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Is the lower shade tolerance of Scots pine, relative to pedunculate oak, related to the composition of photosynthetic pigments?

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Abstract

Foliage of Scots pine (*Pinus sylvestris* L.) and pedunculate oak (*Quercus robur* L.) was collected in a mixed pine/oak forest at canopy positions differing in radiation environment. In both species, chlorophyll (Chl) *a/b* ratios were higher in foliage of canopy positions exposed to higher irradiance as compared to more shaded crown layers. Throughout the growing season, pine needles exhibited significantly lower Chl *a/b* ratios than oak leaves acclimated to a similar photon availability. Hence, pine needles showed shade-type pigment characteristics relative to foliage of oak. At a given radiation environment, pine needles tended to contain more neoxanthin and lutein per unit of Chl than oak leaves. The differences in pigment composition between foliage of pine and oak can be explained by a higher ratio of outer antennae Chl to core complex Chl in needles of *P. sylvestris* which enhances the efficiency of photon capture under limiting irradiance. The shade-type pigment composition of pine relative to oak foliage could have been due to a reduced mesophyll internal photon exposure of chloroplasts in needles of Scots pine, resulting from their xeromorphic anatomy. Hence, the higher drought tolerance of pine needles could be achieved at the expense of shade tolerance.

Additional key words: chlorophyll; lutein; neoxanthin; *Pinus sylvestris*; *Quercus robur*; shade tolerance.

Introduction

Shade tolerance is one of the most important ecological factors with respect to inter-specific competition among forest trees of the temperate climate zone. The ability of plants to grow in deeper shade than others can be attributed to a variety of physiological properties, such as a specific carbon allocation pattern, certain growth characteristics, or a higher efficiency of photosynthetic carbon acquisition under limiting irradiance. The characteristics of photosynthetic reactions differ between shade tolerant species grown in the shade and shade intolerant species acclimated to higher photon levels (reviewed by Björkman 1981). Anyway, from these differences no conclusion can be drawn concerning the contribution of specific features of photosynthesis to shade tolerance, because also within a species the physiological properties of leaves are modulated by the radiation environment. Similar acclimation reponses occur among genetically uniform plants grown at different irradiances and among leaves of individual plants acclimated to different photon supply (Björkman 1981). Hence, attempts to address the question whether shade tolerance is related to certain characteristics of photosynthetic reactions require an experimental set-up through which the comparative measurements on shade tolerant and shade intolerant species can be carried out on foliage acclimated to a similar irradiance.

Several studies have focused on both the acclimation of photosynthetic properties along irradiance gradients and the comparison of tree species differing in shade tolerance. A study on seedlings of several moderately shade tolerant oak species and the more shade tolerant *Fagus grandifolia* (Teskey and Shrestha 1985) revealed a positive relationship between the growth irradiance and P_{Nmax}, the maximum rate of photosynthesis at photon saturation and ambient CO_2 concentration of the air, within each species. At a given growth irradiance, lower P_{Nmax} values were detected on the species with higher shade-tolerance. Coinciding results were obtained by Kubiske and Pregitzer (1996) on seedlings of *Quercus rubra* and *Betula papyrifera*: at a given radiation environment, the more shade tolerant oak showed shade-type CO_2 gas-exchange characteristics relative to the less

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Abbreviations: A, antheraxanthin; CC, core complex; Chl, chlorophyll; f.m., fresh mass; LHC, light-harvesting-complex; Lut, lutein; Neo, neoxanthin; P_{Nmax}, photon saturated net photosynthetic rate; PPFD, photosynthetic photon flux density; rel.PPFD, PPFD expressed as a percentage of the PPFD above the canopy; PS, photosystem; V, violaxanthin; Z, zeaxanthin.

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shade tolerant birch. Bond *et al.* (1999) determined the acclimation of foliage physiology along the canopy irradiance gradient in conifers of varying shade tolerance. P_{Nmax} and chlorophyll (Chl) *a/b* ratios were higher in foliage of canopy positions exposed to higher irradiance as compared to shaded crown layers. The shade tolerant species showed relative shade-type characteristics, as, at a given radiation environment, both P_{Nmax} and the Chl *a/b* ratio were lower in needles of the more shade tolerant species. Corresponding results were obtained on deciduous tree species by Hansen *et al.* (2002): the determination of the pigment composition of leaves of mature *Fagus sylvatica* and *Quercus petraea* trees in a mixed beech/oak forest revealed shade-type pigment characteristics for shade leaves, relative to sun leaves. At a given radiation environment, leaves of the more shade-tolerant beech showed lower Chl *a/b* ratios than those of the less shade-tolerant oak.

The objective of the presented study was to investigate whether the lower shade tolerance of Scots pine (*Pinus sylvestris* L.), relative to pedunculate oak (*Quercus robur* L.), is related to certain characteristics of the leaf pigment composition. *P. sylvestris* is usually found in open locations, sometimes in half-shade, but not in deep shade. *Q. robur* more frequently occupies half-shaded habitats and oak crowns cast a deeper shade than those of pine (Ellenberg 1986). Both species form mixed forests under natural conditions in the eastern part of North Germany (Röhrig 1991). Scots pine is a natural associate of the deciduous tree species in open mixed birch/oak woodlands in the north-western German plains. In eastward direction the abundance of pine increases. Under the more continental climate conditions of north-eastern Germany the higher frost tolerance of pine *versus* oak may play a role for the competitive strength of pine (Ellenberg 1986). The co-occurrence of these tree species differing in shade tolerance but exposed to similar environmental factors in the mixed forest allowed us to investigate the physiology of shade tolerance under natural conditions. We compared the pigment composition of pine needles and oak leaves acclimated to a similar irradiance, and, in order to investigate whether the species show sun- or shade-type pigment characteristics, relative to each other, we determined the variation of the pigment composition along the canopy irradiation gradient.

Adjustments of the leaf pigment composition in response to the irradiance have been described in numerous studies. Chl-based contents of photo-protective carotenoids and Chl *a/b* ratios are higher in sun *versus* shade leaves of individual plants (*e.g.* Thayer and Björkman 1990, Garcia-Plazaola and Becerril 2000, Lichtenthaler *et al.* 2000, Hansen *et al.* 2002) and in sun-grown *versus* shade-grown plants (*e.g.* Logan *et al.* 1998). Chl *b* is enriched in outer antennae, relative to the core complexes (CC) of photosystems (PS) 1 and 2, and in PS2 *versus* PS1. A higher contribution of outer antennae Chl to the total Chl, leading to lower Chl *a/b* ratios, enhances the efficiency of photon capture under limited photon supply. The photosynthetic capacity usually increases with irradiance to which leaves are acclimated, but the relative increase in the energy demand of photosynthesis is lower than the relative increase in irradiance (*e.g.* Björkman 1981). Hence, compared to shade leaves, in sun leaves the rate of photon absorption is more frequently in excess of the capacity of the energy utilising reactions. Excess photon absorption enhances the formation of reactive oxygen species and radicals in chloroplasts that may have deleterious effects on cell constituents (Asada 1999). Carotenoids photoprotect through quenching of triplet Chl and singlet oxygen (Siefermann-Harms 1987, Choudhury and Behera 2001). They are involved in processes through which over-excitation is avoided: Antheraxanthin (A) and zeaxanthin (Z), built up at the expense of violaxanthin (V), are involved in processes leading to the protective dissipation of excess excitation energy (Demmig-Adams *et al.* 1996). Leaves of deciduous trees which have been exposed to excessive irradiance contain higher amounts of xanthophyll cycle pigments (V+A+Z) per unit of Chl than shade acclimated leaves (Niinemets *et al.* 1998). The pools of β-carotene and lutein (Lut) show a less pronounced acclimation response, whereas the Chl based content of neoxanthin (Neo) and in some cases of Lut does not vary markedly among leaves acclimated to different irradiance levels (Königer *et al.* 1995, Demmig-Adams *et al.* 1996, Hansen *et al.* 2002). The contribution to photoprotection, photon harvesting, and stabilisation of Chl-protein complexes is still under debate for some carotenoids. Irrespective of functional relationships, we expected that the comparison between foliage of pine and oak, acclimated to a similar irradiance, would reveal shade-type pigment characteristics for the more shade tolerant pedunculate oak, relative to Scots pine.

Materials and methods

Study site and sampling: In the mixed pine/oak forest on dry sandy soil, the tree layer is dominated by about 140-year old pine trees (*P. sylvestris* L.) with a height of up to 25 m. The younger oaks (*Q. robur* L.) reach a maximum height of approximately 15 m. On pine, foliage was restricted to the upper sun-exposed crown layer. Oaks had leaves at intermediate irradiance levels and in shaded parts of the canopy, where pine needles were shed. The study site is part of the Grunewald, Berlin, Germany (52°27'N, 13°12'E). A detailed description of ecosystem characteristics is given in Cornelius *et al.* (1997) and Marschner *et al.* (1998). A measuring tower provided access to different canopy positions (Table 1). At each selected sampling position, leaf or needle samples of about 0.5 g fresh mass (f.m.) were taken on six days between May and September 2000 (Table 2). A mixed sample of current and previous year pine needles was taken and divided in five sub-samples. On oak, five individual leaves were sampled. After the determination of f.m., samples were frozen in liquid nitrogen and stored at 77 K until the biochemical analysis was carried out.

Radiation environment: The photosynthetic photon flux density (PPFD) was synchronously detected at the respective sampling position and above the canopy. These measurements were carried out on days with diffuse radiation using *LI-190S* sensors (*LI-COR*, USA) and a data logger (*DA 3000, Delta-T Devices*, UK). The relative PPFD (rel.PPFD) represents the PPFD detected at a canopy position, expressed as a percentage of the PPFD above the canopy.

Pigment analysis was carried out using HPLC as described in Hansen *et al.* (2002) with the modification that the material was homogenised with a *MM2000* mill (*Retsch*, Haan, Germany). The pigment contents are expressed on the basis of Chl, since structural leaf properties differed markedly between *P. sylvestris* and *Q. robur*: pine needles had greater f.m. per projected area than oak leaves (Table 1) and the area-based Chl content tended to be larger in pine *versus* oak foliage (Tables 1 and 2).

Statistical analysis: The significance of differences in the mean pigment composition between foliage of pine and oak exposed to similar irradiance was tested using the two-sided Welch test. Significance (s) refers to $p \leq 0.05$.

Table 1. Height and rel.PPFD (PPFD at the canopy position expressed as a percentage of the PPFD above the canopy) of the sampling positions in a mixed pine/oak forest consisting of mature *Pinus sylvestris* L. and young (position at 0.5 m) and semi-mature (positions at 4.1-13.4 m) *Quercus robur* L. trees. Fresh mass (f.m.) and chlorophyll (Chl) content are given per projected leaf area. Means and standard deviations (n = 4-5).

	Height [m]	rel.PPFD [%]	f.m./proj. area [g m^{-2}]		Chl $a+b$/proj. area [μmol m^{-2}]		Chl b/Chl $a+b$ [mmol mol^{-1}]	
			26 June	18 August	26 June	18 August	26 June	18 August
P. sylvestris	20.2	58	372	398	541 ± 17	520 ± 37	260 ± 5	262 ± 3
	17.7	35	323	393	590 ± 21	631 ± 22	272 ± 3	268 ± 3
	17.0	29	344	387	644 ± 23	656 ± 19	272 ± 9	273 ± 3
	13.1	30	313	341	630 ± 46	639 ± 30	283 ± 6	283 ± 3
Q. robur	13.4	32	183	179	518 ± 66	603 ± 57	266 ± 9	256 ± 6
	13.3	19	150	144	485 ± 80	586 ± 131	286 ± 10	270 ± 6
	4.1	15	104	101	483 ± 44	467 ± 30	293 ± 10	284 ± 7
	0.5	13	108	114	439 ± 53	408 ± 16	281 ± 6	278 ± 8

Table 2. Chlorophyll (Chl) content per projected area and Chl b/Chl $a+b$ ratios of *Pinus sylvestris* needles and leaves of *Quercus robur* acclimated to a similar irradiance (32 and 30 % of the PPFD above the canopy for oak and pine, respectively) on six days during the growing season 2000. Mean values (n = 4-5) and standard deviations are given.

	Chl $a+b$/proj. area [μmol m^{-2}]		Chl b/Chl $a+b$ [mmol mol^{-1}]	
	P. sylvestris	*Q. robur*	*P. sylvestris*	*Q. robur*
16 May	714 ± 60	363 ± 59	288 ± 2	271 ± 6
29 May	698 ± 40	551 ± 52	269 ± 6	255 ± 7
26 June	630 ± 46	518 ± 66	283 ± 6	266 ± 9
24 July	713 ± 29	535 ± 48	280 ± 2	250 ± 6
18 August	639 ± 30	603 ± 57	283 ± 3	256 ± 6
26 September	577 ± 32	633 ± 62	283 ± 7	262 ± 6

Results

The comparison of pigment characteristics of pine needles and oak leaves, acclimated to a similar irradiance in the canopy, revealed significantly lower Chl *a/b* ratios in needles of *P. sylvestris* (Fig. 1*A*) throughout the growing season. Low Chl *a/b* is typical for foliage of shaded canopy positions, as a close positive relationship was found between the Chl *a/b* ratio and the rel.PPFD at the respective crown position for both species (Fig. 2*A,B*). Hence, with respect to the Chl *a/b* ratio, foliage of *P. sylvestris*, the less shade tolerant species, showed shade-type pigment characteristics relative to the more shade tolerant pedunculate oak. In both species the Chl *a/b* ratio varied synchronously over the growing season (Fig. 1*A*): a slight decrease in the Chl *a/b* ratio from 29 May to 26 June was followed by an increase from 26 June to 24 July and a subsequent decrease from 24 July to 26 September.

The mean Chl-based contents of Neo and Lut were about 10 % higher in pine *versus* oak foliage on most of the sampling days (Fig. 1*B,C*). The natural variability among neighbour leaves, due to the fact that they slightly differ with respect to irradiance and development phase, is displayed by the standard deviation data. Due to this variability, differences in the pigment composition between pine and oak were not always significant. Despite the high standard deviation, the data show that Neo and Lut contents per unit of Chl tended to vary synchronously in pine and oak (Fig. 1*B,C*). If periods are disregarded during which the pigment composition of oak leaves was influenced by leaf development (16 and 29 May), a shift from higher to lower Neo/Chl and Lut/Chl ratios tended to be connected with a decrease in the Chl *b*/Chl ratio (Table 2) and an increase in the Chl *a*/*b* ratio (Fig. 1*A*). Along the canopy irradiation gradient, the Chl-based Neo and Lut contents (Fig. 2*E-H*) as well as the Chl *b*/Chl ratios (Table 1), varied only to a minor extent.

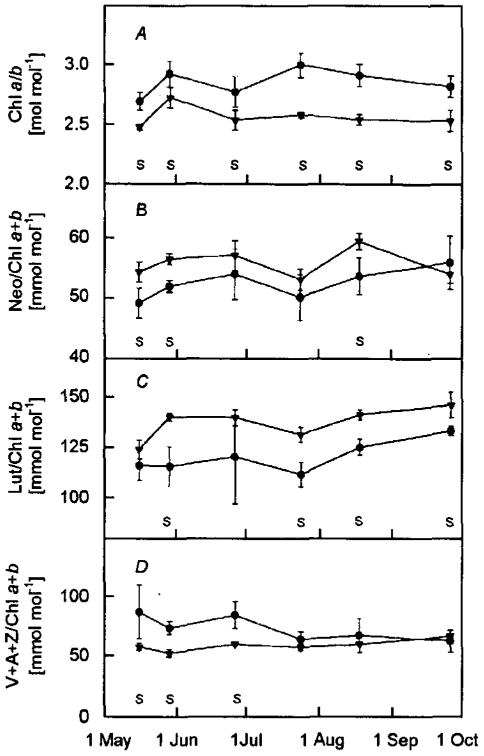

Fig. 1. Variation in chlorophyll (Chl) *a*/*b* ratios (*A*), and Chl-based contents of neoxanthin (*B*), lutein (*C*), and xanthophyll cycle pigments (*D*) in foliage of *Quercus robur* (*circles*) and *Pinus sylvestris* (*triangles*) trees over the growing season 2000. Samples were taken in a mixed pine/oak forest at canopy positions with similar photon reception (32 and 30 % of the PPFD above the canopy for oak and pine, respectively, see Table 1). Means (n = 4-5) and standard deviations are given. "s" indicates significant differences ($p \leq 0.05$) between pine and oak.

The pool of xanthophyll cycle pigments, expressed per unit of Chl, was significantly lower in pine *versus* oak foliage from May to the end of June (Fig. 1*D*). On 24 July and 18 August, pine needles showed slightly lower mean V+A+Z pools per Chl than oak leaves, but the difference was not significant. The V+A+Z/Chl ratio was positively related to the rel.PPFD in oak (Fig. 2*C*). This acclimation response was also present, but less pronounced, in needles of Scots pine (Fig. 2*D*). The V+A+Z content of oak leaves varied markedly over the growing season (Fig. 1*D*). Large contents of photo-protective xanthophyll cycle pigments were present on 16 May, when leaves were not fully green. On 29 May and 26 June, two other sampling days during which oak leaves contained relatively high amounts of xanthophyll cycle pigments, the leaves were exposed to the lowest air temperatures (data not shown).

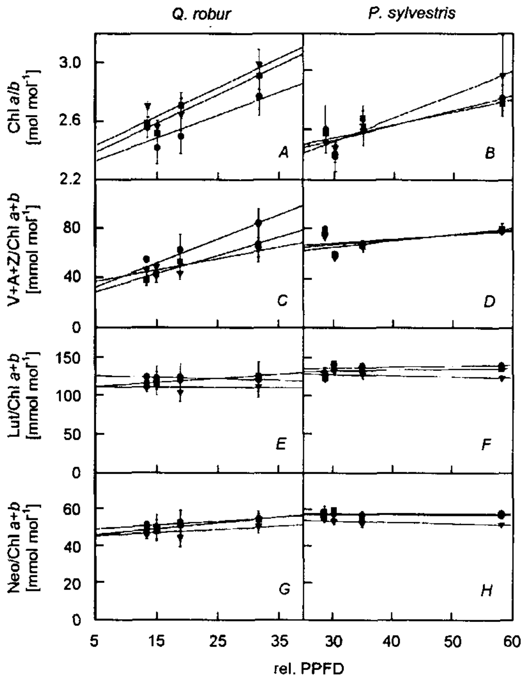

Fig. 2. Acclimation of leaf pigment characteristics along the gradient of canopy irradiance (Table 1) in *Quercus robur* leaves and needles of *Pinus sylvestris* determined in a mixed pine/oak forest during the growing season 2000 (26 June: *squares*, 24 July: *diamonds*, 18 August: *triangles*). Similar gradients were found on 16 and 29 May and 26 September. Means and standard deviations (n = 4-5). For abbreviations see Fig. 1.

Discussion

As pointed out in the Introduction, shade tolerance is not necessarily related to specific features of the photosynthetic reactions. For the tree species investigated here, clear differences in pigment characteristics between the less shade tolerant Scots pines and more shade tolerant pedunculate oaks were found. Leaves acclimated to higher irradiance usually show greater Chl *a/b* ratios than leaves of more shaded canopy positions. This adjustment of the pigment composition in response to photon availability was present in both species (Fig. 2*A,B*). Low Chl *a/b* ratios can therefore be assigned to shade-type pigment characteristics. At a given radiation environment, needles of *P. sylvestris* exhibited lower Chl *a/b* than *Q. robur* leaves (Fig. 1*A*). Hence, in contrast to our expectation, the species with lower shade tolerance showed shade-type Chl *a/b* ratios relative to the species with higher shade-tolerance. Obviously there is no unique relationship between shade tolerance and pigment properties valid for all species. Coinciding results were obtained in a field study on various plant species differing in shade tolerance which revealed no close relationship between the Chl *a/b* and the irradiance of the habitat from which the plants originated (Johnson *et al.* 1993).

The pigment characteristics indicate particular structural features of the photosynthetic apparatus in foliage of *P. sylvestris* and *Q. robur*. Chl *b* is located in the outer antennae of both photosystems and is enriched in PS2 *versus* PS1 (Yamamoto and Bassi 1996). Therefore, the lower Chl *a/b* of pine needles as compared to leaves of oak (Fig. 1*B*) can be attributed to a higher contribution of light-harvesting-complex (LHC) bound Chl to the total Chl in pine, or to a higher PS2/PS1 ratio, or to a combination of both. Neo and Lut are enriched in the outer antennae relative to the core complexes, Neo in PS2 and Lut in PS1 and PS2 (Yamamoto and Bassi 1996). The finding that the higher relative contribution of Chl *b* to the total Chl in pine (Table 2) was connected with higher Chl based Neo and Lut contents (Fig. 1*B,C*) therefore suggests that the pine needles contained higher amounts of LHC-bound Chl relative to the CC-Chl than oak leaves. An increased antenna size enhances the efficiency of photon absorption under low irradiance and is a typical feature of the photosynthetic apparatus of leaves acclimated to limited photon supply.

The synchronous changes in the Chl based contents of Neo, Lut (Fig. 1), and Chl *b* (Table 2) over the growing season, detected in fully developed oak leaves, display post-expansion acclimation processes which can be explained by adjustments of the antenna size in response to internal or external factors. Such adjustments were also reported by Öquist *et al.* (1978), who studied seasonal effects on Chl-protein-complexes isolated from *P. sylvestris*. The authors found inverse seasonal changes in the Chl *a/b* ratio and the abundance of LHC relative to the CC of PS1: an increase in Chl *a/b* was related to a decrease in the LHC/CC_{PS1} and *vice versa*. Irradiance plays an important role among the internal and external factors inducing post-expansion acclimation processes in fully developed leaves (data not shown).

Contents of photoprotective carotenoids are adjusted to the excess of radiant energy over the energy demand of energy utilising reactions. Therefore the higher photoprotective demand in foliage of canopy positions with higher irradiance results in a positive relationship between the Chl-based V+A+Z pool and the rel.PPFD in both species (Fig. 2*C,D*). The relatively large contents of xanthophyll cycle pigments (Fig. 1*D*) present in oak leaves when daily mean temperatures were below 15 °C can be assigned to the low capacity of photosynthetic photon utilisation at lower temperatures.

In summary, we found shade-type pigment characteristics for needles of *P. sylvestris*, relative to leaves of *Q. robur,* when foliage acclimated to similar irradiance levels was compared. The pigment characteristics can be explained by higher LHC-Chl to CC-Chl ratios in pine *versus* oak, suggesting that the photosynthetic apparatus in pine is characterised by a higher contribution of outer antennae Chl to the total Chl. From our results we cannot decide whether the relative shade-type pigmentation in pine needles was due to genetically determined differences in the regulation of chloroplast responses to irradiance or to differences in the mesophyll internal radiation environment to which chloroplasts are exposed. Anyway, differences in the leaf internal irradiance regime between foliage of pine and oak are likely to occur. On average, the fraction of incident photons reaching the chloroplasts of pine needles might be smaller than in oak leaves. The epidermis of needles of *P. sylvestris* consists of extremely thick-walled lignified cells and is covered with a thick cuticle (Fahn 1990). Furthermore, a hypodermis of sclerified parenchyma cells is present except in the areas below stomata. Therefore, photon absorption and scattering by cell walls may be greater in pine than in oak. The needle geometry might have an additional effect on the photon availability within pine needles. Due to the semicylindrical cross-sectional shape of *P. sylvestris* needles, under high irradiance only a part of the needle surface is exposed to the maximum PPFD, whereas each leaf section of a laminar *Q. robur* leaf is exposed to the same high irradiance (Jordan and Smith 1993). Hence, the specific structural features of xeromorphic pine needles could be responsible for the relative shade-type character of their pigment composition. The results imply that the higher drought tolerance of pine needles, resulting from their xeromorphic anatomy, is achieved at the expense of shade tolerance. Therefore, shade tolerance of Scots pine could be limited by the somehow limited ability of the photosynthetic apparatus to compensate for internal photon shortage by an increase in the efficiency of photon collection.

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