Adverse Effects of Epiphytic Crustose Lichens upon Stem Photosynthesis and Chlorophyll of *Populus tremula* L.

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Abstract

Dry cork layer (phellem) in stems of *Populus tremula* transmitted 35–55 percent of incident irradiation, depending upon moisture content. A cover of crustose *Lecanora* lichens reduced transmission through phellem to 10 percent or less of incident irradiation. The bark contains photosynthetically active cells. Apparent quantum yield for photosynthetic O_2-evolution was 0.017 in bark covered with dry *Lecanora* compared with 0.070 in naked bark. The capacity for gross photosynthesis in high light (1090 μmol photons m^{-2} s^{-1}) was reduced by 50 percent in *Lecanora*-covered bark. *Lecanora* did not reduce the ratio between variable and maximal chlorophyll *a* fluorescence (F_v/F_m). Chlorophyll content per unit area was similar in leaves and naked bark of *Populus tremula*. The chlorophyll content in the bark decreased with increasing chlorophyll content in *Lecanora*. Chlorophyll *a/b* ratio was 2.5 in the bark compared with 4.0 in leaves and in *Lecanora*, and the ratio decreased down the stems. The *a/b* ratio was 2.3 in *Lecanora* covered bark compared with 2.6 in naked bark. The changes in bark photosynthesis below a *Lecanora* crust were probably due to acclimation of bark photosynthesis to shade, since the lichen acids in the measured lichens neither suppressed photosynthetic O_2-evolution nor changed the F_v/F_m in bark disks.

Key words

Bark photosynthesis, epiphytic *Lecanora* lichens, lichen acids, phellem light transmission, *Populus tremula*.

Introduction

Twigs and stems of many trees have photosynthetically active cells beneath the cork cambium in the bark. The chlorophyll content per unit bark area can be as high as in leaves (Pearson and Lawrence, 1958). Bark photosynthesis probably has an ecological significance in reducing stem respiratory loss (Keller, 1973; Foote and Schaedle, 1976). Epiphytic lichens are often abundant on bark (Ochsner, 1928). The discussion whether lichens damage their host or not (Barkman, 1958; Brodo, 1973), often concludes that large quantities of lichens are a consequence rather than a cause of slow growth (Barkman, 1958). However, some fruticose lichens with deep penetration tissue into xylem vessels, seem to damage their host (Ascaso et al., 1980; Legaz et al., 1988).

The present study focuses on effects of crustose lichens on photosynthesis and chlorophyll in the bark of *Populus tremula* L., since this type of interaction in a tree-lichen association has been neglected. Epiphytic lichens possibly influence the host through shading that may reduce bark photosynthesis. The photosynthetic apparatus adapts to different light intensities. One objective is to study shading directly through measurements of light transmission through phellem, and through determination of apparent quantum yields for photosynthetic O_2 evolution for bark with and without lichens. Indirectly shading will be studied through chlorophyll *a/b* ratios as shade-adapted leaves (Lichtenthaler et al., 1981; Anderson, 1986) or shade-adapted cells within a leaf (Terashima and Saeki, 1985) have lower chlorophyll *a/b* ratios than leaves or cells adapted to high light. Another objective is to study adverse effects of lichen extracts on bark photosynthesis, as some lichen phenols can inhibit photosynthesis and cause irreversible membrane damage to the host (Kinraide and Ahmadjian, 1970; Vavasseur et al., 1991).

Materials and Methods

Site description

Populus tremula trees were selected in a 40–50-year-old stand at Ås (59°30′N, 10°47′E, 85 m altitude). The stand was a successional stage with a dominance of deciduous trees and eutrophic ground vegetation. The climax vegetation will probably be a *Picea abies* (L.) Karst. forest. The trees were slow growing, and a major portion of the stem (40–80% of surface area) was covered with foliose and crustose lichens with green algae as photobiont. The epiphytic community belonged to *Xanthorion parietinae* (Ochsner, 1928; Barkman, 1958). Lichens containing usnic acid were few and contributed insignificantly to the total epiphytic lichen biomass. Fruticose lichens that have the deepest pentrating tissue extending into the cambium of the host and the youngest cells of the wood (Porter, 1917; Ascaso et al.,

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1980) were absent. The dominant *Lecanora subfusca* (coll.) is partially hypophloedal, according to Ozenda and Clauzade (1970).

Plant material

The bark of *P. tremula* has a continuously active cork cambium as long as it remains smooth; smooth bark can change to rough, but not in opposite direction. Smooth and photosynthetically active bark dominated the upper 5 m of the trunk. Below, there was a gradual increase of rough bark down to 10–15 m below the top, where the rough bark was continuous. The lowest position of smooth bark concurred with the position of the lowest living branches. This level corresponded to an age of about 45 years as shown by annual rings, and to a stem diameter of 16 cm (Fig. 1). Total bark area for both main stem and twigs for one typical tree was 10 m^2.

Lecanora carpinea (L.) Vainio and *L. subfusca* (Brodo, 1984) were the only abundant species covering the whole altitudinal section of a stem with smooth bark. Most other lichens seemed to colonize rough parts of the bark surface, and only secondarily spread to adjoining smooth bark areas, and were therefore scarce or absent in the uppermost part of the stem. Since the chlorophyll content was similar in these two crustose species, they were not separated before measurements. Uppermost samples of *Lecanora* were often sterile.

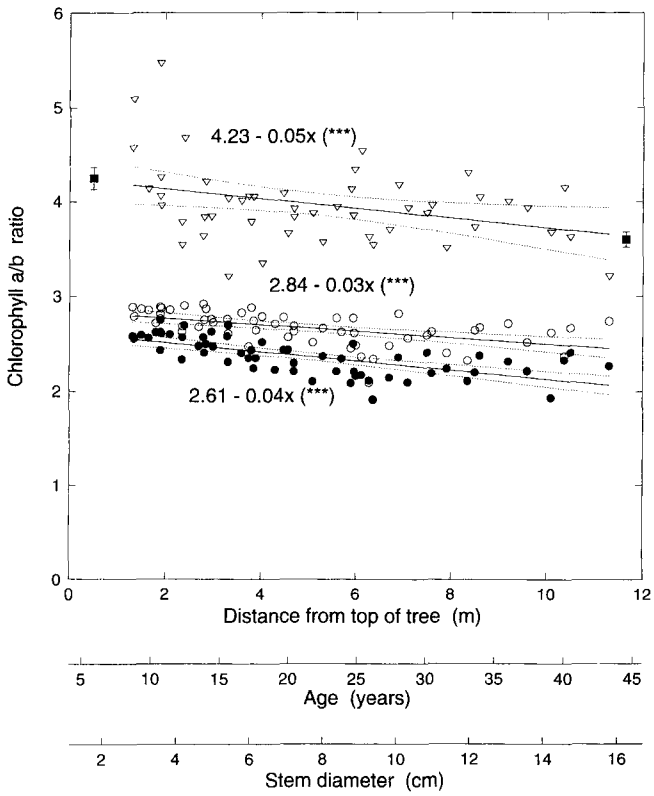

Fig. 1 Chlorophyll *a/b* ratios at different distances from the top of the *Populus tremula* trees for bark which had been covered with lichens (●), for bark which had not been covered with lichens (○), and for lichens (▽). Linear regression curves with 95 % confidence intervals are fitted to the data points. Regression equations with significance level for the regression coefficients are shown beside the curves. (***), $P < 0.001$. Chlorophyll *a/b* ratios ± SE (n = 9) for leaves from top (left) and bottom (right) of the crown are shown by "■".

All measurements were done from June to early September. Trunks of trees were cut into 1 m long sections from the top and downwards until no more smooth bark could be detected. Sections were brought to the laboratory. Samples for chlorophyll determination, chlorophyll fluorescence and light transmission were taken within 3 h, while photosynthetic O_2 evolution was measured within 8 h.

Chlorophyll measurement

Samples were selected on uniform thin phellem with adjoining areas of 100% covered *Lecanora* bark and uncovered bark. Bark disks completely covered with *Lecanora* species and adjoining naked bark disks were cut with a cork borer at each location. Each sample consisted of three disks, each with an area 0.67 cm^2. Bark disks were soaked in distilled water for 10 min before the crust of lichens was carefully scraped off the phellem under a dissecting binocular microscope. Disks were sliced into 1 mm thin sections and were immediately put into separate aluminium foil-covered vials with 5 ml N,N-dimethylformamide. Soaking of lichens was required because chlorophyll was not completely extracted from dry samples. Leaf disks from the uppermost and lowermost twigs were sampled for comparison. Extraction of chlorophyll was complete after two days in a refrigerator. Extracts were then centrifuged a few minutes at 2000 g before measurement of absorbance at 647 and 664 nm. The amount of chlorophyll *a* and *b* was calculated according to Moran (1982).

Light transmission through the phellem

The phellem was removed with a cork borer and a scalpel. Since the cork cambium was active during the measurement period in June, the phellem loosened easily with no damage. The phellem was pressed with a glass plate (microscopy slide) towards a LiCor model LI-190SB quantum sensor, and light transmission was measured by illuminating it with a halogen lamp producing 800 μmol photons m^{-2} s^{-1} at the surface of the bark. Eight different Kodak glass filters with band peaks from 430 to 675 were used one by one to measure light transmission at different wavelengths. Light transmission through wet phellem was measured on samples soaked for about 1 h in water. It was difficult to remove lichen-covered phellem without damaging phellem and especially the lichens. Therefore, light transmission through phellem with *Lecanora* was measured only on the few samples that had been successfully removed. However, some lichen fragments, especially apothecia, dropped off, and the measured light transmission might therefore be too high.

Photosynthetic O_2 evolution

Oxygen evolution was measured with a leaf disc electrode (Model LD2, Hansatech King's Lynn, Norfolk UK) at 20 °C and about 5 % CO_2. One bark disc with an area of 5.0 cm^2 was placed in the cuvette and O_2 evolution was measured with increasing photon fluence rates in the range from 0–1090 μmol m^{-2} s^{-1} using light emitting diodes (LH36U, Hansatech).

Gas diffusion resistance probably does not limit photosynthesis with this method, first because of the high CO_2 concentration used, and second because CO_2 may diffuse to the photosynthetic active cells through the cut edges of the bark discs. The net photosynthetic rates observed in bark with this method will probably not occur under field conditions due to CO_2 diffusion resistance through the phellem. Since only a small area of the stiff, slightly curved bark disks was in direct contact with the temperature-controlled glass above the discs there might have been some warming at high light intensities.

Apparent quantum yields were calculated from the linear portions of the light response curves.

Chlorophyll a fluorescence

Chlorophyll *a* fluorescence induction curves were recorded with a portable fluorometer (Plant Efficiency Analyser (PEA), Hansatech). The phellem was carefully removed from bark samples that were then dark-adapted for at least 15 min before measurement. Fluorescence induction curves of 5 s duration were recorded during illumination with light of 1500 μmol m^{-2} s^{-1} from light emitting diodes.

Lichen acid treatment

Presence of usnic acid in *Lecanora* species was checked by thin-layer chromatography, according to the method of Culberson and Kristinsson (1970) with later modifications (White and James, 1985).

About 300 mg of dry *L. carpinea* were extracted with 50 ml 100% acetone. The extract was filtered and, after evaporation of the acetone, 150 ml 1.0 mM $NaHCO_3$ was added and the flask was placed on a magnetic stirrer for 24 h for maximal solubilization of lichen acids. Solutions of lichen acids from *Usnea longissima* and of pure (+) usnic acid (Sigma) in 1.0 mM $NaHCO_3$ were prepared in the same way. The pure usnic acid solution had a concentration of 25 mg l^{-1}.

The phellem was carefully removed from bark disks of *P. tremula* and the bark disks were put into the solutions of usnic acid, *Lecanora* extract, *Usnea* extract, or control solution with 1.0 mM $NaHCO_3$. After one day at room temperature chlorophyll fluorescence was measured, and after two days photosynthetic O_2 evolution was recorded.

Results

Anatomy of bark and light transmission

The *Lecanora* thalli seemed to be attached only to the outer surface of the phellem. No penetration of hyphae through the phellem was seen (Fig. **2**).

Dry, intact phellem transmitted 36.6 ± 1.4% white light, wetting increased the transmission to 56.6 ± 1.6%. Phellem modified the spectral distribution of the light, as light transmission through dry phellem increased from 10% of blue light to 50% of red light (Fig. **3 A**). Wet phellem showed a similar trend from about 20 to nearly 70% light transmission. Light transmission through *Lecanora* covered phellem was reduced to about one forth of that without lichens (Fig. **3 B**). Light transmission did not change markedly with the distance from the top of the trees.

Chlorophyll content and a/b *ratio*

Chlorophyll *a/b* ratios were highest (≈4.0) in high light-exposed components such as leaves and in *Lecanora* (Fig. **1**). Bark without *Lecanora* had an *a/b* ratio of 2.6 (Fig. **1**), while the lowest value (2.3) was in *Lecanora*-covered bark (Fig. **1**). The difference between *Lecanora*-free and covered bark is small, but highly significant.

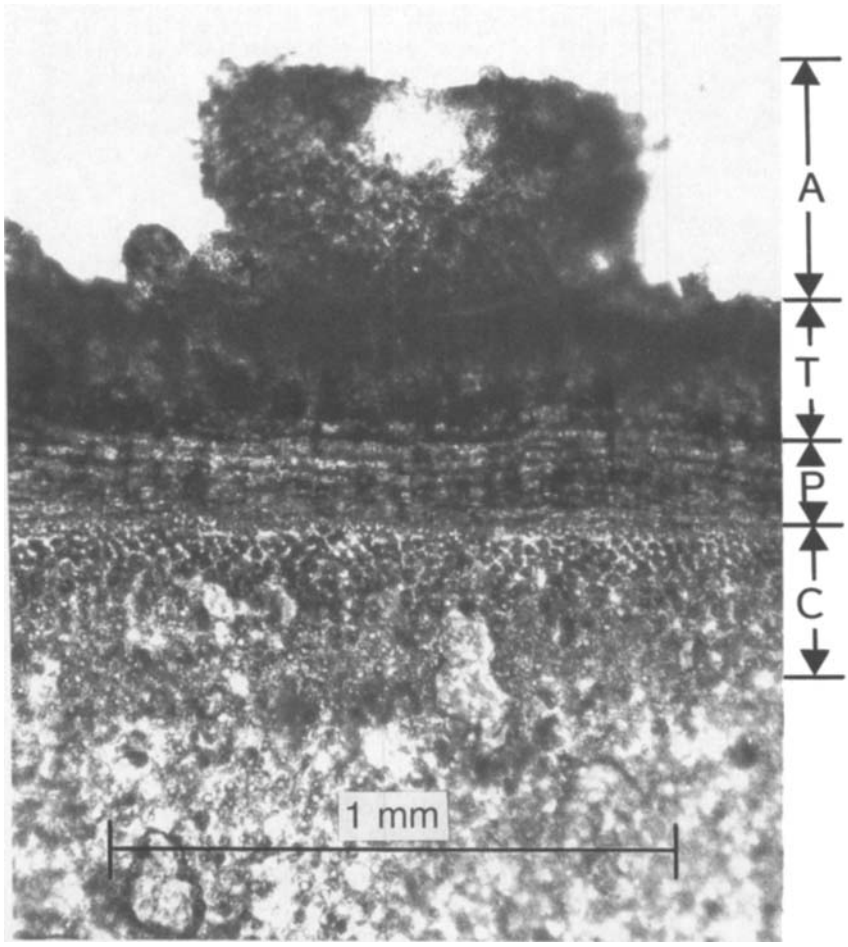

Fig. 2 Light micrograph of *P. tremula* bark covered with *L. carpinea*. A, apothecium; T, thallus; P, phellem; C, chlorophyll-containing cells in the bark. 25 μm thick sections were cut from fresh bark with a freeze microtome.

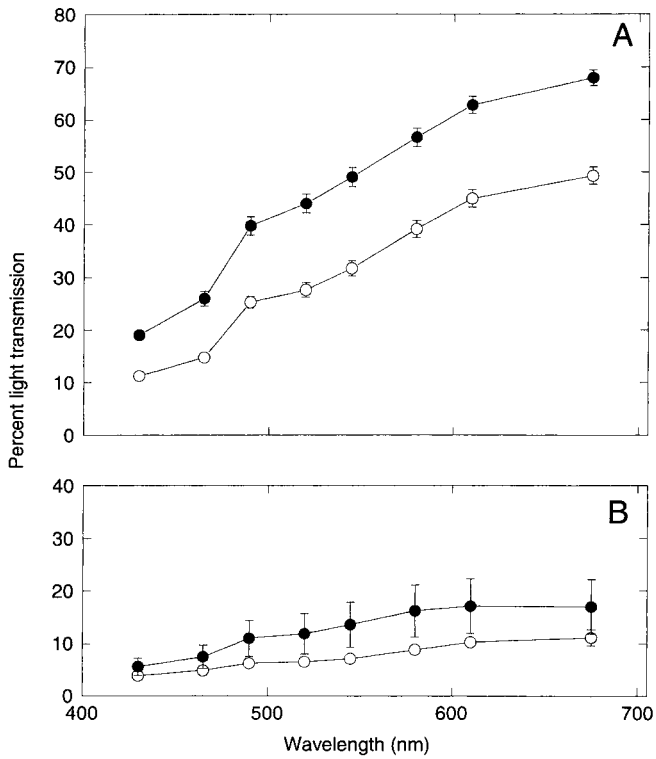

Fig. 3 Percent light transmission at different wavelengths through phellem only (**A**), through phellem covered with lichens (**B**) for dry phellem (○) and for phellem soaked in water (●). The error bars show ± SE (if larger than symbol). n = 24 for phellem only, and n = 5 for phellem covered with lichens.

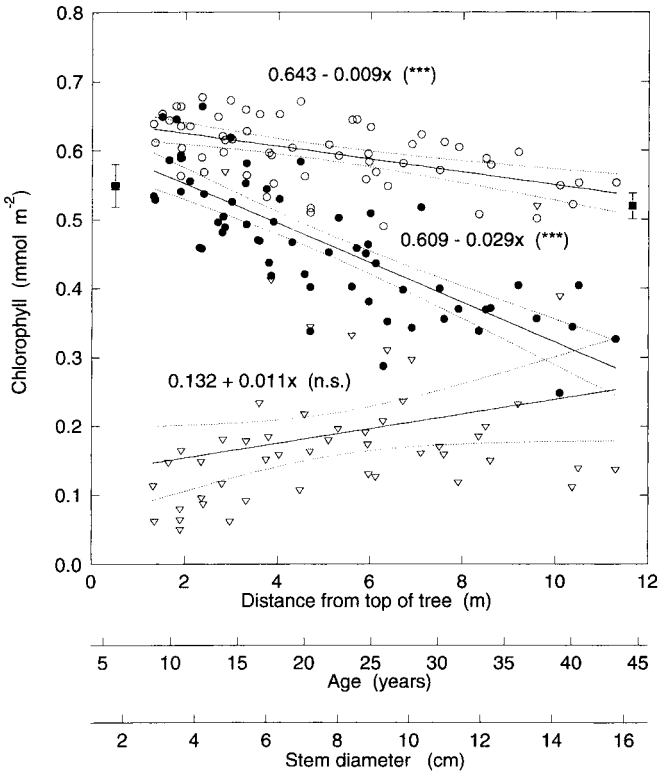

Fig. 4 Chlorophyll content per unit area of bark at different distances from the top of *Populus tremula* trees in bark which had been covered with lichens (●), in bark which had not been covered with lichens (○), and in lichens (▽). Linear regression curves are shown as in Fig. **1**. (***), $P < 0.001$; (n.s.), not significant. Chlorophyll content ± SE (n = 9) for leaves from top (left) and bottom (right) of the crown are shown by "■".

Chlorophyll *a/b* ratios decreased with increasing distances from the top of the canopy. Regression coefficients were similar in the two categories of bark, and in lichens (Fig. **1**). A similar decrease also appeared in leaves, but only leaves from the top and lower part of the canopy were measured.

Bark without a lichen cover had as much chlorophyll per unit area as leaves (Fig. **4**). The chlorophyll content in the bark decreased with increasing chlorophyll content in *Lecanora* ($r = -0.452$, $P < 0.001$, $n = 49$; linear regression analysis). The chlorophyll content in uncovered bark decreased down the stem (Fig. **4**). There was a steeper gradient in chlorophyll content along the stem in bark covered with *Lecanora*. Bark chlorophyll content increased with increasing chlorophyll *a/b* ratio to an *a/b* ratio of about 2.5, especially in *Lecanora*-covered samples (Fig. **5**). Chlorophyll content in the lichens tended to increase down the trees ($P = 0.062$) (Fig. **4**), as there is a succession starting with a sterile thallus crust on bark at 10 years old. The uppermost 1 m of the stem was bare. Thalli increased in thickness with increasing distance from the top. The most obvious change, however, was the increase in size and number of apothecia down the stem to a certain level where the thalli became completely crowded with apothecia.

Photosynthesis

A *Lecanora* cover significantly reduced bark photosynthesis (Fig. **6**). Apparent quantum yield was 0.070 ± 0.004 in uncovered bark compared with 0.017 ± 0.003 in bark covered with *Lecanora* (Fig. **6**). Apparent quantum yield increased to 0.085 ± 0.003 after wetting the phellem (Fig. **6**). Removal of the phellem increased the quantum yield to 0.109 ± 0.004. Quantum yield for leaves that were just fully expanded (1. June) was 0.084 ± 0.006, and 14 d later quantum yield for leaves was 0.095 ± 0.007. Apparent quantum yields for bark covered with phellem determined with red light (660 nm) from light emitting diodes are slightly overestimated compared with daylight since light transmission through the phellem increases with wavelength (Fig. **3**). Photosynthetic capacity for bark in high light was reduced to 50% in lichen-covered bark. Bark photosynthesis in high light was lower than leaf photosynthesis in mature leaves of June 14th, while it was about equal to leaf photosynthesis for just fully expanded leaves 14 d earlier (Fig. **6**).

The ratio F_v/F_m was 0.810 in bark without *Lecanora* compared with 0.837 in *Lecanora*-covered bark. For the leaves F_v/F_m was 0.807. No gradient in chlorophyll fluorescence parameters along the stem was detected.

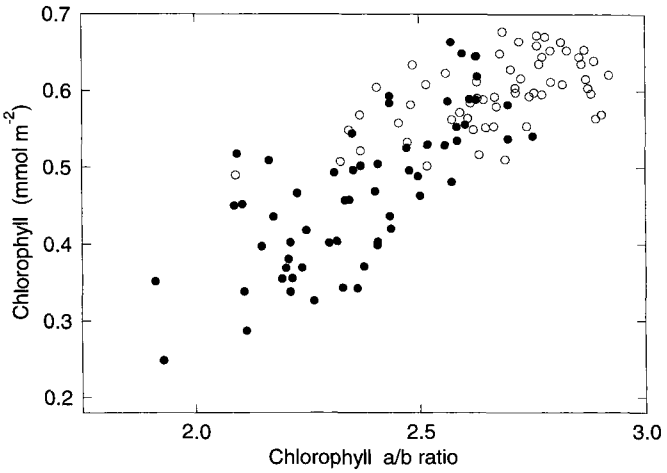

Fig. 5 Relationship between chlorophyll contents and chlorophyll *a/b* ratios in naked bark (○) and in bark covered with lichens (●).

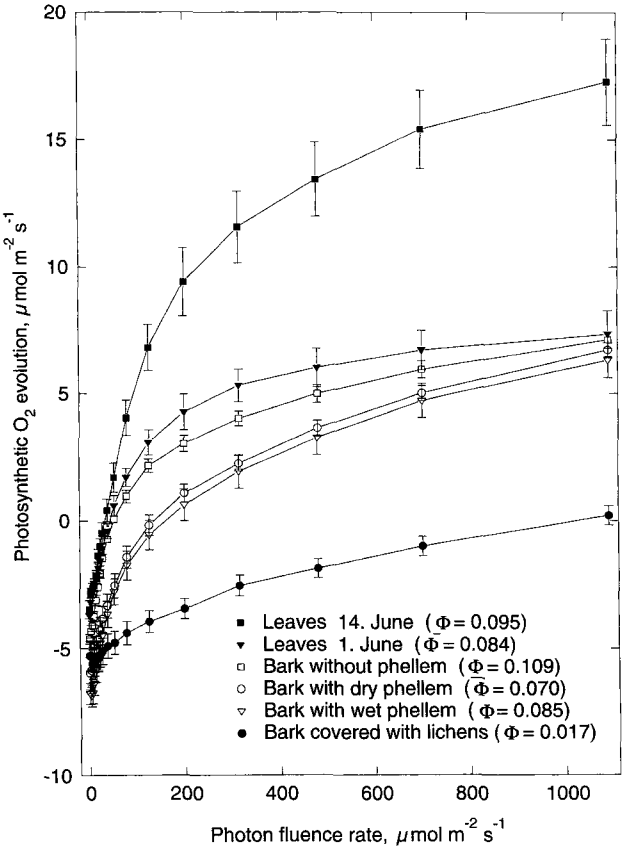

Fig. 6 Photosynthetic O_2 evolution for leaves and bark discs from *P. tremula*. Apparent quantum yields (Φ) are shown in brackets. n = 6.

None of the *Lecanora* species in analysed samples contained usnic acid. Photosynthesis and the ratio F_v/F_m in bark disks treated with usnic acid or extract from *U. longissima* was severely reduced, while photosynthesis in bark disks treated with lichen substances extracted from *L. carpinea* was not reduced (Fig. 7).

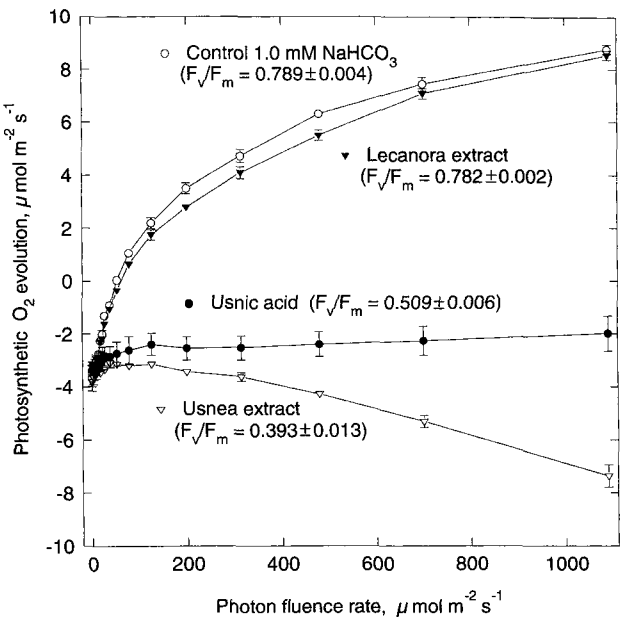

Fig. 7 Photosynthetic O_2 evolution for bark discs without phellem exposed to various extracts for 2 d. F_v/F_m ± SE after one day exposure to the extracts are shown in brackets. n = 5.

Discussion

Light transmission through phellem from *P. tremula* was as high as 35–55% (Fig. 3). Apparent quantum yield measurements (Fig. 6) confirm the high light transmission measurements in *P. tremula*. Assuming a minimum quantum requirement of 8 photons per CO_2 fixed (e.g. Walker, 1992) the maximum quantum yield is 0.125. Since the apparent quantum yield for bark covered with phellem was 0.070 (Fig. 6), at least 56% of incident light must have passed through the phellem. Light transmission through phellem was considerably higher than reported from other trees, such as *P. tremuloides* (Strain and Johnson, 1963) and *Betula* spp. (Kauppi, 1991). Light transmission through the phellem did not change with age of the bark as long as the bark remained smooth. This means that light intensity below phellem decreases down the stems as a function mainly of canopy shading and shading of lichens. The transparent phellem, even on thick stems, suggests that bark photosynthesis may be more important in *P. tremula* than in other species with thicker phellem.

Light transmission was about 50% higher in wet phellem than in dry (Fig. 3), and apparent quantum yield increased from 0.070 to 0.085 after moistening (Fig. 6). Water reduces reflection between the cells in the phellem and in the cortex of the lichens (Gauslaa, 1984). Therefore light transmission increases.

Photosynthesis in high light was more than 50% lower in *Lecanora*-covered bark than in uncovered (Fig. 6), while the average chlorophyll content was only 22% lower than in uncovered bark (Fig. 4). According to Gabrielsen (1948), an increase in chlorophyll content beyond 0.5 mmol m^{-2} does not influence the rate of photosynthesis. Photosynthetic rate increases linearly with chlo-

rophyll content only up to about 0.2 mmol m^{-2}. Therefore, the reduction in chlorophyll content in bark covered with lichens probably does not reduce photosynthesis. Bark photosynthesis is probably not light saturated when the bark is shaded by leaves. Therefore, in low light, lichens affect bark photosynthesis to a similar extent as the reduction in quantum yield from 0.070 in uncovered bark to 0.017 in *Lecanora*-covered bark. Therefore, lichens probably affect bark photosynthesis significantly.

Some lichen phenols like usnic acid have been shown to inhibit photosynthesis and cause irreversible membrane damage in leaves of some hosts (Kinraide and Ahmadjian, 1970; Vavasseur et al., 1991) as well as defoliation (Giménez and Vicente, 1989). In contrast, photosynthesis and F_v/F_m were not reduced in samples treated with an extract from *Lecanora* species, while the usnic acid and especially the *U. longissima* extract treatment severely reduced photosynthesis and F_v/F_m (Fig. 7). For untreated bark F_v/F_m was not reduced when covered with *Lecanora*. The effect of *Lecanora* species on apparent quantum yield is therefore probably an effect of reduced light transmission only, and not a result of inhibitory lichen phenols.

The low chlorophyll *a/b* ratio in the bark (Fig. 1) indicates that bark photosynthesis is shade-adapted (Lichtenthaler et al., 1981; Anderson, 1986), and Dale and Causton (1992) have proposed that the ratio could be used as a bioassay for the light environment. In both cortex, xylem and pith in twigs from the more shade tolerant *Fagus sylvatica* the chlorophyll *a/b* ratio varied from 1.7 to 1.9, indicating shade adaptation (Larcher et al., 1988). Decreasing chlorophyll *a/b* ratios with increasing distance from the top of the trees, as well as lower *a/b* ratios in bark covered with lichens (Fig. 1), can also be explained as shade adaptation. The lichens are probably exposed to similar light levels as the leaves, and they have similar chlorophyll *a/b* ratios (Fig. 1). The phellem modifies the spectral distribution of the light since transmission increases with increasing wavelength (Fig. 3). The red/far-red ratio (660/730 nm) decreased from 1.03 for incident light to 0.85 for light transmitted through the phellem (pers. comm.; I. P. Björnseth, University of Trondheim). A modified light quality could be an additional explanation for reduced chlorophyll *a/b* ratio in the bark since red light stimulates development of shade-type chloroplasts with low chlorophyll *a/b* ratios (Lichtenthaler et al., 1980). Bark photosynthesis substantially reduces respiratory loss of CO_2 in stems (Keller, 1973; Foote and Schaedle, 1976). However, net photosynthesis rates are low, probably because the dense phellem outside the chlorophyll cells has a low gas permeability (Foote and Schaedle, 1976). It has been estimated that annual contribution of bark photosynthesis to total carbohydrate supply in *P. tremuloides* is approximately 1 to 2 percent (Foote and Schaedle, 1978). Bark photosynthesis may be ecologically significant because it provides carbohydrates when phloem transport is low and when deciduous trees have lost their leaves (Foote and Schaedle, 1978). Lichens reduce light transmission through phellem (Fig. 3), apparent quantum yield and photosynthetic rate considerably (Fig. 6). Therefore, lichens, that often cover a large portion of the bark, probably substantially reduce bark photosynthesis and reassimilation of CO_2 in the bark, and thus may affect growth and survival of *P. tremula*.

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