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Original article

Effect of shade on stomatal conductance, net photosynthesis, photochemical efficiency and growth of oak saplings

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Summary — The European oak species, pedunculate (*Quercus robur*) and sessile oak (*Q. petraea*), both considered to be light demanding, were tested for their shade tolerance. Two- and 3-year-old nursery grown seedlings were planted either in the open field or with 50% reduction in sun irradiance, in the spring of 1992. During the following 3 years, growth was monitored. In the third summer, the following ecophysiological parameters were measured: stomatal conductance, net photosynthesis, photochemical efficiency of dark-adapted leaves, as well as carotenoid and chlorophyll content. Stomatal conductance and photosynthesis were increased in the open field treatments, while the shaded plants had larger leaves with fewer stomates per unit leaf area, more chlorophyll per unit dry weight and increased chlorophyll/carotenoid ratio. The photochemical efficiency of photosystem II as measured on dark-adapted leaves was 3–4% lower in the open field plants as compared to the shade grown ones. During the day it exhibited a decrease at noon in plants of both treatments; this decrease recovered completely at the end of the afternoon. There was no difference in overall height of the plants between the two treatments; however, the root collar diameter was significantly smaller in the shade grown plants. Thus, results of some other investigations, according to which young oak plants grow better under shade, could not be confirmed.

***Quercus* / stomatal conductance / net photosynthesis / photochemical efficiency / shade tolerance**

Résumé — Effets de l'ombrage sur la conductance stomatique, l'assimilation nette de CO₂, l'efficacité photochimique et la croissance de semis de chênes. Les chênes européens (*Quercus robur* et *Q. petraea*) sont considérés comme des espèces de lumière. Nous avons testé leur tolérance à l'ombrage, en plantant au cours du printemps 1992 des semis de 2 et 3 ans en plein découvert ou sous une ombrière réduisant le rayonnement de 50 %. La croissance de ces semis a été suivie pendant 3 ans.

Abbreviations: F_v/F_m : photochemical efficiency of photosystem II as measured on dark-adapted leaves; g_w : leaf conductance to water vapour (cm s⁻¹); PS: net photosynthesis (μmol m⁻² s⁻¹).

Lors de la troisième année, des paramètres écophysologiques ont été mesurés : conductance stomatique, assimilation nette de CO_2 , efficacité photochimique de feuilles maintenues à l'obscurité, ainsi que les teneurs en caroténoïdes et en chlorophylles. Conductance stomatique et assimilation nette étaient plus élevées en plein découvert, alors que les plants d'ombre présentaient des feuilles plus grandes avec moins de stomates, plus de chlorophylles par unité de poids sec, et un rapport chlorophylle/caroténoïdes plus élevé. L'efficacité photochimique mesurée sur des feuilles préconditionnées à l'obscurité était plus faible de 3–4% en plein découvert. Pendant la journée, ce paramètre présentait une décroissance dans les deux traitements, avec une bonne récupération à la fin de l'après-midi. La hauteur finale des plants était identique dans les deux traitements, mais le diamètre au collet était plus faible sur les plants d'ombre. La croissance des jeunes plants n'a donc pas été sensiblement meilleure à l'ombre qu'en plein découvert.

Quercus / conductance stomatique / photosynthèse nette / efficacité photochimique / tolérance à l'ombrage

INTRODUCTION

The European oak species, pedunculate (*Quercus robur* L) and sessile (*Quercus petraea* [Matt] Liebl) oak, are generally described in textbooks of silviculture as being light demanding tree species. This view dominates the silvicultural practice of German forestry. As a rule, oak trees are cultivated in open areas from seeds or by planting, because of evidence that oak seedlings in the shade of old stands are stunted or die within a few years. The results of Röhrig's (1967) shade experiments appear to confirm this experience. According to this author, young oaks respond already to "little shading (78% relative light intensity, ie, light intensity as a percentage of that in full daylight) for 2 years with a noticeable reduction of the length of the seedling, its stem diameter and dry mass production". Natural renewal of oak stands is thus only possible in gaps or under a loose canopy (Lüpke, 1987). In the latter case, the mother trees must be cleared within 3–5 years after the appearance of the young plants, thus sacrificing further growth of old stands and some wood quality in favour of young trees.

In contrast to this practice, other investigations have shown substantial shade tolerance of young oaks. Jarvis (1964), for

example, ascertained during his experiments with artificial shade that relative to the unshaded condition, shading of young *Quercus petraea* seedlings resulted in increased height, leaf area, specific leaf area and chlorophyll content; shading also gave decreased root weight, net assimilation rate (ie, dry weight increment divided by the mean leaf area and time) and relative growth rate. Stem weight was unaffected. For an entire growing season, growth saturation was not reached at full daylight. Seedlings reached maximum net assimilation rate and relative growth rate at 56% relative light intensity in August; values in full daylight were much less. The capacity of the photochemical process and the rate of photosynthesis at light saturation (per unit leaf area) were greater in shade grown than in sun grown leaves. The minimum relative light intensity for net gain in weight, including the weight of fallen and harvested leaves, was approximately 6%. Based on these results, Jarvis (1964) concluded that the degree of adaptation of the oak seedlings is similar to that of other shade plants, and that the seedlings are intolerant of high light intensity. Ziegenhagen and Kausch (1993) arrived at similar conclusions, from their experiments with artificial shade finding a growth optimum for 2-year-

old oaks at 25% relative light intensity. Rousset (1972) even set the threshold for shade tolerance for 1-year-old oaks at 10% relative light intensity. It has remained little known until now to what extent such a growth optimum would shift to higher light requirements with increasing age of the plants.

In order to test the influence of irradiance as a function of age, plants of *Q. robur* (2 years old) and *Q. petraea* (3 years old) obtained from a nursery were planted in the spring of 1992 in the experimental garden of the Institute of Silviculture of the University of Freiburg, Germany, half in the open and half artificially shaded. Since then the growth of the oaks has been monitored continuously. The results of this investigation will be presented in full detail elsewhere. In order to compare the experimental plants of both treatments also at the ecophysiological level, in midsummer of 1994 the saplings were monitored for the following parameters: stomatal conductance, net photosynthesis, photochemical efficiency of photosystem II, photosynthetic pigments, leaf area and stomatal density. The parameters stomatal conductance, net photosynthesis and photochemical efficiency were measured on both oak species. The measurements of the remaining parameters were confined to pedunculate oaks.

MATERIALS AND METHODS

Experimental design

The experiments were conducted during the summer of 1994, with 140 plants, of pedunculate (*Q. robur* (L)) and sessile (*Quercus petraea* [Matt] Liebl) oak in the experimental garden of the Institute of Silviculture of the University of Freiburg, Germany (48°N, 7°51'E, elevation 420 m). The experimental plot (13 m x 55 m) was located in a narrow valley near Freiburg with direct sunshine only between 830 and 1800 hours in midsum-

mer. The terrain was flat with cultivated sandy loam.

In summer 1994, the experimental plants were 4-1/2 (*Q. robur*) and 5-1/2 (*Q. petraea*) years old. They were planted in the spring of 1992 on a 1.5 m x 1.5 m grid. The rows were shifted against each other to result in a triangular pattern of spacing between plants. The plot was subdivided into four equal strips. Two adjacent strips were shaded with a net used in nurseries to give approximately 50% reduction of sunlight (Agroflor, Wolfurt, Austria). The species were planted in two strips each, one in the open field and one in the shade. The shading modifies the sunlight in the following way:

1. Reduction of solar radiation as measured with a portable spectroradiometer LI-1800 (LI-cor, Lincoln, NE, USA)

blue (420–450 nm)	52.4%
green (535–565 nm)	58.3%
red (660–690 nm)	53.4%

2. Reduction of ultraviolet light as measured with a UV-meter (Dr Hönle, München, Germany)

UVA	39%
UVB	30%

3. During the growing season, the differences between the daily minimum and maximum temperature in the shade was approximately 1–2 °C less than in the open area. The soil moisture was marginally higher in the shaded area and the herb layer was reduced.

Parameters measured

Stomatal conductance

Stomatal conductance (g_w) was measured in situ with a steady-state porometer (model LI-1600; LI-cor, USA) calibrated in cm s^{-1} . The measurements were conducted between the end of June and the end of August during 18 predominantly sunny days either at specific hours or as whole day kinetics. The data were taken from ten randomly chosen plants of both treatments and species from leaves in the upper part of the crown (one leaf per plant taken at random). To evaluate the potential effects of water stress on the stomatal conductance, three pedunculate oaks in each treatment were watered daily in the evening with 10 L of water per plant for porome-

ter measurements. The water status of the adjacent plants 1.5 m apart was thereby hardly affected.

Net photosynthesis

Net photosynthesis (PS) was measured in situ with a Leaf Chamber System (Analytical Development Company, Hoddesdon, UK) and expressed on a leaf area basis. Data were collected from five plants of each species from the open field and from the shade, and under both light conditions from one set each of three well-watered plants. For technical reasons, the measurements of PS had to be restricted to only 3 days.

Photochemical efficiency

Photochemical efficiency (F_v/F_m , ie, the ratio of variable and maximal chlorophyll a fluorescence of photosystem II) was measured in situ with a nonmodulated Plant Efficiency Analyser (model 9120; HANSATECH Ltd, King's Lynn, UK) during 6 days at noon or three times during the day as whole day kinetics on leaves which were dark adapted for 30 min (for technical details, see Bolh  r-Nordenkamp and   quist [1993]). Data were taken from 15 randomly chosen plants of both treatments from leaves in the upper part of the crown (one leaf per plant taken at random). In early summer, data were collected from early sprouting leaves; in late summer, from the second flush.

The measurement of daily time courses of the parameters g_w , F_v/F_m and PS always began shortly after disappearance of dew. Thus, it was impossible to measure these parameters before exposure to direct sun irradiance in the morning.

Growth

Root collar diameter and total height were measured during the whole experimental period for all experimental plants. The mean increments in height and diameter were calculated as the difference between values measured at the beginning of the experiment in spring 1992 and end of 1994 for each individual plant. These differences expressed in percent of the initial status (values of spring 1992) yielded the relative increment in height and diameter.

Leaf parameters

Leaves from the same developmental stage were collected from ten different pedunculate oaks from open field and shade conditions for determination of i) dry weight, ii) leaf area, iii) pigment composition (after Lichtenthaler, 1987) and iv) stomatal density.

RESULTS

Stomatal conductance

Although most days were hot during the experimental period (June–August 1994), frequent thundershowers prevented the soil from drying. Nevertheless, the well-watered pedunculate oaks in the open field always had higher average g_w values than the non-watered ones in both oak species. Thus, the nonwatered plants in the open field may have experienced slight water stress (fig 1). In the shade, however, the g_w values were altogether lower than in the open field and showed no differences between well-watered and nonwatered plants, indicating that water supply was not limiting (figs 1, 2 and 3, table I). Thus, the value of g_w depended both on water supply and on photon fluence. No significant differences in the response of both oak species could be detected.

Net photosynthesis

The net photosynthesis per unit leaf area as measured on watered and nonwatered pedunculate oaks on 2 cloudy days, was higher on two replicates in the open field. As with stomatal conductance, there was a positive effect of watering only in the open field (table II). In contrast, the time course data on 16 August 1994 (fig 2B, C) revealed

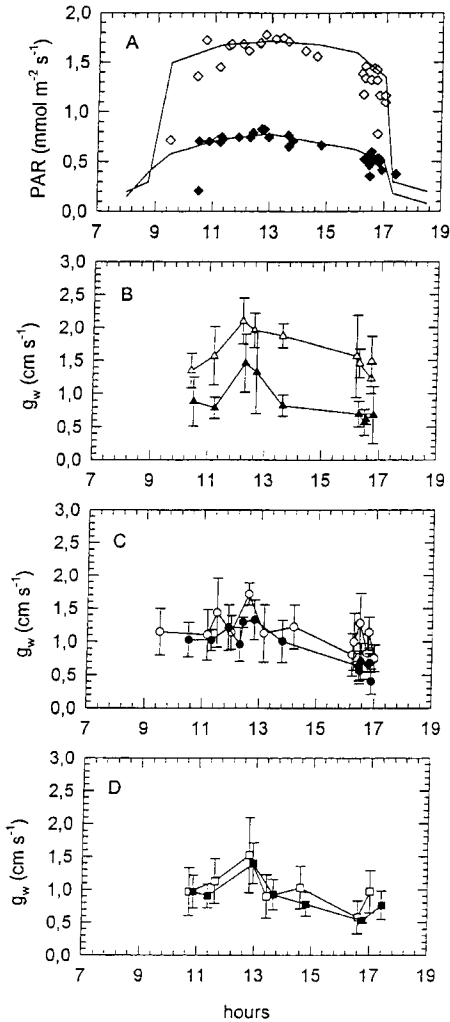


Fig 1. Variations in photosynthetic active radiation (PAR) and stomatal conductance (g_w) of shaded and nonshaded, watered and nonwatered young oaks. The data were collected at various times of the day during July 1994 on sunny days and were plotted together as a single daily time course. (A) PAR (\diamond , \blacklozenge); (B) g_w of well-watered pedunculate oaks (Δ , \blacktriangle); (C) g_w of nonwatered pedunculate oaks (\circ , \bullet); (D) g_w of nonwatered sessile oaks (\square , \blacksquare). Values represent means, with vertical bars indicating standard deviations. Open symbols: open field; closed symbols: shaded area.

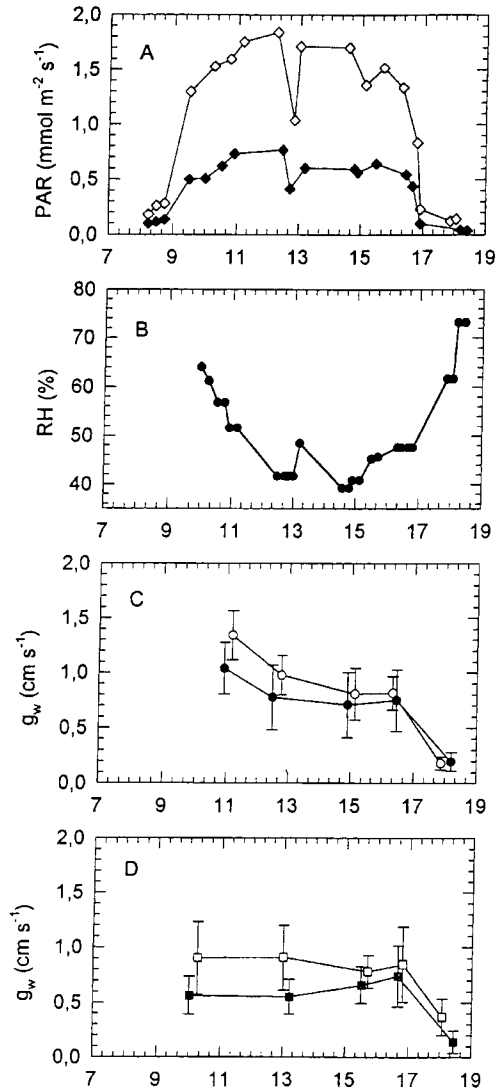


Fig 2. Daily time course recorded on 14 August 1994 on the nonshaded (open symbols) and the shaded (closed symbols) areas of (A) photosynthetic active radiation (PAR) (\diamond , \blacklozenge); (B) relative humidity (RH) as obtained from porometer measurements; (C) stomatal conductance (g_w) of nonwatered pedunculate oaks (\circ , \bullet); (D) g_w of nonwatered sessile oaks (\square , \blacksquare). Values represent means, with vertical bars indicating standard deviations.

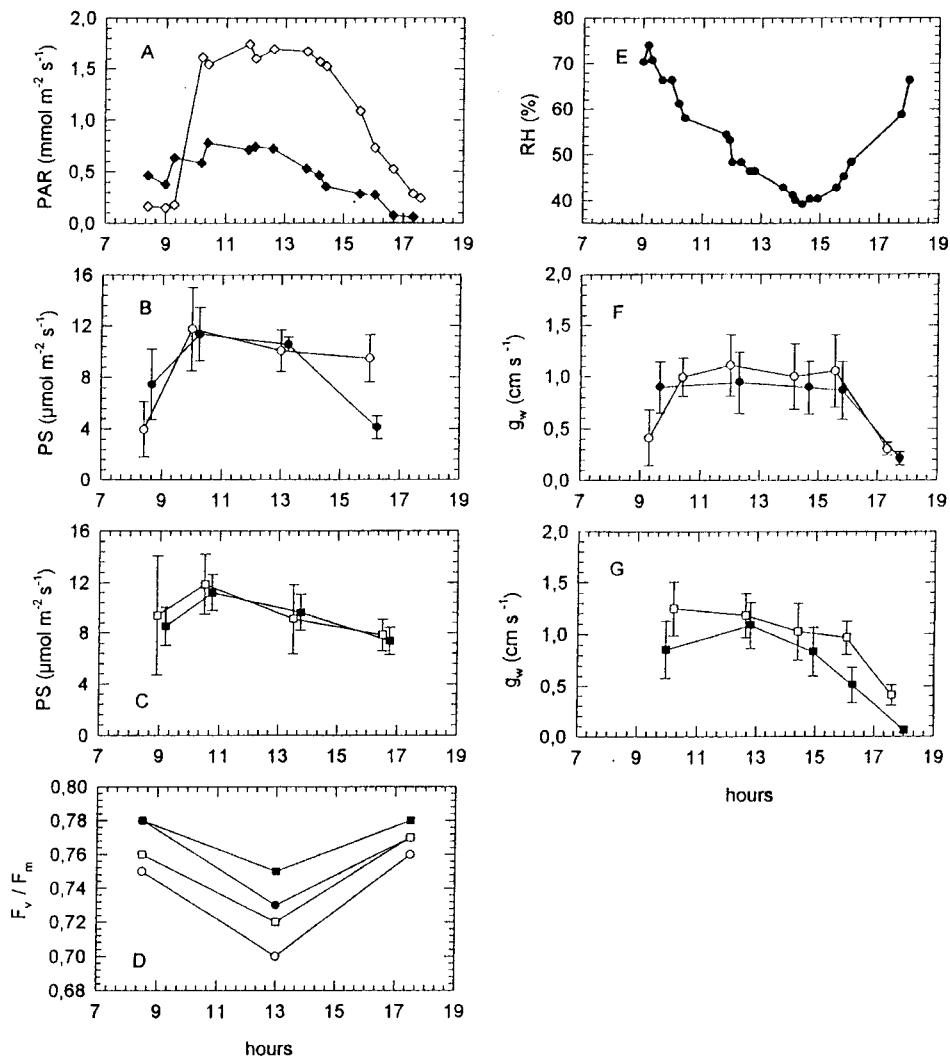


Fig 3. Daily time course recorded on 16 August 1994 on the nonshaded (open symbols) and the shaded (closed symbols) areas of (A) photosynthetically active radiation (PAR) (◇, ◆); (B) net photosynthesis of nonwatered pedunculate oaks (O, ●); (C) net photosynthesis of the nonwatered sessile oaks (□, ■); (D) photochemical efficiency of both oak species (F_v/F_m) (symbols as for B and C); (E) average change in relative air humidity (RH) as obtained from porometer measurements; (F) stomatal conductance (g_w) of nonwatered pedunculate oaks (O, ●); (G) g_w of nonwatered sessile oaks (□, ■). Values represent means, with vertical bars indicating standard deviations (because of their small size, the vertical bars were omitted in D).

Table I. Photosynthetic active radiation (PAR) and stomatal conductance (g_w) as measured on leaves of nonshaded and shaded, nonwatered pedunculate oaks on cloudy days (mean values with standard deviations).

Day	Time (h)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_w (cm s^{-1})	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	g_w (cm s^{-1})
		Nonshaded		Shaded	
07.07	1045	440	0.880 ± 0.32	190	0.600 ± 0.33
08.07	1030	614	1.000 ± 0.27	240	0.810 ± 0.26
	1650	508	0.780 ± 0.20	160	0.521 ± 0.27
24.07	1230	430	1.290 ± 0.10	196	0.739 ± 0.47
	1305	497	1.530 ± 0.26	244	1.000 ± 0.44

no differences in net photosynthesis between open field and shade plants although the corresponding average values of g_w were different (fig 2F, G). A certain water stress as a possible cause for that phenomenon seems to be probable, since g_w values of well-watered plants (data not shown) were slightly higher (at about 0.3 cm s^{-1}) than the corresponding g_w values of the nonwatered plants. The irregularities of the initial values and the final values of the

time courses in figures 3B and 2F can be explained by the fact that the time of both the beginning and the end of direct sunshine were not the same for the whole area of the experimental field (fig 3A). Thus, the lowest values in the morning were not measured on shaded plants but rather on plants of the open field where the direct sunshine began later.

Table II. Net photosynthesis as measured on leaves of nonshaded and shaded, well-watered and nonwatered pedunculate oaks in late morning and afternoon of 22 July and 4 August 1994 (mean values with standard deviations).

Treatment	Time (h)	Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)		
		Nonshaded	Shaded	Stat signif
Watered	1000–1100	15.48 ± 2.68	10.43 ± 1.40	**
	1400–1500	13.73 ± 1.72	9.10 ± 1.23	**
Nonwatered	1000–1100	14.83 ± 1.50	10.98 ± 1.50	**
	1400–1500	11.02 ± 1.30	9.95 ± 1.43	ns

** Values differ significantly at the 0.01 level; ns: not significant.

Photochemical efficiency

The mean values of photochemical efficiency of photosystem II (F_v/F_m) as measured on dark-adapted leaves of pedunculate oaks during 6 days at midday varied between 0.81 and 0.73 in shaded plants and between 0.78 and 0.70 in nonshaded plants (table III). Thus, F_v/F_m was always approximately 3 to 4% lower in the nonshaded plants. On 16 August, the lowest values of F_v/F_m were measured. The daily time course showed a significant decrease at noon in plants of both species and treatments (fig 3D). The differences between the values measured in the morning and at midday on nonshaded and shaded plants were more clearly expressed in pedunculate oak (7 and 6%, respectively) than in sessile oak

(5 and 4%, respectively). The decreased values of F_v/F_m at midday completely recovered at the end of the afternoon in both treatments.

Morphological and biochemical differences

Morphological and biochemical differences of leaves from open field and shade plants were considerable. The leaves of shaded plants were larger (table IV) and had fewer stomata per unit area (table V), as well as different pigment composition (table VI). The total chlorophyll content as well as the contents of chlorophyll a and b per unit leaf dry weight were higher in shaded plants. Values of chlorophyll a and b related to leaf

Table III. Photochemical efficiency as measured on dark-adapted leaves (F_v/F_m) (30 min) of nonshaded and shaded pedunculate oaks on various days at midday (mean values with standard deviations).

Day	Time (h)	F_v/F_m	
		Nonshaded	Shaded
14.06	1230	0.74 ± 0.03	0.76 ± 0.02
28.06	1230	0.78 ± 0.02	0.81 ± 0.01
04.07	1230	0.75 ± 0.04	0.78 ± 0.01
10.07	1300	0.74 ± 0.02	0.76 ± 0.01
02.08	1300	0.75 ± 0.03	0.79 ± 0.01
16.08	1300	0.70 ± 0.03	0.73 ± 0.01

Table IV. Average values of leaf area, leaf dry weight and the leaf dry weight to leaf area ratio for leaves collected on 16 August 1994, from nonshaded and shaded pedunculate oaks. Values were measured from 20 leaves per treatment.

Pedunculate oak leaves	Average leaf area (cm ²)	Average leaf dry weight (g)	Leaf dry weight/leaf area ratio (mg/cm ²)
Nonshaded	33.10	0.278	8.4
Shaded	53.42	0.348	6.5

Table V. Stomatal density of leaves from nonshaded and shaded pedunculate oaks (mean values with standard deviations; six leaves per treatment).

Pedunculate oak	Stomatal density (stomata/mm ²)	
	Nonshaded	Shaded
Leaf tip	500 ± 64	360 ± 16
Leaf middle	449 ± 70	388 ± 37
Leaf base	377 ± 64	377 ± 45

area and the chl a:b ratio were not significantly different between the treatments. With regard to the content of carotenoids, the very opposite could be observed. The value related to leaf area was lower in shaded plants. Consequently, the chlorophyll/carotenoids ratio was higher in shaded plants.

Growth

Total height showed only small variations for both oak species with no significant differences between open field and shaded plants. However, root collar diameter was significantly higher in plants from the open field (table VII).

DISCUSSION

Some of our results agree with certain data of the investigations by Jarvis (1964) and Ziegenhagen and Kausch (1993), as mentioned above. This is especially true for the parameters leaf area and chlorophyll content of the leaves per unit dry weight. We found

here that both values were substantially higher in the shaded saplings than in the nonshaded ones, as also reported by Jarvis (1964). Following Jarvis (1964) and Ziegenhagen and Kausch (1993), it seems certain that here a light or shade adaptation is involved. As shading was paralleled by a change in light quality (see *Materials and methods*), an additional photomorphogenetic effect cannot be excluded.

We were not able to confirm the reduced net photosynthesis reported by Jarvis (1964) for nonshaded plants. This was evident from our measurements of net photosynthesis per unit leaf area and the stomatal conductance data, which – although not always statistically significant – were lower in the shaded saplings. Net photosynthesis and stomatal conductance are well correlated parameters as shown by Epron (1993) for oak plants. Furthermore, in contrast to the growth in height, differences in diameter at the root collar were highly significant (ie, lower in the shaded saplings after three vegetation periods than in the open field). The shaded oaks were thus noticeably slimmer.

Regarding our measurements of photochemical efficiency of photosystem II (parametrized as F_v/F_m) taken from dark-adapted leaves, one could distinguish between two effects: i) F_v/F_m values as measured at midday on sunny midsummer days were lower in the nonshaded plants from the open field than in the shaded ones and ii) the F_v/F_m values showed a daily course with a pronounced decrease at noon which completely recovered at the end of the afternoon. The midday depression was observed on plants of both treatments (fig 3). Very similar results on both effects were obtained, for example, with sun-exposed and artificially shaded French bean plants (Bolhàr-Nordenkamp and Öquist, 1993). Quite recently, Greer (1995), studying the susceptibility of kiwifruit plants to photoinhibition, has also shown that attenuation of light in the kiwifruit canopy created a sustained sunshade gra-

Table VI. Results of the pigment analysis of leaves collected on 16 August 1994 from nonshaded and shaded pedunculate oaks (mean values with standard deviations; ten leaves were used for each measurement).

Pedunculate	Total chlorophyll content per dry weight (mg/g) per leaf area ($\mu\text{g}/\text{cm}^2$)	Chl a per dry weight (mg/g) per leaf area ($\mu\text{g}/\text{cm}^2$)	Chl b per dry weight (mg/g) per leaf area ($\mu\text{g}/\text{cm}^2$)	Chl a:b ratio	Carotenoids per dry weight (mg/g) per leaf area ($\mu\text{g}/\text{cm}^2$)	Chl _{total} : carotenoids ratio	
Nonshaded	1.20 \pm 0.07 (10.11 \pm 0.05)	335	920 \pm 54 (7.74 \pm 0.46)	478 \pm 27 (4.02 \pm 0.23)	1.92	216 \pm 7 (1.82 \pm 0.06)	5.54
Shaded	1.53 \pm 0.09 (9.19 \pm 0.05)	490	1 160 \pm 64 (7.52 \pm 0.41)	614 \pm 38 (3.98 \pm 0.24)	1.89	210 \pm 7 (1.36 \pm 0.05)	6.75

chl: chlorophyll.

Table VII. Relative growth increment of root collar diameter and total height of the nonshaded and shaded test plants of both oak species since start of the experiment in 1992 (mean values with standard deviations).

Species	Parameter	Growth increment since 1992 (in %)		
		Nonshaded	Shaded	Stat signif
Pedunculate oak	Root collar diameter	344 ± 64	208 ± 153	**
	Total height	360 ± 83	333 ± 73	ns
Sessile oak	Root collar diameter	244 ± 42	153 ± 112	**
	Total height	205 ± 55	213 ± 47	ns

** Values differ significantly at the 0.01 level; ns: not significant.

dient in fluorescence, with F_v/F_m universally higher in shade than in sun leaves. Such decreases of F_v/F_m may reveal either disorders (photodamage) in photosystem II (Powles, 1984) or the onset of protective mechanisms against excess light energy (Demmig and Björkman, 1987). According to Osmond (1994), both effects could be interpreted as photoinhibition (ie, light dependent loss in photosynthetic functioning of photosystem II, which is manifest in whole leaves as a decline in the quantum efficiency of photosynthesis under limiting light intensities). In contrast to this view, Epron et al (1992) pointed out that the decreases in F_v/F_m should be reversible as soon as irradiance decreases to nonsaturating levels. In analysing the diurnal time course of fluorescence parameters and net photosynthesis on adult trees of *Q petraea* in summer, they showed indeed that the observed transient midday depressions of F_v/F_m revealed the onset of mechanisms for thermal de-excitation of photosystem II. Although these mechanisms transiently reduced photosystem II efficiency (midday depression), the increase in thermal de-excitation of photosystem II protected the photosynthetic apparatus from permanent damage. Thus, the full recovery of the midday depression of

F_v/F_m in our experimental plants gave evidence that the protective mechanisms were functioning. Similar conclusions were drawn by Bilger et al (1995) and Valentini et al (1995), who did not observe any signs for sustained photodamage after exposure of beech or oak leaves to high values of photosynthetic photon flux densities. Adams et al (1995) also emphasized that photoinhibition, at least in nature, is quite possibly predominantly a reflection of a photoprotective (eg, xanthophyll cycle dependent) energy dissipation process. Thus it seems quite incongruous to refer to such a phenomenon as photoinhibition of photosynthesis. As indirect confirmation for this interpretation, one should look at the pigment proportions: the total content of carotenoids (per unit leaf area) was higher in leaves of nonshaded plants. Correspondingly, the chlorophyll/carotenoid ratio was clearly lower in the unshaded plants (5.54) than in the shaded plants (6.75).

Overall, from the comparison of the young oak plants in the open field and in shade up to an age of 5–6 years at the end of 1994, we could not confirm the results of Jarvis (1964) and Ziegenhagen and Kausch (1993), according to which young oak plants in the shade grew better than those in full

sunlight. Jarvis (1964) described less than 1-year-old oak seedlings as intolerant to high light intensity (above a relative intensity of 56%); Ziegenhagen and Kausch (1993) demonstrated with 2-year-old oak plants an increase in growth with increased shade down to a relative light intensity of 25%. In contrast, our oaks showed a substantial reduction in growth already at 50% relative light intensity for the last three vegetation periods. Regarding the question raised at the beginning as to the light requirement of young oaks over 2 years old, it can be concluded that in spite of the adaptations mentioned earlier, the growth optimum must be situated at a relative light intensity substantially greater than 50%. Thus, previous experience as to an increase in light requirement with increasing age of young oak trees is substantiated. In addition, differences in growth between open field and shade plants could be modified by water supply, as indicated by effects of watering in open field plants.

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