.59
WD_s (Qu)	864	0.001	−123	0.05	86	ns.	0.18

*Ac — *A. platanoides*, Qu — *Q. robur*.

Several allometric ratios were also affected by tree size (Table 3), and the inclusion of LnH into the statistical models significantly increased the explained variance (cf. Fig. 2 and Table 3). In general, H was a more important determinant of biomass partitioning in *A. platanoides* (significantly altering seven allometric ratios) than in *Q. robur* (significant in four cases). Total height varied eight-fold in *A. platanoides* and four-fold in *Q. robur*, and this may have resulted in statistically less significant effect of H on biomass partitioning in *Q. robur*. However, M_t varied 250-fold in *A. platanoides* and 190-fold in *Q. robur*, but no relationship was qualitatively altered by using either M_t or H as a size estimate. Therefore, it is unlikely that low height range of the sampled saplings in *Q. robur* was responsible for any of the detected noncorrelations. The proportion of roots in total plant mass decreased with increasing height in *A. platanoides* (Table 3), permitting to increase the biomass investment in stem growth and to keep the proportion of biomass in foliage constant. In contrast, the fractions of stem and root biomass were invariable, but the amount of supported foliage decreased with increasing tree size in *Q. robur*. This brought about also decreasing LAR in this species (Table 3), because LMA was independent of H ($P>0.6$ for both species). The changes in biomass distribution with irradiance and sapling size were not attributable to plant ageing, since sapling age was independent of irradiance (in both species $P>0.3$), and only a weak positive correlation existed between A and LnH in *A. platanoides* ($r^2=0.22$, $P<0.05$). Moreover, A was never significant in statistical models with biomass ratios.

LMA was larger at a common RI in *Q. robur* than in *A. platanoides* (Fig. 3B, $P<0.001$). When the variation in biomass partitioning with tree size and relative irradiance was accounted for, it appeared that LMR was greater in *A. platanoides* ($P<0.05$). Accordingly, *A. platanoides* had also larger LAR (LMR/LMA) than *Q. robur* ($P<0.001$). Though *Q. robur* had significantly larger stem mass ratio than *A. platanoides* ($P<0.05$), the proportion of total biomass in roots, and biomass partitioning between roots and stem were similar in both species ($P>0.05$).

Stem density increased with increasing both H and RI in *A. platanoides*, but decreased with increasing H and was independent of RI in *Q. robur* (Table 3). *A. platanoides* had less dense wood in stem (mean±SE=662±16 kg m^{-3}) than *Q. robur* (898±19) ($P<0.001$). Biomass density of roots was independent of *H* and RI in both species, and was greater ($P<0.001$) in *Q. robur* (918±28) than in *A. platanoides* (758±21). Mean root density was similar to stem density in *Q. robur* ($P>0.5$), but was larger than stem density in *A. platanoides* ($P<0.01$). To gain further insight into the variation in stem density, correlations of low-density components of stem (pith and bark) with RI and *H* were also studied. In *A. platanoides* the proportions of pith and bark decreased with increasing Ln*H* ($r^2=0.32$, $P<0.01$ for pith and $r^2=0.60$, $P<0.001$ for bark) and were independent of RI. In *Q. robur*, only the proportion of bark decreased with increasing Ln*H* ($r^2=0.18$, $P<0.05$). The proportion of pith in stem was similar between the species, however, *Q. robur* had significantly larger proportion of stem biomass in bark ($P<0.001$).

To distinguish between the effects of light and tree size on stem allometry, it may be useful to examine the sources of variation in M_s in more detail. Provided the stem cross-section is circular in shape, M_s is given by:

$$M_s = \frac{1}{4} \mathrm{WD}_s \times H \times \Pi D_m^2 . \qquad (4)$$

Accordingly, M_s increases with increasing irradiance in *A. platanoides* due to increasing both WD_s and mean stem diameter (D_m) (Table 2–3), and in *Q. robur* due to a change in D_m with irradiance (Table 2).

Sapling growth

Minimum growth irradiance, arbitrarily calculated as the average of the lowest three RI values, was lower ($P<0.05$) in *A. platanoides* (mean±SE=0.07±0.02) than in *Q. robur* (0.13±0.01). Hence, the saplings of *A. platanoides* were likely to sustain growth under lower irradiances than those of *Q. robur.*

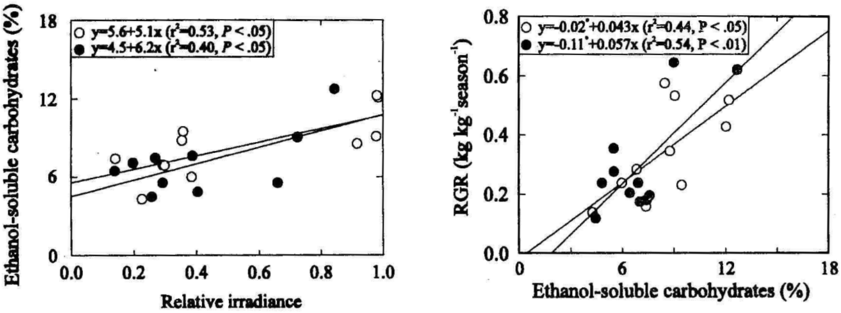

Fig. 4. Dependence of ethanol-soluble carbohydrates in current-year twigs (ESC_s) on relative irradiance, and the relationship between relative growth rate and ESC_s. Data presentation as in Fig. 1.

Net assimilation rates on both area and mass basis increased with increasing irradiance in both species (Fig. 3D,E). The increase in net assimilation rate was larger than the decline in LAR (Fig. 3A), resulting also in greater RGR ($\mathrm{NAR}_a \times \mathrm{LAR}$) at higher irradiance in both species (Fig. 3F). At equal irradiance both NAR_a and NAR_m were greater in *Q. robur* than in *A. platanoides* ($P<0.001$). Yet RGR was not significantly different between the species ($P>0.5$, Fig. 3F), because larger LAR and LMR counterbalanced lower NAR in *A. platanoides.* Tree size did not influence RGR, NAR_a or NAR_m ($P>0.2$). However, annual stem mass increment per foliage area increased with increasing Ln*H* in *Q. robur* ($r^2=0.33$, $P<0.01$).

When the variation in RGR was examined in better resolution, it appeared that NAR_a ($r^2=0.76$, $P<0.001$ for *A. platanoides* and $r^2=0.77$, $P<0.001$ for *Q. robur*) and NAR_m ($r^2=0.68$, $P<0.001$ for *A. platanoides* and $r^2=0.75$, $P<0.001$ for *Q. robur*) were the major determinants of

RGR. However, RGR of *A. platanoides* was significantly larger at a common NAR_a ($P<0.01$) and NAR_m ($P<0.05$). There was also a tendency of RGR to decrease with increasing biomass investment in the construction of foliage (LAR and LMR, data not shown), and to increase with increasing LMA ($r^2=0.61$, $P<0.001$ for *A. platanoides* and $r^2=0.56$, $P<0.001$ for *Q. robur*). This largely resulted form the negative correlations between LAR and NAR_a ($r^2=0.50$, $P<0.001$ for *A. platanoides* and $r^2=0.41$, $P<0.001$ for *Q. robur*), and LMR and NAR_m in *Q. robur* ($r^2=0.35$, $P<0.001$). When the variation in RGR with net assimilation rate was accounted for, RGR increased with both LMR ($P<0.001$) and LAR ($P<0.001$).

The concentration of ethanol-soluble carbohydrates (ESC) in current-year twigs (ESC_s) was positively related to irradiance (Fig. 4). Though starch content in current-year twigs was independent of RI in both taxa, it was significantly lower ($P<0.05$) in *A. platanoides* (mean±SE= 9.0±0.8%) than in *Q. robur* (11.8±0.8%). RGR (Fig. 4), and NAR_m and NAR_a (data not shown) were correlated with the availability of ethanol-soluble carbohydrates in current year twigs in *A. platanoides* and *Q. robur*.

Discussion

Influence of irradiance on sapling allometry and biomass partitioning

Irradiance positively affects both diameter and height increment (Greis and Kellomäki 1981, Chan and Walstad 1987). However, as trees get taller, light becomes increasingly available (King 1990) and height growth loses in priority (Lieffers and Stadt 1994). Hence, biomass investment for increase in total height seems to be more important under lower irradiance. This hypothesis received strong support from the current study, where in both *A. platanoides* and *Q. robur* all biomass compartments as well as mean stem diameter at the same *H* were less in environments with lower irradiance (Table 2), signifying the paramount importance of biomass allocation for height gain in shaded habitats.

In saplings of both species irradiance also significantly influenced dry matter partitioning between the biomass compartments. Increased proportion of roots with increasing irradiance (Fig. 2) is a major modification in biomass distribution across light gradients (Brix 1967, Drew and Ferrell 1977, Walters *et al.* 1993a). This change is frequently accompanied by parallel decreases in stem mass ratio (Brix 1967, Walters *et al.* 1993a, and *A. platanoides* in the current study). However, it is not clear what factors cause dry matter partitioning to change across light gradients. Soil water availabilities, which generally decrease with increasing irradiance (Bazzaz and Wayne 1994), may alter root mass ratio (Brouwer 1983). If further to consider that even at constant soil water content evaporative demand is higher in environments where radiation loads are greater, limited water availability seems to provide the explanation. Madsen (1994), studying the growth and biomass partitioning in seedlings of *Fagus sylvatica* along a gap-understory continuum, concluded that water availability is the major determinant of dry matter distribution across light gradients. Other studies indicate that, because reduced carbon becomes increasingly available with increasing irradiance, nutrient requirements for growth increase in proportion with irradiance (Ingestad and McDonald 1989). In *Betula pendula*, irradiance had no direct influence on biomass allocation, but a feedback through enhanced carbon accumulation rate resulted in lower plant nitrogen concentration at a constant nitrogen addition rate, and caused greater fractional biomass investment in roots (Ingestad and McDonald 1989). There is also evidence that nutrient availability is generally lower in environments where more light is available (Tilman 1993), but even if nutrient availability in soil was unaffected by irradiance, greater nutrient demand at higher irradiance is likely to result in more severe nutrient deficiencies there. Accordingly, the observed changes in root to stem partitioning with RI in *A. platanoides* and

Q. robur (Fig. 2) may reflect both the decreased water availability and increased nutrient requirement with increased irradiance.

Since leaf mass ratio is relatively constant (Brix 1967, Walters *et al.* 1993a, Fig. 2) and leaf mass per area increases with increasing irradiance (Drew and Ferrell 1977, Kull and Niinemets 1993, Fig. 3B), the combination of these effects leads to a strong negative relationship between LAR (LMR/LMA) and RI in both shade-tolerant and intolerant species (Rincón and Huante 1993, Fig. 3A). However, if the proportion of leaves in current-year rather than in total biomass is examined, a different picture emerges: in both *A. platanoides* and *Q. robur* the fraction of aboveground production in leaves increases with decreasing irradiance (Fig. 3C). King (1991) found similar relationship of LA on irradiance for several shade-tolerant tropical saplings, but not for intolerant ones. In the current study there were no such qualitative difference between the shade-tolerant *A. platanoides* and intolerant *Q. robur*. Nevertheless, the proportion of total production in leaves was consistently lower in intolerant *Q. robur* (Fig. 3C). In like manner, LA was lower in saplings of intolerant species in the King's (1991) study.

Effects of sapling size on biomass partitioning

Biomass distribution changes also dramatically during plant ontogeny (Walters *et al.* 1993b). Because plant growth rate, and consequently size, are positively related to irradiance, one may argue that the increasing root to shoot mass ratio with increasing irradiance is rather a size effect than an intrinsic response of dry matter partitioning to irradiance (Ledig *et al.* 1970). In general, the proportion of total biomass in roots (Whittaker 1962, Chalmers and van den Ende 1975) and leaves (Whittaker and Woodwell 1968, Ledig and Perry 1969, Chalmers and van den Ende 1975) decreases, and in stem (Whittaker 1962, Whittaker and Woodwell 1968, Chalmers and van den Ende 1975) increases with increasing plant age or dimensions. However, the positive correlation between tree size and irradiance may have confounded the exact distinction between size and irradiance effects in several earlier studies: depending on experimental design, either the influences of size or irradiance may have been oversignified. In the current study, where H and RI were orthogonal, the partitioning of standing biomass was shifted towards the expected directions with changing sapling size only in shade-tolerant *A. platanoides* (Table 3). LMR, in contrast, was independent of H in *A. platanoides* and decreased with increasing size in *Q. robur*. This resulted in declining LAR with increasing LnH in *Q. robur* (Table 3), because LMA was not related to H in this species.

Interspecific differences in wood density may play a central part in determining different responsiveness of various biomass fractions to height. Higher biomass density in *Q. robur* than in *A. platanoides* indicates that *Q. robur* needs on average higher biomass investments per unit volume gain than *A. platanoides*. This may decrease the plasticity of this species in environments where above- and belowground resources are scarce. Furthermore, there exists a good negative correlation between sapling wood density and leaf support efficiency (leaf area per unit woody cross-sectional biomass, $L/(\mathrm{WD}_s \Pi D_m^2/4)$) (King 1994), and thus the cost in terms of woody tissue for similar foliar display should be larger in *Q. robur* than in *A. platanoides*. Given the lower stem density and less responsive D_m with respect to irradiance and H in *A. platanoides* (Table 2), lower safety margin for disproportionately increasing requirements for mechanical stability may have caused greater stem density with increasing tree height and irradiance in this species (Table 3).

Sapling growth and survival in understory

The saplings of *Q. robur*, which survived at irradiances as low as RI_{min}=0.13, appeared to be more tolerant than reported previously (Ellenberg *et al.* 1991: for its seedlings and saplings RI_{min}=0.3–0.4). Malkina *et al.* (1970), growing six-year old saplings of *Q. robur* under different irradiances, reported that after four years growth none survived under RI<0.09, whereas at

RI=0.09 39% and at RI=0.8 89% of the saplings survived. Nevertheless, as may be suggested from the sapling dispersal in the understory (RI_{min}=0.13), it is still less shade-tolerant than *A. platanoides* (RI_{min}=0.07).

This is the only study on sapling growth across a natural light gradient I am conscious of, where also below-ground production has been taken into account. Because current growth was also a good estimate of previous growth (see Material and methods), this was performed in a relatively simplistic way, assuming a constant root mass ratio during the sapling ontogeny. In *A. platanoides*, where stem to root partitioning was also affected by tree size (Table 3), the root production may be overestimated in several cases. However, inasmuch as *H* and RI were orthogonal, this should not affect species comparisons along the irradiance gradient.

In general, dry matter accumulation and growth rates are positively related to irradiance (Ingestad and McDonald 1989, Kamaluddin and Grace 1993, Madsen 1994). Because the scatter in RGR vs. RI relationships, probably due to microheterogeneity in soil water and nutrient availabilities, is remarkable in understory environments (Fig. 3), whole plant growth vs. light response curves represent a powerful tool for studying species-specific growth response to incident irradiance. In seedlings, maximal RGR or dry matter accumulation may occur under intermediate light availabilities (Brix 1967, Drew and Ferrell 1977), or they may plateau at higher irradiances (Ingestad and McDonald 1989). However, much higher light levels are necessary to saturate sapling canopy, where self-shading within the foliage is considerably larger than that in seedlings. Increasing self-shading with increasing size provides an explanation for quasi-linear relationships between tree productivity and intercepted irradiance (Jarvis and Leverenz 1983, Chan and Walstad 1987). Linear fits of RGR vs. RI relationships in *A. platanoides* and *Q. robur* resulted in physiologically unrealistic growth rates at RI=0 (Fig. 3). Larger than zero growth at RI=0 may have resulted from the inability of the used method to take into account the losses of standing biomass due to accidental damage or death of branches during the season. This explanation receives support from a study on seedlings of *Q. robur*, where plant height decreased continuously due to the death of apical shoots during the first four years of growth at low irradiance (RI<0.05) (Malkina *et al.* 1970). Other stress factors such as water and nutrient limitations may also have acted in decreasing the growth rates at higher irradiances, and by lowering the slope values of the regression line, they may have caused greater intercepts than expected for a constant slope.

Because LAR decreases with increasing irradiance (Fig. 3A and the references above), the enhancement of relative growth rates across irradiance gradients must result from an increase in net assimilation rate (Brix 1967, Kamaluddin and Grace 1993, Rincón and Huante 1993, Fig. 3E and 3F) as was also found for *A. platanoides* and *Q. robur*. This contrasts to studies at constant irradiance, where RGR is negatively correlated with NAR and LMA, and positively to LAR and LMR (Poorter 1990). The discrepancy arises from the reverse correlation of NAR and LAR with RI (Fig. 3A,D,E). When the variability in NAR is accounted for, both LAR and LMR positively affect growth in both *A. platanoides* and *Q. robur*.

An increase in ethanol-soluble carbohydrate content with increasing RI has been frequently observed (Fjeld 1992, Niinemets 1995, 1996b), and attributed to increasing photosynthetic production at greater irradiance (Takahashi *et al.* 1993). As may be suggested from the relationships between ethanol-soluble carbohydrate concentration and irradiance (Fig. 4), higher NAR at higher RI most likely results from greater photosynthetic carbon acquisition there. Early successional species generally have higher photosynthetic capacities than late-successional ones (Bazzaz 1979, Oberbauer and Strain 1984), an observation, which may be the mechanistic reason for their higher NAR values across light gradients (Pons 1977). For a RI of about 0.9 the light-saturated photosynthesis at an ambient CO_2 (*ca.* 300 ppm) was 7.3 μmol m^{-2} s^{-1} for *Q. robur* (Malkina 1983) and 5.1 μmol m^{-2} s^{-1} for *A. platanoides* (Tselniker 1979). Moreover, leaf nitrogen concentrations, which scale with leaf photosynthesis (Field and Mooney 1986), were also higher at a common irradiance in *Q. robur* than in *A. platanoides* (Niinemets 1996c). Greater starch pools in current-year twigs in *Q. robur*, which had less biomass in leaves than *A. platanoides*, give another evidence for higher photosynthesis in this species. Thus, available photosynthesis and foliar chemistry data are in line with the argument that the observed differences in net assimilation rate (Fig. 3D,E) are caused by interspecific differences in foliage photosynthetic capacities.

Sapling shade-tolerance depends on biomass investment in foliage

RGR was significantly greater for the same NAR_a and NAR_m in *A. platanoides*, manifesting the relevance of greater biomass allocation in leaves (Fig. 2, 3C) and lower biomass requirement for surface area construction (Fig. 3B), which did effectively compensate for lower assimilation rates in this species. Greater allocation of annual production to foliage in shade-tolerant relative to intolerant species (Fig 3C, Nicola and Pickett 1983, King 1991), which brings about greater LMR in shade-tolerant species, may be a fundamental difference between the saplings of tolerant and intolerant species. Lambers and Dijkstra (1987) proposed that not RGR but rather its components (NAR, LAR, LMR) may be the target of selection in different environments. Maintenance of high LMR, which allows to compensate for low net assimilation rate due to the scarcity of light, may be of paramount significance for growth and survival under low irradiance. However, it is important to recognise that low LMR cannot necessarily be substituted by higher biochemical capacities for carbon acquisition — in low irradiances there may not simply be enough light to supply enhanced potentials for carbon assimilation with energy. Of course, in terms of competitive relations in understory it is not just greater foliar area that counts, but improved ability to capture light: additional investment in foliage is of little use if it results in increased self-shading within the canopy. In this sense, it is relevant that a previous work (Niinemets 1996a) has shown that the canopy architecture of the studied species responds to irradiance very differently: foliage distributions are adjusted with declining irradiance in *A. platanoides* to display more foliar area, but they are independent of irradiance in *Q. robur*. Furthermore, leaf area and weight per unit stem length are larger in *Q. robur*, resulting in greater light gradients across and higher self-shading within the canopy in this species (Niinemets 1996a). Accordingly, differences in canopy architecture may provide an explanation why *Q. robur* has lower LMR and less responsive LAR with respect to irradiance than *A. platanoides*.

Implications of different allometries for shade-tolerance

Albeit LMR inevitably decreases with increasing tree size due to disproportionately increasing demands of support tissues for mechanical stability, the velocity of this decrease, and accordingly species shade-tolerance, may be altered by the differences in allometry. The current study demonstrates that, because the conflicting requirements for height growth vs. biomass investment in leaves start to decrease the competitive ability of the saplings of *Q. robur* earlier, saplings of similar height of *Q. robur* may need greater irradiances than those of *A. platanoides* for survival.

Leaf mass ratio may be as low as 1–4% in trees (Körner 1994), but the saplings in the current study had considerably higher LMR-s (Fig. 2). Though LMR was independent of size in saplings of *A. platanoides*, it may begin to decrease with further increases in plant dimensions. It is discussionable if constant LMR in *A. platanoides* is at the expense of lowered allocation of biomass in roots, because root to leaf ratio decreased with H in *A. platanoides* (Table 3). *Q. robur* relative to *A. platanoides*, had higher proportion of biomass in stem and similar in roots, even if the height range of the saplings of *Q. robur* was lower. Therefore, it is likely that a conservative investment pattern of assimilates in standing biomass vs. leaves during sapling ontogeny may have led to decreasing foliar biomass with increasing tree size in *Q. robur* (Table 3). To keep the proportion of total biomass in foliage constant and higher than that in

Q. robur during sapling ontogeny, *A. platanoides* may need to cut down the investments for standing biomass. This may inversely affect volume gain and competitive ability in environments where irradiance is high.

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VI

Niinemets, Ü. 1996. Changes in foliage distribution with tree size and relative irradiance: differences between the saplings of *Acer platanoides* and *Quercus robur*. Ecological Research. (In Press)

Changes in foliage distribution with relative irradiance and tree size: differences between the saplings of *Acer platanoides* and *Quercus robur*

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Abstract

Dependencies of foliage arrangement and structure on relative irradiance and total height (TH) were studied in saplings of *Acer platanoides* and *Quercus robur*. Distribution of relative foliar area and dry weight (leaf area and weight in a crown layer per total tree's leaf area and weight, respectively) were examined with respect to relative height (RH, height in the crown per TH) and characterised by Weibull function. Distributions of relative area and weight were nearly identical, and the differences between them were attributable to a systematic decline in leaf dry weight per area with increasing crown depth. Foliage distribution was similarly altered by tree size in both species: RH at foliage maximum was lower and relative canopy size (RCS, length of live crown per TH) greater in taller trees. However, the distribution was more uniform in *Acer* than in *Quercus*. Apart from size effects, relative irradiance also influenced canopy structure: RCS increased in *Acer* and decreased in *Quercus* with increasing irradiance. As crown architecture was modified by irradiance, foliage distribution was shifted upwards with decreasing irradiance in *Acer*, but it was independent of irradiance in *Quercus*. Higher foliage maximum at lower irradiance in more shade-tolerant *Acer* is likely to contribute towards more efficient foliar display for light interception and thus increase the competitive ability of this species in light-limited environments. Consequently, these differences in crown architecture and foliage distribution may partly explain the superior behaviour of *Acer* in understory.

Key Words: foliar area, foliar biomass, leaf distribution, leaf morphology, Weibull function.

Introduction

Spatial variability in the distribution of foliar surface, which significantly alters light interception by and light gradients across the crown, plays an important part in determining the light-use efficiency of the whole canopy. Inasmuch as a positive relationship exists between relative growth rate and irradiance (Canham 1988; Oberbauer *et al.* 1988; King 1991; Washitani & Tang 1991), more efficient utilisation of light enables to sustain the growth under lower irradiances, and therefore, is likely to improve the species potential to compete successfully in low-light environments.

Due to a tight connection between branching patterns and foliage distribution, modifications in crown geometry may result in different vertical foliage distributions (Ardhana *et al.* 1988). Many shade-tolerant and late-successional species inherently possess crowns which mostly extend laterally, while intolerant and early-successional taxa maximise vertical rather than horizontal growth (Boojh & Ramakrishnan 1982; Hara *et al.* 1991; Yamamura *et al.* 1993). These interspecific differences in growth patterns give rise to crowns which are efficient for light harvesting under shade in shade-tolerant and in open in intolerant species. Unfortunately, the matters are not so simple, because apart from genetic effects the species exhibit considerable morphological plasticity, e.g. relative irradiance (Steingraeber *et al.* 1979; Kohyama 1980; Canham 1988; Hashimoto 1990; O'Connell & Kelty 1994) and tree dimensions or age (Borchert & Tomlinson 1984; Hagihara & Hozumi 1986; Hashimoto 1990; Mori & Hagihara 1991) influence crown structure and foliage distribution. Furthermore, the positive correlation between growth rate and light availability makes it difficult to distinguish between the effects of size and irradiance on canopy architecture. It follows that, to provide insight into species competitive relations across various light environments, it is essential to examine the influences of both irradiance and tree size on species-specific patterns of foliage distribution.

Differences in foliage distribution should also significantly alter biomass costs for formation of canopy foliar surface, because leaf dry weight per area increases linearly with increasing relative irradiance (Čermák 1989; Kull & Niinemets 1993; Niinemets 1995; Niinemets & Kull 1995). Thus, the assessments of interspecific differences in light-use efficiency, which include the estimates of carbon costs for surface area construction, should be even more aggravated than those based on the differences in foliage distribution and crown geometry alone. Furthermore, foliage physiology, which is directly related to plant carbon acquisition, depends on relative irradiance (Koike 1986; Oren *et al.* 1986; Kurachi *et al.* 1992), a finding that again emphasises the importance of explicit characterisation of light gradients and foliar distribution patterns.

The objectives of the current study were twofold: (i) to gain a better understanding upon the influences of relative irradiance and tree size on the distribution and morphology of the assimilative surface in the saplings of temperate deciduous species *Acer platanoides* L. and *Quercus robur* L.; and (ii) to examine the variability in crown architecture in relation to species shade-tolerance rank. Both species often grow in the understory, but *A. platanoides* which has an Ellenberg's light figure of 4, tolerates lower light availabilities and may grow under heavier shade than *Q. robur* which has a light figure of 7 (Ellenberg *et al.* 1991). Though phenomenological differences in foliage distribution and crown architecture in "sun" and "shade" have been identified previously (cf. refs. above), comparison of the species response to light availability requires quantitative relationships between plant architecture and irradiance.

Methods

Plant material

The study was carried out in the understory of a mixed forest dominated by about 100-yr-old trees of *Picea abies* (L.) Karst. on gleyic and gleyed pseudopodzolic soils at Tôrvandi (58° 20' N, 26° 42' E; elevation 60–65 m above sea level), Estonia in August 1993. Solitary individuals of *Betula pendula* Roth., *Pinus sylvestris* L., *Populus tremula* L. and *Salix caprea* L. were also found in the overstory, whereas understory was dominated by *Padus avium* Miller, *P. tremula*, *Salix myrsinifolia* Sal. and *Vaccinium myrtillus* L.

Saplings exclusively of seed origin, 22 for *A. platanoides* and 27 for *Q. robur*, were sampled across the understory habitats of various exposure. Sapling age (yr), which was estimated by counting the growth rings at the butt, ranged from four to 21 (9.1±0.6, mean±SE (standard error of the mean)) in *Acer* and from three to 15 (10.2±0.9) in *Quercus*. Saplings ranged in total height (TH, m) from 0.30 to 2.63 (1.04±0.11) in *Acer* and from 0.30 to 1.53 (0.93±0.06) in *Quercus*. Mean sapling age and TH were not significantly different between the species ($p>0.05$, t-test). The studied taxa at our latitudes usually have determinate growth, producing annually only one flush of leaves. Few plants of *Quercus*, which had a small number of second-flush leaves, were discarded from the analysis.

Estimation of relative irradiance

Several hemispherical photographs were taken at the top of the crown of every sapling and the differences between the sample trees in relative irradiance (RI) quantified after Anderson (1964) as modified by Nilson and Ross (1979). From every photograph relative area of canopy gaps was measured with respect to zenith angle and relative amount of penetrating diffuse solar radiation, always laying within the range of 0.0–1.0, was calculated. A value of RI equal to 1.0 corresponds to the diffuse irradiance above the stand, and RI is zero with no canopy gaps. To examine the contribution of different sky bands to RI in more detail, lateral (RI_l), and vertical

(RI_v) components of RI, which were defined as the parts of RI penetrating between the zenith angles of 0° to 35° and 55° to 90°, respectively, were also calculated. Though the contribution of RI_v to RI over the range of measured relative irradiances was similar between the species, *Acer* received slightly greater proportion of RI from sky bands at lower zenith angles than *Quercus* ($p<0.001$, Fig. 1). However, since RI was positively correlated with both RI_l and RI_v (Fig. 1), like RI_l was with RI_v ($r=0.933$, $p<0.001$ for *Acer* and $r=0.825$, $p<0.001$ for *Quercus*), no relationship of plant morphology vs. relative irradiance was qualitatively altered by considering different indices of light availability. Thus, RI was always used as the estimate of relative light conditions. TH was not correlated with RI ($p>0.05$) in both species, and accordingly, the effects of tree size and light availability on leaf and crown architecture could be studied independently.

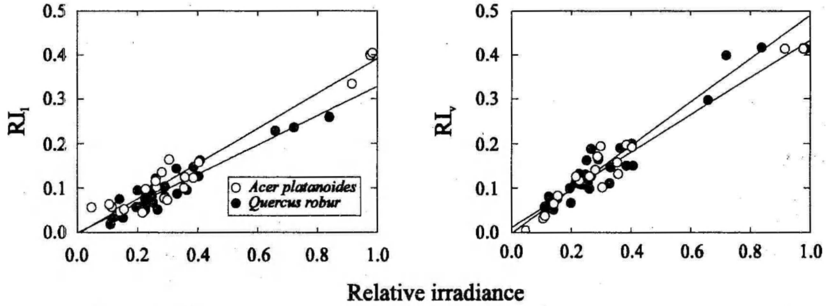

Fig. 1. Relationships between the relative irradiance above the canopy (RI), and the lateral (RI_l) and vertical (RI_v) components of RI. RI_l and RI_v are the contributions to RI of the sky bands between the zenith angles of 0° to 35° and of 55° to 90°, respectively. *Acer platanoides* (N=22): $RI_l=-0.004+0.40RI$ ($r^2=0.953$, $p<0.001$), $RI_v=0.011+0.42RI$ ($r^2=0.968$, $p<0.001$); *Quercus robur* (N=27): $RI_l=-0.002+0.33RI$ ($r^2=0.891$, $p<0.001$), $RI_v=-0.003+0.47RI$ ($r^2=0.910$, $p<0.001$). In all regressions, intercepts are not significantly different from zero ($p>0.2$). The slope of RI_l vs. RI relationship is larger in *Acer* than in *Quercus* ($p<0.001$) but the slopes of RI_v vs. RI regressions are not different ($p>0.3$).

Analysis of leaf distribution and morphological parameters

Starting from the top of the trees, crown layers of 0.1 m were harvested. From every layer a random sample, consisting at minimum of five, and if there were less than five, of all leaves, was taken. Contours of sample leaves were traced manually with a computer digitizer (QD–1212, Qtronix, Taipei, Taiwan) and the surface areas of images determined using self-developed computer software. All leaves in a layer were weighed after oven-drying at 70 °C for 48 h, and total leaf area of a layer was calculated from dry weight of all leaves in the layer and leaf dry weight per area of the sample leaves (LWA).

Leaf area and dry weight distributions were fitted by Weibull function (Schreuder & Swank 1974) as modified by Mori and Hagihara (1991):

$$\gamma(x)=\frac{\mathrm{TLA}\times m}{\alpha}\left(\frac{\mathrm{TH}-x}{\alpha}\right)^{m-1}e^{-\left(\frac{\mathrm{TH}-x}{\alpha}\right)^{m}} \qquad (1),$$

where $\gamma(x)$ is foliar area per unit stem length (m^2m^{-1}) at the height x, TH and TLA are total tree height (m) and leaf area (m^2), respectively, and α and m are the parameters of Weibull function ($\alpha>0$, $m>0$). For the approximation of the distribution of leaf dry weight by Weibull function, TLA in equation 1 has to be replaced by total foliage weight (TLW, kg). To compare the distribution shapes in trees varying in size as well as the distributions for area and weight, I defined relative leaf area (RLA) and leaf weight (RLW) as leaf area and weight per unit total foliage area and weight, respectively, and relative tree height (RH) as height in the crown per TH. This allowed me to examine relative distributions, i.e. the distributions of RLA and RLW along RH. Since both total height and area become equal to 1, Eq. 1 simplifies to:

$$\mathrm{RD}_a(\mathrm{RH}) = \frac{m_a}{a_a}\left(\frac{1-\mathrm{RH}}{a_a}\right)^{m_a-1} e^{-\left(\frac{1-\mathrm{RH}}{a_a}\right)^{m_a}} \qquad (2),$$

where $\mathrm{RD}_a(\mathrm{RH})$ is RLA per layer thickness (ΔRH) (Fig. 2). To change between the equations 1 and 2, $m=m_a$, but α must scale with total tree height such that $\alpha=a_a \times \mathrm{TH}$. Both a_a and m_a determine the shape of foliage distribution. Leaf area distribution has a maximum at a relative height:

$$\begin{aligned} \mathrm{RH}^{\max}{}_a &= 1 - a_a \sqrt[m_a]{1-\frac{1}{m_a}}, && \text{if } m_a \geq 1 \\ \mathrm{RH}^{\max}{}_a &= 1, && \text{if } m_a < 1 \end{aligned} \qquad (3).$$

$\mathrm{RH}^{\max}{}_a$ declines with increasing both a_a and m_a, though the distribution is sharper at higher m_a and flatter at greater a_a (Fig. 2A). Eq. 3, modified to include the coefficients for Weibull function for RLW (a_m and m_m), was also used to calculate the maxima of RLW distributions ($\mathrm{RH}^{\max}{}_m$). It is possible to show (Mori & Hagihara 1991) that relative cumulative foliar area ($\mathrm{RLA}_c(\mathrm{RH})$) and weight ($\mathrm{RLW}_c(\mathrm{RH})$) from top to given RH may be expressed as:

$$\mathrm{RLA}_c(\mathrm{RH}) = 1 - e^{-\left(\frac{1-\mathrm{RH}}{a_a}\right)^{m_a}} \qquad (4),$$

and

$$\mathrm{RLW}_c(\mathrm{RH}) = 1 - e^{-\left(\frac{1-\mathrm{RH}}{a_m}\right)^{m_m}} \qquad (5).$$

Accordingly, the parameters of Weibull distribution for relative area (a_a and m_a) and weight (a_m and m_m) were obtained from a single non-liner least-squares fit of the data to equations 4 and 5 (Fig. 2B,C). Explained variance was high and similar for the cumulative relative area (r^2=0.937–1.000, on average 0.989) and weight (r^2=0.937–1.000, on average 0.987) distributions, signifying the suitability of Weibull function for modelling of canopy architecture in *Acer* and *Quercus*.

Since the differences between foliar area and weight distributions, e.g. shifting maxima (Fig. 2B, C), are caused by changes in LWA with cumulative foliar area and relative tree height, the variability in LWA within the crown must be identified explicitly. Combining the positive linear relationship between LWA and relative irradiance (cf. Introduction), and the exponential decline in irradiance with increasing cumulative foliar area (Monsi & Saeki 1953), the variation in LWA across the crown with increasing leaf area was described by empirical relationships between LWA and $\mathrm{RLA}_c(\mathrm{RH})$:

$$\mathrm{LWA} = C_1 + C_2 \times e^{\mathrm{RLA}_c(\mathrm{RH})} \qquad (6),$$

and LWA and RH:

$$\mathrm{LWA} = C_3 + C_4 \times \mathrm{RH} \qquad (7),$$

where C_1, C_2, C_3 and C_4 are tree-specific coefficients. In the case of a linear relationship between LWA and RI, C_1 is related to RI above, C_3 to RI below the sapling canopy, and C_2 and C_4 characterise the light gradient across it (Fig. 3). Only regressions statistically significant at $p<0.05$ were used. Nevertheless, LWA always tended to decrease with $\mathrm{RLA}_c(\mathrm{RH})$ and to increase with RH also for insignificant regressions (19 of 49 for $\mathrm{RLA}_c(\mathrm{RH})$ and 24 of 49 for RH), where mostly due to low TH the number of leaf layers was less than or equal to four. Nevertheless, incorporation of insignificant regression coefficients into the analysis did not alter the conclusions qualitatively. Explained variance (r^2) for significant regressions ranged from

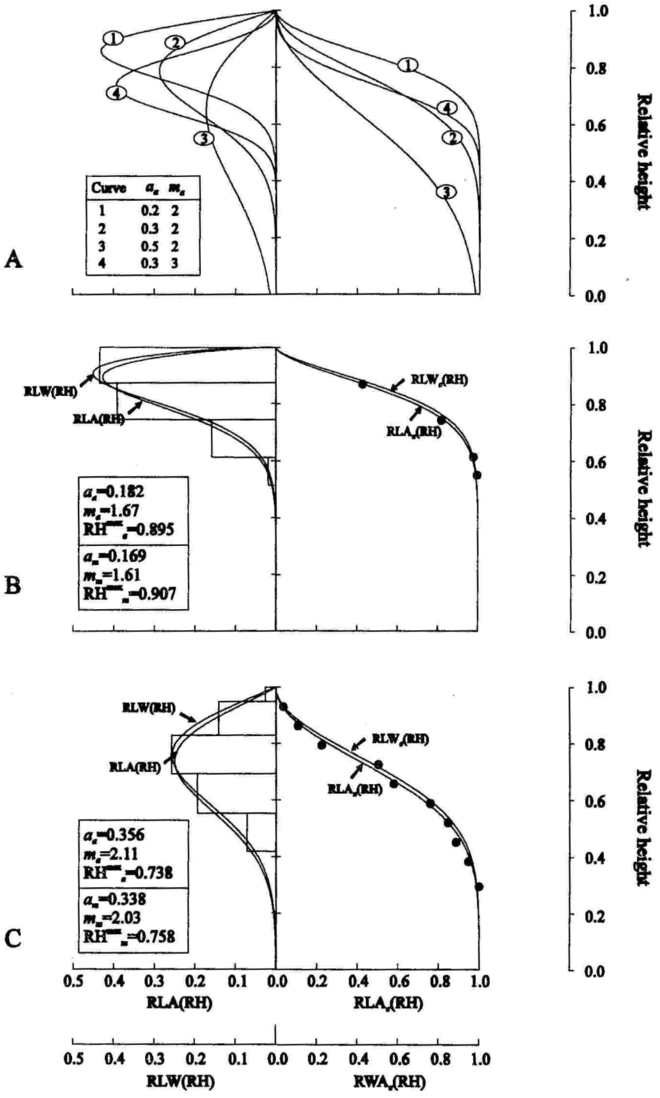

Fig. 2. Distribution of relative foliar area (RLA(RH) — leaf area at a given relative height, RH (height in a tree per total height), per total leaf area) and weight (RLW(RH) — leaf weight at RH per total foliar weight), and cumulative relative foliar area (RLA$_C$(RH)) and weight (RLW$_C$(RH)) from top to RH at different parameter values of Weibull function (Eqs. 2 and 4–5), and examples of the data fitting for two trees of *Q. robur*. Eq. 2 was multiplied by the layer thickness (ΔRH) to obtain RLA(RH) and RLW(RH). **A**. Theoretical distributions of RLA(RH) and RLA$_C$(RH). a_a and m_a are the parameters of Weibull distribution for relative area (Eqs. 2 and 4–5). **B**. Foliar distribution for a tree with a total height (TH) of 0.78 m and with a relative canopy size (RCS, length of live crown per TH) of 0.45. Relative irradiance above the canopy (RI) was equal to 0.33, total leaf area (TLA) to 0.065 m^2 and total foliar weight (TLW) to $3.85 \cdot 10^{-3}$ kg. For comparison also the fitted curves for foliar weight are drawn. a_m and m_m are the parameters of Weibull function for foliar weight, RH$^{max}_a$ and RH$^{max}_m$ are the maxima (Eq. 3) for relative area and weight distributions, respectively. r^2-s for area and weight distributions were both equal to 1.000. **C**. TH=1.46 m, RCS=0.71, RI=0.66, TLA=0.57 m^2, TLW=$3.25 \cdot 10^{-2}$ kg. r^2(area)=0.994, r^2(weight)=0.995.

0.629 to 0.996 (on average 0.883) for LWA vs. $RLA_c(RH)$ and from 0.441 to 0.854 (on average 0.854) for LWA vs. RH. Since equation 6 usually resulted in higher proportion of explained variance, and C_1 and C_3, and C_2 and C_4 behaved similarly along the light gradient, only LWA vs. $RLA_c(RH)$ relationship is further demonstrated in more detail.

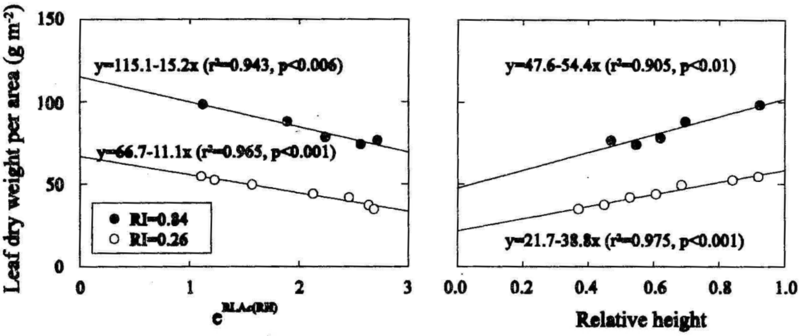

Fig. 3. Examples of the data fitting to describe the variation of LWA across the canopy: relationships between LWA and $e^{RLAc(RH)}$ (Eq. 6), and LWA and RH (Eq. 7) in two trees of *Q. robur*. $RLA_c(RH)$ is relative cumulative leaf area from top to RH (exponential transformation is used to agree with theoretically exponential decline of irradiance with increasing cumulative foliar area in the canopy).

Linear correlation and linear and non-linear regression techniques were used for data analysis. To linearise the relationship and/or improve normality (Lilliefors test, Wilkinson 1990), it was necessary in several cases to transform the variables using natural logarithmic transformation (Ln). Interspecific differences in the parameter means were examined by t-test, and in statistical relationships by ANCOVA (Wilkinson 1990). All dependencies were considered significant at $p<0.05$. Frequently used symbols with definitions and respective units are listed in Table 1.

Table. 1. Explanation of used abbreviations*.

Symbol	Definition
C_1	parameters (g m^{-2}) of LWA vs. $RLA_c(RH)$ relationship (Eq. 6)
C_2	
LWA	leaf dry weight per area (g m^{-2})
LWA_m	mean LWA (TLW/TLA, g m^{-2})
RCS	length of live crown (m) per TH
RI	relative irradiance
RI_l	part of RI between the zenith angles of 0° to 35°
RI_v	part of RI between the zenith angles of 55° to 90°
RH	relative height (height in crown (m) per TH)
RH^{max}	RH at foliage maximum (Eq. 4)
$RH^{max}{}_a$	RH^{max} for RLA distribution
$RH^{max}{}_m$	RH^{max} for RLW distribution
RLA	relative leaf area (leaf area (m^2) per TLA)
$RLA_c(RH)$	cumulative RLA from the top to RH
RLW	relative leaf dry weight (leaf dry weight (kg) per TLW)
$RLW_c(RH)$	cumulative RLW from the top to RH
TLA	total leaf area (m^2)
TLW	total leaf dry weight (kg)
TH	total tree height (m)

*The symbols not included in Table 1, the parameters of Weibull distribution for relative leaf area and weight (a_a and m_a, and a_m and m_m, respectively) and for actual foliage area (α, m), are defined by equations 1–2 and 4–5.

Results

Crown allometry and foliage distribution

Relative canopy size (RCS), defined as the length of live crown (the distance from canopy top to the lowest leaves) per TH, was dependent on both RI and TH. RCS was greater in taller trees in both species, but decreased in *Quercus* and increased in *Acer* with increasing RI (Table 2). Allometric relationships between TH, and foliar area and weight were also affected by irradiance: the trees, which were exposed to higher irradiances, had more foliage at a common TH (Table 2).

Table 2. Effects of relative irradiance above the crown, RI, and total tree height, TH (m), on crown structure, foliar morphology, and total leaf area and weight: multiple linear regression analysis

Species (sample size	Dependent variable*	Intercept	p	Slopes				r^2
				RI	p	TH**	p	
A. platanoides (22)	RCS	0.162	0.092	0.341	0.023	0.258	0.004	0.556
	LWA (g m^{-2})	26.8	0.001	39.0	0.001	7.24	0.027	0.797
	Ln(TLA)	−1.64	0.001	0.991	0.001	2.18	0.001	0.950
	Ln(TLW)	−5.13	0.001	1.81	0.001	2.22	0.001	0.955
Q. robur (27)	RCS	0.067	0.47	−0.352	0.039	0.555	0.001	0.607
	LWA (g m^{-2})	18.2	0.001	71.09	0.001	14.1	0.001	0.885
	Ln(TLA)	−2.02	0.001	1.35	0.006	1.78	0.001	0.802
	Ln(TLW)	−5.39	0.001	2.31	0.001	1.83	0.001	0.856

* RCS — relative canopy size (length of live crown per TH), LWA — leaf weight per area of the leaves from the uppermost 0.1 m crown layer, TLA — total leaf area (m^2), TLW — total leaf weight (kg).

** TH was transformed using natural logarithmic transformation, Ln(TH), in regressions with logarithmed leaf area, Ln(TLA), and weight, Ln(TLW).

Tree size, influencing all parameters of Weibull function, was an important determinant of the shape of foliage distribution. The parameters of relative leaf area distribution, a_a and m_a (Eq. 2), both increased, and the maximum of it, RH^{max}_a (Eq. 3), decreased with increasing TH (Fig. 4, Table 3). Dependencies of a_a on TH were not significantly different between the species ($p>0.2$), however, the slope of m_a vs. TH was lower in *Acer* than in *Quercus* ($p<0.01$, Fig. 4). a_a and m_a were correlated with each other in both species (Fig. 5), whereas *Acer* had significantly higher values of a_a for the same m_a than *Quercus* ($p<0.01$).

Table 3. Dependence of the parameters of Weibull function (Eq. 2) for the distributions of relative foliar area (a_a, m_a) and weight (a_m, m_m), and the distribution maxima (RH^{max}_a and RH^{max}_m, maxima for relative area and weight, respectively, Eq. 3) on relative irradiance above the canopy, RI, and on total tree height, TH (m).

Species (sample size)	Dependent variable	Intercept	p	Slopes				r^2
				RI	p	TH (m)	p	
A. platanoides (18)	a_a	0.120	0.038	0.167	0.016	0.0861	0.040	0.484
	m_a	0.809	0.001	0.404	0.046	0.381	0.007	0.556
	RH^{max}_a	1.053	0.001	−0.152	0.014	−0.102	0.011	0.583
	a_m	0.095	0.056	0.177	0.005	0.0872	0.02	0.573
	m_m	0.746	0.001	0.419	0.036	0.366	0.007	0.560
	RH^{max}_m	1.077	0.001	−0.156	0.008	−0.101	0.008	0.617
Q. robur (23)	a_a	−0.0264	0.70	−0.127	0.18	0.308	0.001	0.542
	m_a	0.576	0.30	0.109	0.88	1.101	0.05	0.205
	RH^{max}_a	1.143	0.001	0.0171	0.89	−0.281	0.003	0.378
	a_m	−0.0354	0.61	−0.127	0.18	0.306	0.001	0.528
	m_m	0.509	0.38	0.0739	0.92	1.100	0.053	0.191
	RH^{max}_m	1.148	0.001	0.0131	0.91	−0.270	0.005	0.355

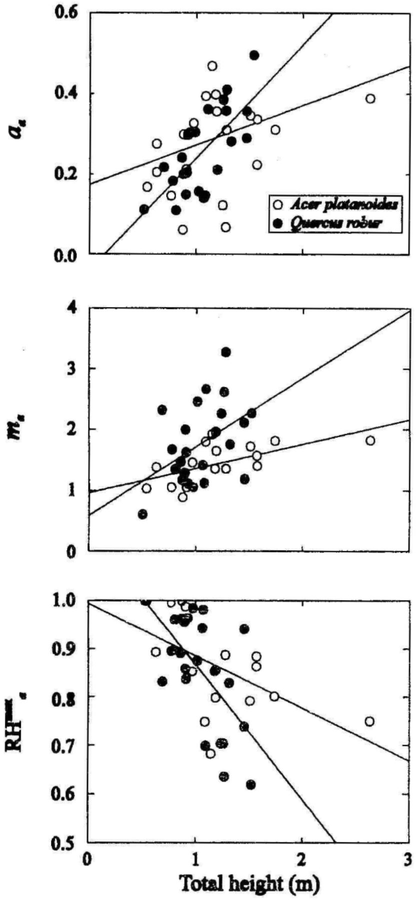

Fig. 4. Effect of total tree height (TH, m) on the distribution of relative foliar area (Eq. 2): parameters of Weibull distribution for leaf area (a_a and m_a) and changes in distribution maximum, RH^{max}_a. *A. platanoides* (N=18): a_a=0.174+0.0986TH (r^2=0.231, $p<0.05$), m_a=0.965+0.398TH (r^2=0.390, $p<0.01$), RH^{max}_a=0.994–0.109TH (r^2=0.322, $p<0.05$); *Q. robur* (N=23): a_a=–0.0413+0.283TH (r^2=0.496, $p<0.001$, intercept is not significantly different from zero), m_a=0.588+1.12TH (r^2=0.205, $p<0.05$, intercept is not significantly different from zero), RH^{max}_a=1.15–0.277TH (r^2=0.377, $p<0.002$).

The effect of relative irradiance on foliage distribution varied qualitatively between the species: it was insignificant in *Quercus* and significant in *Acer*, where both parameters of Weibull function increased and RH^{max}_a decreased with increasing RI (Table 3). Since RI positively altered the slopes of a_a vs. TH and m_a vs. TH relationships, and negatively the slope of RH^{max}_a vs. TH in *Acer*, RI shifted the slope values of the relationships between TH and the parameters of Weibull function in *Acer* towards those in *Quercus*. Accordingly, the interspecific differences in foliage distribution vs. TH at common irradiance should be even more aggravated than is necessarily apparent in Fig. 4.

In *Acer*, both parameters of Weibull function increased with increasing RCS (r^2=0.487, $p<0.001$ for a_a and r^2=0.340, $p<0.02$ for m_a). In *Quercus*, a_a behaved similarly (r^2=0.371, $p<0.01$) but m_a was not related to RCS (r^2=0.160, $p>0.06$). Dependence of the parameters of foliage distribution on RCS resulted in decreasing RH^{max}_a (Eq. 3) with increasing RCS in both *Acer* (r^2=0.401, $p<0.01$) and *Quercus* (r^2=0.200, $p<0.05$). The distribution patterns of relative foliar weight were very similar to those of relative area (e.g., Fig. 2), and the relationships of RCS, RI and TH with the distribution parameters were not qualitatively changed by using parameters for either area or weight (Table 3). Nevertheless, the maxima of the distributions of relative leaf weight (0.886±0.024 for *Acer* and 0.869±0.024 for *Quercus*, means±SE) were always higher ($p<0.01$ for the means) than the maxima of relative area (0.861±0.024 for *Acer* and 0.854±0.025 for *Quercus*). These differences in area and weight distributions resulted from decreasing LWA with increasing crown depth and cumulative foliar area (Fig. 3).

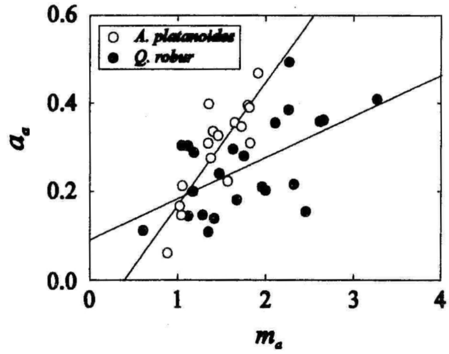

Fig. 5. Relationship between the parameters of Weibull distribution for relative foliar area (Eq. 2). *A. platanoides*: a_a=–0.110+0.278m_a (r^2=0.703, $p<0.001$, N=18); *Q. robur*: a_a=0.0909+0.0932m_a (r^2=0.333, $p<0.005$, N=23). For both regressions the intercept is not significantly different from zero.

Leaf structure across sample sites and canopies

Leaf size (area per leaf) was independent of RI and TH, but LWA of the uppermost 0.1 m layer increased with increasing both RI and TH (Table 2). Sapling mean LWA (LWA_m, Fig. 6) was independent of TH, whereby relative irradiance above the crown was still a fairly good predictor of LWA_m (Fig. 6). *Acer* had significantly larger leaves (62.1±6.1 cm^2, mean±SE) than *Quercus* (34.0±2.4 cm^2) ($p<0.05$), but *Quercus* had higher LWA (Table 2) and LWA_m (Fig. 6) at common RI ($p<0.001$). Thus, *Quercus* has costlier foliar area in terms of leaf biomass than *Acer*.

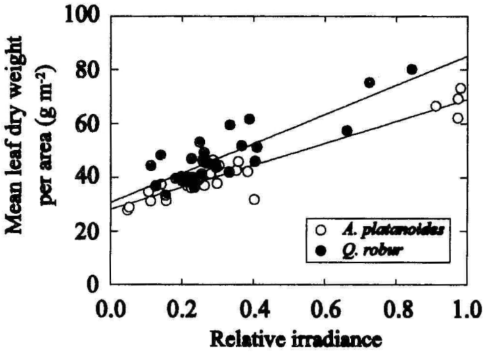

Fig. 6. Dependence of mean leaf weight per area, (total tree's foliar weight per area, LWA_m, g m^{-2}) on relative irradiance above the canopy, RI. *A. platanoides*: LWA_m=27.7+40.9RI (r^2=0.890, $p<0.001$, N=22); *Q. robur*: LWA_m=30.8+54.3RI (r^2=0.732, $p<0.001$, N=27).

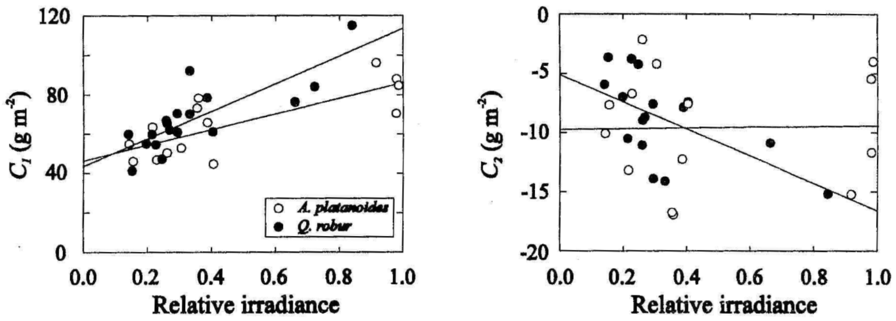

Fig. 7. Relationships between RI and the parameters, C_1 (intercept, g m^{-2}) and C_2 (slope, g m^{-2}), of the linear regressions between LWA and $e^{RLAc(RH)}$ (Eq. 6, Fig. 3). *A. platanoides*: C_1=46.2+40.0RI (r^2=0.605, $p<0.001$, N=14), C_2=–9.70+0.307RI (r^2=0.000, $p>0.9$, N=14); *Q. robur*: C_1=43.4+70.0RI (r^2=0.646, $p<0.001$, N=18), C_2=–5.09–11.5RI (r^2=0.347, $p<0.01$, N=18).

The variation of LWA across the canopy with cumulative foliar area was also affected by incident irradiance (Fig. 7). The intercept of LWA vs. $e^{RLAc(RH)}$ (C_1, Eq. 6), which is related to the irradiance above the crown, increased with increasing RI in both species (Fig. 7). The slope (C_2, Eq. 6), which provides an estimate of the light gradient across the crown, was significantly related to RI only in *Quercus* (Fig. 7). The correlation between C_1 and C_2 was insignificant for *Acer* (–0.507, $p>0.05$) but statistically relevant for *Quercus* (r=–0.763, $p<0.001$). There were no significant correlations of C_1 and C_2 with TH, RCS and the distribution parameters for foliar area and weight.

Discussion

Crown allometry and foliage distribution

Similarly to the current study the parameters of Weibull function for leaf area distribution (Eq. 1) were dependent on tree size in *Chamaecyparis obtusa* (Hagihara & Hozumi 1986; Mori & Hagihara 1991). Unfortunately, α in Eq. 1 is equal to TH×a_a, and therefore, the changes in α with tree size (Hagihara & Hozumi 1986; Mori & Hagihara 1991) cannot be interpreted in terms of distribution shape. Nevertheless, m_a (Eq. 2) is the same for both actual and relative distributions, and an increase in m_a with increasing tree size in small trees of *C. obtusa* (Mori & Hagihara 1991) does match my results (Fig. 4).

An increase in relative canopy size (RCS) with increasing TH in *Acer* and *Quercus* (Table 2) may have caused the foliage distributions to change with TH (Fig. 4), because foliage can be distributed more uniformly within a canopy which is relatively longer. Inasmuch as a_a and a_m control the distribution sharpness (Fig. 2A), whereby increasing values of these parameters are compatible with gradually more flattened distributions, this hypothesis was supported by increasing a_a and a_m with increasing RCS. Analogously, the declining maxima of foliage distributions with increasing TH (Fig. 4) are likely to result from relatively longer canopies in tall trees. However, it appears that the influence of TH on foliage distribution is variable among woody species: RCS decreased with TH and stand age in *Abies mariesii* and *Abies veitchii* (Kohyama *et al.* 1990), and the maxima for the distributions of green phytomass in *Ulex europaeus* (Ojea *et al.* 1988) and of foliage weight in *Picea sitchensis* (Ford 1982) increased with TH. Since the height range of the saplings of *Acer* and *Quercus* (cf. Methods) was considerably less than that of the trees of *P. sitchensis* (Ford 1982) and *Abies* (Kohyama *et al.*

1990), positive relationship between RCS and TH in the current study (Table 2) may have caused by low maximal height of studied saplings.

Light availability affected RCS and foliage distribution in *Acer* and *Quercus* in a very different way. With decreasing RI (Table 2) canopy became relatively shorter in *Acer* and longer in *Quercus*. One would expect the patterns of foliage distribution to follow light-related changes in RCS, and thus *Quercus* to have an increasing and *Acer* a decreasing foliage maximum with increasing RI. This was exactly the case for *Acer* (Table 3), but RI had no effect on foliage distribution in *Quercus*. Like in *Acer*, heavier shading resulted in shorter canopy in *Pinus strobus* (O'Connell & Kelty 1994) and in *A. mariesii* (Kohyama 1980), and shifted foliage distributions towards higher crown heights in *A. mariesii* (Kohyama 1980) and *Castanopsis fargesii* (Cornelissen 1993). In a *Cryptomeria japonica* stand understory trees also had foliage distributions skewed more upwards than the trees in overstory (Hashimoto 1990). However, no RI values are available from this study, and it is therefore impossible to conclude if this was a size effect or a response of crown morphology to incident irradiance.

The increase in a_a with increasing RI in *Acer* corresponds to a progressively more stretched canopy with profusely distributed branches. This architectural response fits well to observed changes in bifurcation ratio (the number of terminal branches to the number of branches on the next order) in *Acer saccharum*, where the bifurcation ratio was higher (many terminal branches on a parental branch) in open-grown and lower (highly bifurcating parental branches) in understory saplings (Steingraeber *et al.* 1979; Boojh & Ramakrishnan 1982; Canham 1988). The forest-grown saplings of *A. saccharum* had also on average shorter shoots than open-grown saplings (Steingraeber *et al.* 1979), a pattern which is in good agreement with low bifurcation ratio with frequently forking parental shoots. However, average branch length decreased with increasing irradiance in seedlings of *Quercus petraea* (Ovington & MacRae 1960). In comparison to *A. saccharum*, this would imply a reverse pattern in light-related changes in bifurcation ratio. Assuming that *A. platanoides* and *Q. robur* behave similarly to *A. saccharum* and *Q. petraea*, respectively, the differences, which were detected between the foliage distribution vs. RI relations in *A. platanoides* and *Q. robur*, may have ultimately resulted from species-specific responses of branching architecture to irradiance.

Higher a_a and a_m for the same m_a and m_m, respectively, in *Acer* than in *Quercus* (Fig. 5, Table 3) signify that the foliage is more uniformly distributed in *Acer* (see also Fig. 2A). Furthermore, as may be suggested from lower m_a and m_m in *Acer*, the maxima of foliage distributions in *Acer* are located higher in the crown than those in *Quercus* at a common TH (Eq. 3, Fig. 4). On the basis of foliage distribution, Horn (1971) distinguished between two canopy invasion strategies: 'monolayer' and 'multilayer'. At low irradiance, 'monolayer', which possesses a foliar display composed of leaves arranged non-randomly side by side in a single layer, minimises shading between the leaves and offers an efficient strategy for light interception. 'Multilayer', which has leaves distributed more uniformly across the canopy, takes advantage of penumbra effect, and can expose more foliar area than 'monolayer'. However, due to the random foliage arrangement, 'multilayer' does not intercept incident light as completely as 'monolayer'. Self-shading within the canopy is also higher in 'multilayer', which therefore requires higher irradiances than 'monolayer' to have all leaves illuminated adequately. This is why 'monolayers' are typically late-successional and shade-tolerant, 'multilayers' early-successional and intolerant species (Horn 1971). Higher maxima of foliage distributions are likely to contribute to 'monolayer' strategy, while more uniform distributions to 'multilayer' strategy. In general, light becomes increasingly available with increasing total height (King 1990), and thus the decreasing distribution maxima with increasing TH (Table 3) in both species may signify the declining importance of 'monolayer' strategy. On the other hand, lower distribution maxima in taller saplings may also point to allometric restrictions, because irradiance and TH were not related in the current study.

In addition to ontogenetic effects, *Acer* also exhibits considerable morphological plasticity. Increasing distribution maxima with decreasing irradiance (Table 3), which manifest a simultaneous shift from 'multilayer' to 'monolayer' strategy, may optimise the light use efficiency of the canopy in different light environments in this species. *Quercus*, with a crown composed of branches which are longer in shade (Ovington & MacRae 1960), may have a limited potential for adjusting the foliage distributions to low irradiances: long branches, if they are coupled with high bifurcation ratio, allow less flexibility in organising the foliar display towards a planar array of leaves. Indeed, the adaptability of canopy architecture to irradiance was limited in *Quercus* (Table 3). Invariable foliage distribution with declining RI, which is likely to decrease canopy performance under shade, may therefore constrain *Quercus* to more open habitats. Moreover, the distance between leaf layers for penumbra significantly to influence light interception increases with increasing leaf size (Horn 1971) and thus *A. platanoides*, which has considerably larger leaves than *Q. robur*, may inherently be destined to 'monolayer' strategy. However, less sharper foliage distribution in *Acer* than in *Quercus* (cf. Fig. 2A and Fig. 5) does not fit, because it is rather a trait of a 'multilayer' than of a 'monolayer'. Because large leaves need less woody supporting twigs than small leaves (Givnish 1979), and branching increases with decreasing leaf size (White 1983), interspecific differences in leaf size may provide an explanation for this discrepancy. *Acer*, which was demarcated by larger leaves and likely had also less frequently bifurcating branches than *Quercus*, may consequently have leaves distributed more uniformly across the crown. Furthermore, *A. platanoides* has also much longer petioles (5–20 cm) than *Q. robur* (0.5–2 cm). This may result in functional 'monolayer' irrespective of the exact position of leaf attachment, because long petioles allow considerable flexibility in horizontal arrangement of leaves.

Canham *et al.* (1994) concluded that the interspecific variability in the efficiency of light harvesting was more directly related to the differences in crown depth rather than to light interception per unit crown depth. Thus, more uniform foliage distribution in *Acer* may result in greater efficiency of light use, because this species can construct taller canopies than *Quercus* with the same amount of foliage. Furthermore, in understory environments, where a considerable fraction of solar radiation penetrates under low solar inclination angles (Fig. 1), a vertically extended canopy provides additional advantages for light capture. In the current study it was not possible to distinguish between the effects of various components of RI, because the contributions of lateral and vertical sky bands to RI were correlated with RI and with each other. Though the lateral component of RI was significantly larger in *Acer* than in *Quercus* (Fig.1), the differences, which were observed between the species, were small and probably did not cause the large interspecific variability in foliage distributions.

Implications of different foliage distributions for leaf structure

Lower LWA (Table 2) and LWA_m (Fig. 6) in *Acer* than in *Quercus* agree with the reported tendency of shade-tolerant species to have lower biomass requirement for construction of unit foliar area than intolerant species do (Jurik 1986; Abrams & Kubiske 1990; Niinemets & Kull 1994). This difference may be relevant in terms of light interception, because with similar proportion of total biomass in leaves, *Acer* forms more extensive foliar display than *Quercus*, and may capture more light. However, insofar as there exists a positive correlation between LWA and leaf photosynthesis rate per leaf area (Jurik 1986; Oren *et al.* 1986), low LWA compromises between highly effective light interception and low rate of carbon acquisition per unit leaf area. Nevertheless, to take advantage of higher leaf photosynthetic capacities, higher average irradiances are necessary as well. Accordingly, for a positive plant carbon balance *Quercus* may need higher irradiances than *Acer*.

A linear increase in LWA with increasing RI in both *Acer* and *Quercus* (Table 2, Fig. 6) is compatible with the general trend across many woody species (e.g. Čermák 1989; Kull &

Niinemets 1993; Niinemets 1995; Niinemets & Kull 1995). LWA often also increases with increasing TH (Linder 1985; Kull & Niinemets 1993; Niinemets 1995; Niinemets & Kull 1995), as was found for the uppermost leaves of *Acer* and *Quercus* (Table 2). Relationships between LWA and TH most likely result from an increasing demand for supporting tissues in leaves with increasing TH (Kull & Niinemets 1993; Niinemets & Kull 1995; Niinemets 1996). Higher proportion of supporting tissues, which adds to the foliage tolerance of low water potentials, is essential in large trees, where also water gradients exceed those in small trees. Surprisingly, LWA_m was not related to TH either in *Acer* or in *Quercus*, and was only correlated with relative irradiance above the canopy (Fig. 6). Since the parameters of foliage distribution were affected by TH, light gradients across the canopy are also expected to depend on TH. As TH increases, distribution maxima decrease (Fig. 4), and shading within the canopy, which in turn alters LWA_m, may increase. Therefore, the influence of TH on foliage distribution may offset the effect of TH on LWA. This hypothesis received further support from a study on saplings of shade-intolerant *Dipteryx panamensis*, where intra-crown variability in irradiance was related to canopy and tree size (Oberbauer *et al.* 1988). However, in the same study no effects of plant and crown size on light gradients across the crown were apparent for saplings of shade-tolerant *Lecythis ampla*. Moreover, the coefficients, C_1 and C_2 (Eq. 6), which describe the variation of LWA within the canopy were not related to TH or RCS in either *Acer* or *Quercus*.

Accompanied by gradually decreasing irradiance, the decline in LWA with increasing canopy depth is one of the most characteristic canopy features (Hollinger 1989; Ellsworth & Reich 1993). Due to the exponential nature of the relationship of light absorption vs. cumulative foliage area (Monsi & Saeki 1953), light gradient across the canopy should be greater for higher values of incident irradiance. However, the gradient in LWA was related to relative irradiance above the crown only in *Quercus*. Different response of LWA in *Acer* may result from (1) light-related adjustments in foliage distribution (Table 3) and (2) from an increase in relative canopy size (Table 2) in this species. Effects (1) and (2) may counterbalance the expected increase in light gradient with RI, and thus explain why no influence of incident irradiance on C_2 was detected in *Acer*. In *Quercus*, where RCS decreased with RI and the slope of foliar area vs. RI relationship was higher than that in *Acer*, the absolute values of leaf area per unit stem length increased also more with RI. This, in combination with the static foliage distribution with variable RI, may have caused the light-dependency of C_2 (Fig. 7) in *Quercus*.

Morphological plasticity of crown architecture and foliage distribution to incident irradiance in *Acer* results in more uniform distribution of irradiance within the canopy, and as such, is likely to improve the light-use efficiency and allow the growth of the saplings of this species under lower irradiance. Low architectural flexibility in *Quercus*, where enhanced foliar area production inevitably results in greater self-shading within the canopy rather than in more advanced light interception, may constrain its saplings to more open habitats. Thus, these differences in irradiance-response of sapling canopies may play a central role in determining the observed niche separation along the understory-gap continuum and the differing abilities to tolerate shade in the studied species.

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VII

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Plant growth-form alters the relationship between foliar morphology and species shade-tolerance ranking in temperate woody taxa

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Abstract

Variation in leaf size (area per leaf) and leaf dry weight per area (LWA) in relation to species shade-and drought-tolerance, characterised by Ellenberg's light (ELD) and water demand (EWD) values, respectively, were examined in 60 temperate woody taxa at constant relative irradiance. LWA was independent of plant size, but leaf size increased with total plant height at constant ELD. Canopy position also affected leaf morphology, leaves from the upper crown third had higher LWA and were larger than leaves from the lower third. Leaf size and LWA were negatively correlated, and leaf size decreased and LWA increased with decreasing species shade-tolerance. Mean LWA was similar for trees and shrubs, but trees had larger leaves than shrubs. Furthermore, all relationships were altered by plant growth-form, and none of the qualitative tendencies was significant for trees, implying the considerably lower plasticity of foliar parameters of trees than those of shrubs. Accordingly, shade-tolerance of trees, having relatively constant leaf structure, may be most affected by the variability in biomass partitioning and crown geometry, influencing foliage distribution and spacing, and finally determining canopy light absorptance. Alteration of leaf form and investment pattern for construction of unit foliar surface area, changing the efficiency of light interception per unit biomass investment in leaves, is a competitive strategy inherent to shrubs. EWD as well as wood anatomy did not control LWA and leaf size, though there was a trend of ring-porous tree species to be more shade-tolerant than diffuse-porous trees. Since ring-porous species are more vulnerable to cavitation than diffuse-porous species, they may be constrained to environments where irradiances and consequently evaporative demand is lower.

Introduction

Influencing foliar surface area exposed to solar radiation at constant biomass investment in leaves, interspecific variation in leaf dry weight per leaf area (LWA) of woody taxa (Abrams & Kubiske 1990; Jurik 1986; Niinemets & Kull 1994) may affect species ability to compete for light, and thus promote diverse canopy invasion strategies. As a contribution to conservative light use, shade-tolerant species have lower values of LWA than intolerant species (Abrams & Kubiske 1990; Jurik 1986; Niinemets & Kull 1994), and may consequently construct cheaper and more extensive light-intercepting foliar display than intolerant species. However, the major trade-offs associated with low LWA involve potentially higher self-shading between the leaves and, since often a positive relationship between photosynthesis and LWA exists (Gutschick & Wiegel 1988; Jurik 1986; Oren et al. 1986), lower photosynthesis per unit area. With increasing light availability enhanced photosynthesis rather than light interception per unit foliar surface area should be favoured, and high LWA, making it possible to invest more photosynthesising weight per area where the irradiances and payback in terms of carbon fixation are largest (Gutschick & Wiegel 1988), may offer a considerable benefit in sunny habitats, where intolerant species have greater carbon gain per unit leaf area than shade-tolerators (Bazzaz & Carlson 1982). Though, canopy of intolerant species, transmitting more light than that of shade-tolerators (Canham et al. 1994; Horn 1971), is open to invasion, and increased LWA, implying increased biomass costs for formation of intercepting surface, may inherently limit efficient light harvesting.

Foliar architecture of both shade-tolerant and intolerant species adaptively responds to light gradients across the canopy (Björkman 1981), and in addition to interspecific differences, LWA close to linearly increases with increasing relative irradiance (Čermak 1989; Niinemets & Kull 1994). Moreover, relative irradiance is an even more important source of variation in LWA than species shade-tolerance rank (Niinemets & Kull 1994). Since light becomes increasingly available with increasing plant height (King 1990) and canopy expansion (Küppers 1989, 1994) LWA is likely to be affected by species growth-form. Trees, growing in overstory and having extensive canopies, should possess greater LWA than shrubs, constrained to understory, or than species lacking self-supporting stems and being thus unable to form massive canopy, e.g. vines and lianas. Indeed, LWA was higher in trees than in shrubs (Körner et al. 1986), in self-supporting mono-and dicots than in lianas (Bigelow 1993), in trees than in vines (Castellanos et al. 1989). However, resulting from increasing water limitation and environmental stresses with increasing plant dimensions, expected to increase the proportion of supporting tissues in leaves, LWA at constant irradiance increases with total plant height (Niinemets & Kull 1995; Schoettle 1994). Therefore, it is not evident to what extent LWA differs between growth-forms due to an intrinsic variability in irradiance, caused by diverse patterns of species dispersal in the canopy that are specific to plant growth-forms, e.g. overstory vs. understory, and to what extent the variability in LWA is induced by changing investment patterns for foliage construction with increasing plant size. Furthermore, with increasing plant height the significance of both the effects of increasing structural requirements for leaf surface formation and of increasing irradiance on LWA is likely to increase in importance. Thus, the influences of irradiance and plant size may override the interspecific variability in LWA, and consequently, the relationship between LWA and species shade-tolerance rank may be less significant for trees than for shrubs. Küppers (1985, 1989, 1994) argues that, in temperate forests, branching and partitioning patterns, determining crown architecture and the limits for vertical and horizontal canopy expansion, are more important long-term competitive attributes than foliar structure and functional activity, e.g. greater canopy light interception by shade-tolerant than by intolerant trees was achieved by increasing canopy depth rather than by adjusting light ex-tinction per unit canopy depth (Canham et al. 1994). Again, since shrubs have inherently limited potential for changing canopy depths, their foliar structure may be of considerably greater relevance for efficient light capture than that of trees.

The purpose of the current study was to test if plant growth-form affects interspecific relationships between species shade-tolerance rank and leaf structural characteristics, and if leaf variables differ between shrubs and trees. Variability in light availability was eliminated and thus only species-specific differences in leaf structure as related to plant stature or tolerance rank could be studied. In addition to LWA, leaf size, influencing leaf energy balance (Givnish 1984; Vogel 1968) and light distribution in the canopy (Horn 1971), was included in the present analysis. Since leaf size is poorly related to relative irradiance (Niinemets & Kull 1994), the species, having inherently large leaves and sustaining therefore higher leaf temperatures with the same radiation loads (Parkhurst & Loucks 1972, Taylor 1975) that may cause leaf transpiratory water loss to increase (Givnish & Vermeij 1976; Parkhurst & Loucks 1972; Taylor 1975), and unless xylem capacity for water transport scales with increasing water requirements, they may be constrained to understory environments where evaporative demand is lower, and accordingly, the water balance of leaves more favourable. Therefore, in addition to the efficacy of light absorption, consideration of variation in leaf form and structure in terms of plant water economy is necessary.

Material and methods

Leaves of 88 natural and naturalised woody taxa, comprising 83% of Estonian native woody flora, were sampled during the summer months in 1986–1988 from 21 stands located between 58 ° N, 21 ° E and 59 ° N, 28 ° E in Estonia (Niinemets & Kull 1994). Fully-expanded undamaged leaves on distal branch position from upper ('sun' leaves) and lower crown third ('shade' leaves) of the southern crown aspect were sampled. On average, 500 leaves per plant (one half from the upper and the other half from the lower crown third) and 3.3 (2 to 6) plants per species were analysed. To reliably estimate mean leaf size, i.e. projected area per leaf, a large number of leaves per sample location was necessary (Tamm & Hannus 1977). For species with compound leaves, leaflets were considered equivalent to simple leaves. Leaves were weighed after oven-drying at 90 °C, and leaf dry weight per projected surface area (LWA, g m^{-2}) was calculated. Further details concerning leaf sampling and estimation of leaf surface area are given in Niinemets and Kull (1994).

Sampled woody species were grouped according to plant growth-form. Species with single stem and with maximum height over 6 m were considered as trees, all others as shrubs (Appendix 1). Mean heights (antilogarithm of mean logarithmed total height) for sampled trees and shrubs were 6.6 ± 1.2 m (range 1.2–19 m) and 1.5 ± 1.1 m (range 0.3–6 m), respectively (means are significantly different at $p<0.001$, t-test). According to plant size, dwarf-shrubs are often treated as an independent group. However, leaf size and LWA of dwarf-shrubs did not differ significantly from those for shrubs (t-test, $p>0.05$), also, separation of dwarf-shrubs did not affect comparisons between trees and shrubs qualitatively.

Since leaf structural parameters were strongly dependent on relative irradiance, characterised by stand canopy cover (SCC, proportion of completely covered sky), and more shade-tolerant species were restricted to lower irradiances than less tolerant species (Niinemets & Kull 1994), the comparison between species was constrained to mean SCC of 0.45–0.55. Leaf parameters for this range of mean SCC were available for 60 species (Appendix 1).

Ellenberg's light demand values (ELD, Ellenberg et al. 1991) were used to order species according to decreasing shade-tolerance, and Ellenberg's water demand values (EWD, Ellenberg et al. 1991) according to decreasing drought-tolerance. The studied species ranked with respect to ELD from 4 to 8, and with respect to EWD from 3 to 8, giving consequently relative five- and six-level tolerance scales for shade and drought, respectively. Light requirements (% of open sky) approximately corresponding to ELD are: 4: 5–10%, 5: 10–20%, 6: 20–30%, 7: 30–40%, 8: 40–50%. Though ELD of trees is given for the seedling stage of development, in the data of Ellenberg (1982, p. 82) a good correlation exists between the ability of tree seedlings to tolerate shade and of mature trees to intercept radiation and cast shadow (Spearmann rank correlation, $r = 0.823$, $n = 42$, $p<0.001$, Figure 1), indicating that also for trees ELD is a good index of efficiency of light interception and consequently of species strength to compete for light.

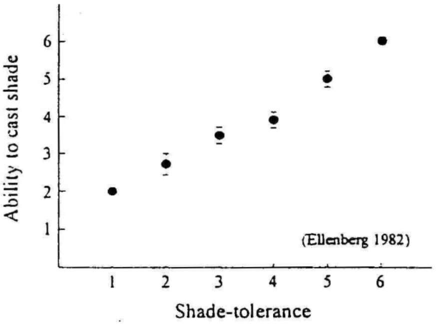

Figure 1. Category plot of species ability to tolerate shade in understory vs. to cast shadow in overstory (data of Ellenberg 1982, p. 82). Numeric classes (1–6) stand for 1: extremely low, 2 very low, 3: low, 4: average, 5: high, 6: very high. Error bars give ± SE.

To test the effect of interspecific variability in wood structure on leaf parameters, diffuse-porous, semiring-porous and ring-porous species were separated. Initially, two species groupings by wood anatomy, the first based on Greguss (1959) and Grosser (1977), and the second on Baas and Schweingruber (1987), were compiled. Though the correlation between the independent sets was not excellent (Spearmann rank correlation, $r = 0.725$, $n = 31$, $p<0.001$), implying the various classification criteria in different wood anatomists and aggravating thus the ecological comparison between the species, significance values of correlations between leaf parameters, EWD, ELD and wood structure were only slightly altered by using different sets, and therefore only species classification of Baas and Schweingruber (1987) was used throughout the study. Distributions of leaf area per leaf (S, cm^2) and total tree height (H, m) were strongly skewed, and therefore both S and H were transformed before statistical analysis using natural logarithmic transformation (LogS and LogH, respectively).

Dependence of leaf structure on LogH, ELD and EWD, and relationships between LWA and LogS were examined by linear regression analysis, effect of wood anatomy on leaf structure as well as relations between wood anatomy, ELD and EWD by Kruskal-Wallis non-parametric analysis of variance and by Spearmann non-parametric rank correlations. LWA and leaf size for different growth-forms were compared using t-test. Statistical relationships were considered significant at $p<0.05$ (Wilkinson 1990).

Table 1. Mean LWA (g m^{-2}) and LogS for the leaves from upper (sun) and lower crown third (shade) with respect to plant growth-form

Growth-form	Mean LWA ± SE			Mean LogS ± SE		
	sun	shade	N	sun	shade	N
Shrubs	66.8 ± 5.2a	60.0 ± 4.7b	23	2.11 ± 0.22a	1.87 ± 0.23b	21
Trees	70.8 ± 3.7a	66.5 ± 4.1a	18	2.39 ± 0.15a	2.35 ± 0.16a	18
Shrubs+trees	68.6 ± 3.3a	62.8 ± 3.3b	41	2.24 ± 0.13a	2.09 ± 0.14b	39

Mean values for sun and shade followed by the same letter are not significantly different ($p>0.05$)

Table 2. Influence of LogH (natural logarithm of total plant height) and Ellenberg's light demand value (ELD, Ellenberg *et al.* 1991) on mean LogS (natural logarithm of mean projected leaf area per leaf)

Growth-form	*n*	Intercept ± SE	*p*	Slope ± SE				r^2
				LogH	*p*	ELD	*p*	
Shrubs	30	6.29 ± 0.97	0.001	0.90 ± 0.24	0.001	−0.80 ± 0.15	0.001	0.590
Trees	18	3.22 ± 1.19	0.02	0.016 ± 0.23	0.95	−0.14 ± 0.16	0.41	0.058
Shrubs+trees	48	4.32 ± 0.83	0.001	0.43 ± 0.13	0.003	−0.47 ± 0.13	0.001	0.419

Results

Mean light and water demand values as well as wood anatomy were not significantly different in shrubs vs. trees ($p>0.05$). Also, mean LWA of trees did not differ from that of shrubs ($p>0.05$). Leaves were smaller (5.0 cm^2, antilogarithm of mean LogS) and more variable in size (Figure 2) in shrubs than in trees (11.3 cm^2) ($p<0.01$). Lower LogS in shrubs was largely attributable to decreased leaf size in lower crown third of shrubs (Table 1). 'Sun' leaves had higher mean LWA and LogS than 'shade' leaves (Table 1), whereas this variation pattern was dependent on plant growth-form: leaf morphological parameters were significantly dependent on leaf position in the canopy in shrubs ($p<0.001$), but not in trees ($p>0.05$) (Table 1). Mean LogS and LWA were negatively correlated ($r^2 = 0.206$, $p<0.001$). However, when shrubs and trees were examined separately, the correlation was significant for shrubs, but LogS was independent on LWA in trees (Figure 2). Mean values of LWA and LogS were altered slightly by consideration of only natural species (53 of 60 Appendix I), though, the exclusion of naturalised species did not change the qualitative tendencies.

LWA pooled for all species increased significantly with increasing species light demand ($r^2 = 0.160$, $p<0.01$). Relationship between LWA and ELD was highly significant in shrubs, but LWA of trees was not related to ELD (Figure 3). Mean LWA and LogH were not correlated ($p>0.05$), but LogS was significantly affected by both LogH and ELD, increasing with LogH

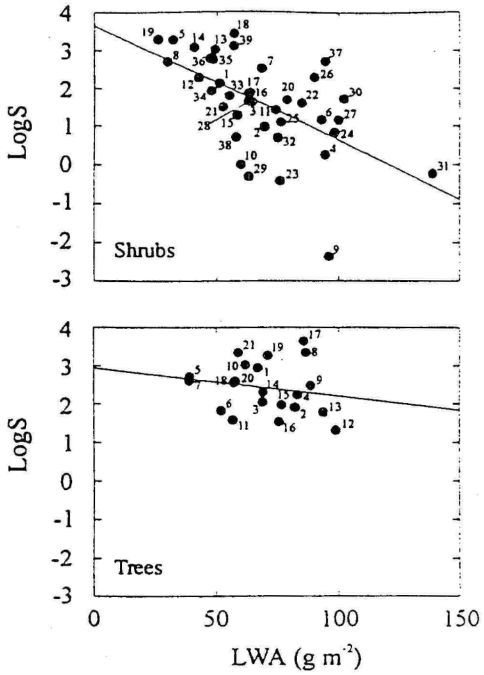

Figure 2. Correlation between mean LogS and LWA at constant relative irradiance (at a stand canopy cover, SCC, range of 0.45–0.55). Shrubs: LogS = 3.66 − 0.0303 × LWA ($n = 39$, $r^2 = 0.329$, $p<0.001$) Trees: LogS = 2.94 − 0.0075 × LWA ($n = 18$, $r^2 = 0.035$, $p>0.4$). Species numbers refer to appendix I.

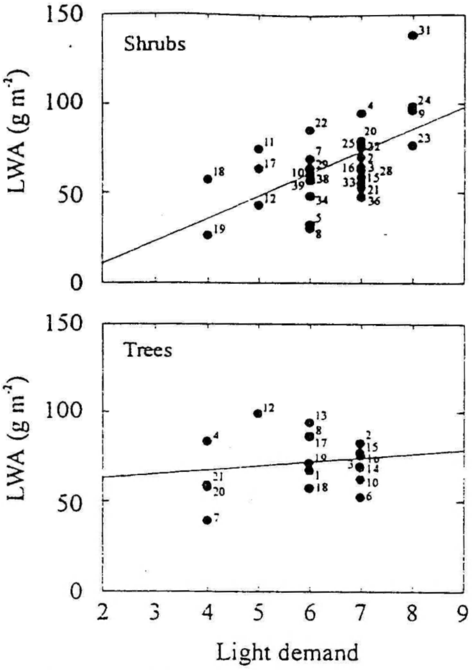

Figure 3. Effect of Ellenberg's light demand value (ELD) on mean LWA (g m^{-2}) at constant relative irradiance (at a SCC range of 0.45–0.55). Shrubs: LWA = 12.59 × ELD − 14.4 ($n = 30$, $r^2 = 0.349$, $p < 0.001$, intercept is not significantly different from zero). Trees: LWA = 58.5 + 2.2 × ELD ($n = 18$, $r^2 = 0.029$, $p > 0.5$).

and decreasing with ELD (Table 2). Again, LogS of trees was not related to ELD and LogH, and ELD and LogH altered LogS significantly only in shrubs (Table 2). Correlation between ELD and LogH was not significant ($p > 0.2$).

LogS and LWA were independent of EWD and wood anatomy. However, mean ELD increased with decreasing ring-porosity ($p < 0.03$), the trend being not significant for shrubs ($p > 0.2$) but important in trees ($p < 0.05$). EWD was correlated neither with wood anatomy nor with ELD. Since LWA-s and LogS-s for 'sun' and 'shade' leaves were correlated for both shrubs ($r^2 = 0.874$, $p < 0.001$ for LWA and $r^2 = 0.929$, $p < 0.001$ for LogS) and trees ($r^2 = 0.654$, $p < 0.001$ for LWA and r^2 $p = 0.960$, $p < 0.001$ for LogS), relationships of LWA and LogS for 'sun' and 'shade' with ELD, EWD, LogH and wood anatomy did not differ qualitatively from those for mean LWA and LogS.

Discussion

Within a species LWA has consistently been found to increase with increasing total plant height (TH) (Niinemets & Kull 1995; Schoettle 1994). However, in current study no correlation between LWA and TH was observed, and also LWA in trees and shrubs, differing in mean TH, was not significantly different. Since environmental gradients and water limitation increase with TH, leaves should become increasingly more resistant, and thus the requirement for supporting structures should increase with TH, e.g. higher wind speed increased the proportion of supporting tissues in leaves of *Phleum alpinum* L. and *P. pratense* L. (Woodward 1983), and water stress the content of foliar cell-wall polysaccharides in *Triticum durum* Desf. (Rascio et al. 1990), resulting in both cases in higher LWA (Rascio et al 1990; Woodward 1983). Thus, trees, having similar LWA as shrubs, but larger TH, may have proportionally less leaf biomass in assimilative structures than shrubs.

With increasing leaf size, mechanical load of leaf lamina on petiole increases, and to keep the leaf at a constant inclination angle, larger investment in supporting tissues is necessary than for a small leaf (Niklas 1992). Increasing LWA would supplementary increase mechanical loads on petiole for the same leaf size, and thus decreasing LogS with increasing LWA in shrubs (Figure 2) may manifest an adaptive modification towards avoiding enhanced costs for leaf support. In trees, no correlation between LWA and LogS was found (Figure 2), but the range of variation in LogS was also considerably narrower than that in shrubs. Thus, with increasing LWA, the adjustment of foliar inclination angles as well as maintenance of blade consistency appears to become increasingly more expensive in terms of leaf support in trees, having constant leaf size than in shrubs, compensatory diminishing the size of their leaves. Furthermore, larger mean leaf size in trees than in shrubs at similar mean LWA (Table 1) implies also higher biomass costs for foliar support in trees.

At constant light availability, lower LWA in shade-tolerant than in intolerant shrub species (Figure 3) may be adaptive, allowing to construct larger foliar surface area with the same investment of biomass in leaves. However, modification of LWA appears to be of no importance in determining species ability to endure shade in trees (Figure 3). For large trees, Ellenberg's light demand values, actually determined for seedlings (Ellenberg et al. 1991), may not be appropriate estimates, since Yevstigneyev (1990) found that species shade-tolerance decreased dramatically in the ontogeny of different woody species. Nevertheless, shade-tolerance ranking was fairly constant, whenever the individuals of similar age were compared (Yevstigneyev 1990). Moreover, a good correlation for a given species between the ability of seedlings to endure and of mature trees to cast shade does exist as well (Figure 1). Thus the results are not likely to be biased by using a scale of shade-tolerance initially proposed for seedlings. Constant LWA in trees (Figure 3) contrasts to the studies, where lower values of LWA or leaf thickness were found in shade-tolerant than in intolerant trees (Abrams & Kubiske 1990; Carpenter & Smith 1981; Jackson 1967; Jurik 1986). Carpenter and Smith (1981) even reported that a trend of decreasing leaf thickness with increasing species shade-tolerance in trees was reversed when shrubs were included. However, since shade-tolerators are expected to grow under lower mean irradiances than intolerant species, and canopies of shade-tolerant trees cast deeper shade (Canham et al. 1994; Figure 1) as well, generalisation of trends in leaf thickness and LWA, both being significantly related to irradiance (Björkman 1981; Čermák 1989; Niinemets & Kull 1994), without specifying the irradiance is impossible. Similarly to current study, leaf thickness of three *Quercus* species, varying in shade-tolerance, differed little within the same irradiance treatment (Ashton & Berlyn 1994). Likewise, such extensive data on foliar parameters at constant relative irradiance, covering most of the local woody flora, have not been analysed so far.

Leaf size was also relatively constant in trees, but decreased significantly with increasing species shade-tolerance in shrubs (Table 2). Large leaves allow construction of a foliar display, monolayer, that efficiently intercepts light and casts deep shade (Horn 1971), and is profitable in understory environments in capturing sunflecks Consisting of small leaves, multilayer takes advantage of penumbra effect, and therefore more foliar area may be exposed than in the case of monolayer (Horn 1971). However, multilayer is penetrated by more light than monolayer and also captures lightflecks less effectively. With increasing species shade-tolerance, the advantages of monolayer strategy should increase, and leaf size of shrubs, related positively to species shade-tolerance, may adjust towards effective light interception. Though, trees had larger leaves than shrubs (Table 1), and monolayer arrangement, in particular, casting of deep shade, may be a more important competitive attribute in trees than in shrubs. Positive relationship between LWA and ELD in shrubs (Figure 3), increasing the biomass costs for lamina support for the same leaf size (cf. above), may also cause leaf size to be inversely related to species shade-tolerance rank. And leaves may optimise a pay-off of having large leaves and efficient light intercepting surface (monolayer) and low LWA with low investment of photosynthesising tissues pear unit area, or]having small leaves and less effective light interception, but high LWA.

Since lateral thermal conductivity, though being generally very low for leaves, depends on leaf thickness (Vogel 1984), negative correlation of LWA with LogS (Figure 2), and positive with leaf thickness (Witkowski & Lamont 1991), may also signify the importance of leaf energy balance in modifying leaf structure. Moreover, leaf boundary-layer conductance for both water and heat transfer at constant wind speed is dependent on characteristic leaf width, i.e. the width of simple leaf or its lobes or leaflets of compound leaves (Parkhurst & Loucks 1972; Taylor 1975). With increasing leaf width, leaf temperature for constant radiation load increases, causing also evaporative potential of leaves to increase and may therefore bring about enhanced water use. Accordingly, species with large leaves may be constrained to shaded environments, where radiation loads are lower and water balance of leaves more favourable. Decreased leaf size of intolerant shrubs may thus be an adaptation to higher mean irradiance in habitats, where these species most likely occur. Analogously, leaves in upper canopy, exposed to greater radiation loads, are often smaller, being consequently more effective heat dissipaters than leaves in lower canopy (Vogel 1968). However, larger leaves of shrubs in sun than in shade (Table 1) do not fit this pattern. Since water gradient across the stem increases with increasing irradiance and evaporative demand, expansion of leaf cells, depending on water availability (Dale 1988), is likely to decrease with increasing height in the canopy. On the other hand, light stimulates the division rate of leaf cells (Baker et al. 1985; Dale 1988), and in shrubs, having a short canopy, the differences in water supply within the canopy may not override the positive effect of light on leaf growth. This may result in greater leaves in upper canopy.

Implicit of using LogS as a determinant of leaf energy balance is the assumption that area per leaf and leaf width are correlated. Indeed, Vasilyev (1988) for a dataset of 35 temperate woody species, of which 89% were included in the current analysis, found that there exists a good interspecific correlation between area per leaf and leaf width ($r^2 = 0.83$, $p<0.001$), proving the convergence in leaf form and the validity of using LogS as an estimate of leaf width.

Increasing leaf size with increasing TH in shrubs may represent a general dependence between whole-plant allometry and leaf size. Similarly to the current study, leaf size increased with TH in *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman (Senn et al 1992), and species with large leaves had greater supporting twigs than species with small leaves in several desert plants (Comstock & Ehleringer 1990). Since large leaves need more mechanical support than small leaves, small plants may not be able to bear large leaves, an accidental loss of a large leaf will be more fatal for the carbon balance of a small than of a large plant. Because supporting woody twigs need to branch less frequently for large leaves, increase in leaf size may be favoured with increasing apical dominance. In contrast, small leaves, minimising the fraction of supporting structures within the leaf, may be more profitable for species invading space mostly by lateral growth and investing intrinsically more biomass for small twigs than for species with mostly vertical growth. However, leaf size cannot increase infinitely, and the benefits of large leaves in terms of short woody twigs should be counterbalanced by increased diameter of these twigs. Accordingly, enhanced supporting costs may cause the relationship of leaf size vs. TH to saturate, and accordingly, limited upper boundary for leaf size may be the reason of independent TH and leaf size in trees.

Variation in LWA and leaf size, nearly constant in trees and significantly dependent on species shade-tolerance rank in shrubs (Figure 3) point to the lower foliar plasticity in trees than in shrubs. Higher light harvesting by the canopy of shade-tolerant than of intolerant trees (Canham et al. 1994; St-Jacques & Bellefleur 1993) was essentially achieved by changes in crown architecture (Canham et al. 1994), demonstrating the decreasing influence of leaf traits on the economy of light harvesting of the canopy with increasing plant dimensions. Furthermore, the effect of leaf-level adjustments on canopy energy balance may also decrease with increasing TH, since both canopy aerodynamic roughness, affecting canopy conductance for water and heat at constant wind speed (Landsberg 1986), and wind speed increase with increasing TH (Brunig 1970; Landsberg 1986). Accordingly, canopy geometry and plant growth-form may be more powerful competitive attributes than foliar structure and physiological activity (Küppers 1989, 1994). Since trees have a potential to reach unshaded overstory, the adaptability of crown architecture in trees may be a more important determinant of competitive strength than foliar plasticity.

Carlquist (1975) concluded that leaf size may be limited by wood anatomy and hydraulic architecture of stems. Low hydraulic conductance of stem should favour small leaves, having lower leaf temperatures and thus lower evaporative demands than large leaves. Furthermore, when transpiration rates are high, low hydraulic conductance of stems may effectively uncouple leaves from the water availability in soil, e.g. during midday the leaves of diffuse-porous *Acer saccharum* Marsh. may be subject to water stress even if soil water is not limiting (Yang & Tyree 1993). Though, trees have larger capacity for water storage than shrubs, they possess also longer water transport pathways and are therefore likely to be more vulnerable to water limitations than shrubs. Consequently, the interspecific differences in xylem anatomy may be more important in trees. Increasing size of xylem vessels, results in enhanced xylem conductivity, but also in higher xylem vulnerability to cavitation (Cochard & Tyree 1990; Zimmermann 1978), and higher proportion of ring-porous trees among shade-tolerators may be caused by their low plasticity in adjusting leaf size, and consequently in controlling the evaporative demand, constraining these tree species to shaded environments.

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Appendix 1. Studied species (number in figures). Nomenclature is given according to Czerepanov (1981)

Trees

Alnus incana (1)
Betula pendula (2)
Betula pubescens (3)
Fraxinus excelsior (4)
Malus domestica (5)
Malus sylvestris (6)
Padus avium (7)
Populus tremula (8)
Pyrus pyraster (9)
Quercus robur (10)
Salix acutifolia (11)
Salix alba (12)
Salix daphnoides (13)
Salix pentandra (14)
Salix triandra (15)
Salix viminalis (16)
Sorbus aria (17)
Sorbus aucuparia (18)
Sorbus intermedia (19)
Ulmus glabra (20)
Ulmus laevis (21)

Shrubs and dwarf-shrubs

Amelanchier spicata (1)
Berberis vulgaris (2)
Betula humilis (3)
Corylus avellana (5)
Crataegus curvisepala (6)
Euonymus europaea (7)
Frangula alnus (8)
Juniperus communis (9)*
Ledum palustre (10)*
Lonicera baltica (11)
Lonicera xylosteum (12)
Pentaphylloides fruticosa (13)
Physocarpus opulifolius (14)**
Prunus spinosa (15)
Rhamnus cathartica (16)
Ribes nigrum (18)
Ribes pubescens (19)
Rosa dumalis (20)
Rosa majalis (21)
Rosa mollis (22)
Rosa spinosissima (23)**
Rosa subcanina (24)
Salix aurita (25)
Salix dasyclados (26)
Salix lapponum (27)
Salix myrsinifolia (28)
Salix myrtilloides (29)
Salix rosmarinifolia (31)
Salix starkeana (32)
Sambucus nigra (33)**
Sambucus racemosa (34)**
Sorbaria sorbifolia (35)**
Swida sanguinea (36)
Syringa vulgaris (37)**
Vaccinium uliginosum (38)
Viburnum opulus (39)

* Evergreen species.
** Naturalised species, i.e. introduced species, dispersing and reproducing naturally.

CURRICULUM VITAE

I. GENERAL FACTS

1. Name: Ülo Niinemets
2. Date and place of birth: March 19, 1970, in Tartu (Estonia)
3. Citizenship: Estonian
4. Address: Ringtee 3–1, EE2430 Tõrvandi, Estonia; phone: 372/7/415229; e-mail: ylo@ut.ee, ylo@zbi.park.tartu.ee, Uelo.Niinemets@bitoek.uni-bayreuth.de
5. Current employment: Doctoral student of the Chair of Ecophysiology, University of Tartu (since Sept. 20, 1993); Researcher at the Institute of Ecology of Estonian Academy of Sciences (since March 15, 1996).
6. Education:

1977–1988, Tartu Secondary School no. 5 (biology class, finished with a silver medal);

1988–1992, biology studies at the Faculty of Biology and Geography of University of Tartu (graduated *Cum laude* as plant ecophysiologist in 18.06.92, Diploma work on 'Variations in leaf morphology and nitrogen content in *Corylus avellana, Lonicera xylosteum* and *Betula pendula*');

May 5, 1991 – March 1, 1992, biology studies and research work at the University of Bayreuth (Federal Republic of Germany);

Sept. 1, 1992 – Sept. 20, 1993, master studies at the Chair of Ecophysiology of University of Tartu, Since Sept. 20, 1993 Master of Biology (Ecophysiology) of University of Tartu (Master thesis on 'Variation in leaf morphology and nitrogen content of woody plants in relation to light availability').

7. Professional experience:

Summers of 1986–1988, assisting in field works of the Department of Ecophysiology of the Institute of Zoology and Botany of Estonian Academy of Sciences;

June–August 1989, research work at Voore Ecological Station of University of Tartu;

July–August 1990, geobotanical research at Kivatsu State Nature Reserve (Karelia, Russia);

May 1991–May 1996 (at intervals, altogether 2.5 years), research on leaf structure, chemical composition and total tree carbon balance at the Chair of Plant Ecology II (BITÖK, University of Bayreuth, Germany);

1992–1996, studies on interspecific variability in woody species shade-tolerance and leaf properties at the Institute of Ecology, Estonian Academy of Sciences (1.10.92–15.03.96 as junior researcher, since 15.03.96 as researcher).

8. Languages: German, English, Russian, Spain, Czech.

II. SCIENTIFIC ACTIVITY

1) Fields of research: Shade-tolerance of woody species, stand carbon balance and stand development, tree size and age effects on foliar structure and function.

2) Related publications (in addition to those reprinted in this Thesis):

1. Niinemets, Ü.; Kull, O. (1995): Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in needle morphology. Tree Physiology 15, 307–315.

2. Niinemets, Ü.; Kull, O. (1995): Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*: variation in shoot structure. Tree Physiology 15, 791–798.

3. Niinemets, Ü. (1996): Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*:. Trees: Structure and Function. (In Press)

4. Niinemets, Ü.; Tenhunen, J. D. (1996): A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade tolerant species *Acer saccharum*. (Submitted)

4) Grants:

1995, 'Potentials and limitations in the annual carbon gain of forest trees: Interspecific variability due to the differences in leaf development, water and light use efficiency' (Estonian Science Foundation, ETF-1597);

1996/97, 'Combined effects of light and temperature on annual net carbon gain of deciduous forest trees' (ETF-2048).

5) Other scientific organisational and biology-related activities:

1985–1989, a member of the School Students Scientific Society of Estonia (SSSE);

1986–1988, chairman of the section of botany of SSSE (arrangement of conferences and expeditions for the school students);

1989–1991, leader of the students' circle of theoretical biology at University of Tartu (organising conferences, spring schools of theoretical biology, and editing and publishing of a students' journal of theoretical biology — "Vita Aeterna").

6) Prizes:

1986, the title 'laureate' of SSSE (the best study in a given branch) in botany ('Analysis of plant cover and floristic composition of the old rivers of Võhandu and S-Emajõgi');

1987, first prize in a competition of research works of school students of Estonia ('Specific leaf mass of Estonian woody species');

1988, 'laureate' of SSSE in zoology ('Estimation of growth rates and a new coefficient of exterior for the Estonian fish species);

1996, *Academia Europea* Baltic Prize to young scholars (for the work on species shade-tolerance — paper I of this Thesis).

CURRICULUM VITAE

I. ÜLDANDMED

1. Nimi: Ülo Niinemets
2. Sünniaeg ja koht: 19. märts 1970, Tartu
3. Kodakondsus: Eesti
4. Aadress: Ringtee 3–1, EE 2430 Tõrvandi, tel. 27/415229
5. Praegune töökoht: TA Ökoloogia Instituudi teadur
6. Haridustee:

   1977–1988 Tartu 5. Keskkool (loodusteaduste süvaõppega klass, lõpetanud hõbemedaliga),

   1988–1992, Tartu ülikooli bioloogia-geograafiateaduskond, bioloogia eriala. Lõpetanud *Cum laude* ökofüsioloogina, diplomitöö teemal: 'Variations in leaf morphology and nitrogen content in *Corylus avellana, Lonicera xylosteum* and *Betula pendula*'

   1. sept. 1992 – 20. sept. 1993 TÜ ökofüsioloogia õppetooli magistrant. 20. sept. 1993 kaitsnud magistrikraadi (bioloogia-ökofüsioloogia alal) teemal 'Variation in leaf morphology and nitrogen content of woody plants in relation to light availability'
7. Teenistuskäik:

   Juuni–august 1986–1988 osalemine Eesti TA Zooloogia ja Botaanika Instituudi ökofüsioloogia töörühma välitöödel Laelatul (juhendaja Kalevi Kull)

   Juuni–august 1989 teadustöö Tartu Ülikooli Voore ökoloogiajaamas (juh. Olevi Kull)

   Juuli–august 1990 geobotaaniline uurimistöö Kivatsu looduskaitsealal (Karjala, Venemaa) (juh. Jaanus Paal);

   Alates maist 1991 kuni maini 1996 (vaheaegadega, kokku 2,5 aastat), teaduslik töö Bayreuthi Ülikoolis (Saksamaa LV) (Maismaa Ökosüsteemide Uurimise Instituut, juh. Thomas Gollan, prof. John D. Tenhunen);

   1. okt. 1993 – 15. märts. 1996 nooremteadur Eesti TA Ökoloogia Instituudi Tartu osakonnas, alates 15. märts. 1996 samas instituudi teadur.

II. TEADUSTEGEVUS

1. Uurimisvaldkonnad: Puittaimede varjutolerants, liikidevahelised erinevused lehe morfoloogias ja keemilises koostises; valguse kättesaadavusest tingitud adaptiivsed muutused lehepinna ja massi jaotumises võras; puu suurusest tingitud puu veebilansi ja lehtede struktuuri varieeruvus.

2. Teaduslik-organisatsiooniline ja erialane tegevus.

Õpilaste Teadusliku Ühingu liige aastail 1985–1989, laureaat botaanika- (1986: Võhandu jõe ja S-Emajõe vanajõgede taimestiku analüüs, juh. Kai Punger) ja zooloogiasektsioonis (1988: Mõnede Eesti mageveekalade kasvukiiruse ja eksterjööri hindamisest, juh. Teet Krause, Tiit Paaver). 1987. a. oli töö puittaimede lehe morfoloogiast (juh. Kalevi Kull) Eesti koolinoorte bioloogiaalaste tööde konkursi parim (vanemas astmes). 1986–1988 olin ÕTÜ botaanikasektsiooni esimees. Igal aastal korraldasime ettekandekoosolekuid ja konverentse, lisaks toimusid sektsiooniga välitööd Endla looduskaitsealal. 1989–1991 olin TÜ teoreetilise bioloogia ringi esimees (ettekandekoosolekud, teoreetilise bioloogia kevadkoolid, teoreetilise bioloogia ajakirja "Vita Aeterna" väljaandmine jne.). 1996. a. autasustati mind *Academia Europea* auhinnaga Balti vabariikide noortele teadlastele (töö eest puittaimede varjutolerantsist).

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu ,1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
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