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Seasonal variation of photoinhibition of photosynthesis in bark from *Populus tremula* L.

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Abstract

In the bark of *Populus tremula* L. photochemical efficiency of photosystem 2 (PS2) determined as F_v/F_m decreased during winter. The strongest reduction was found after cold periods. The degree of reduction depended on irradiance since the lowest levels of F_v/F_m were found on the sun-exposed side of the stem and below thin phellem. Therefore, photoinhibition was partly responsible for the reduction in F_v/F_m. The photochemical efficiency of PS2 recovered in late April about a month before the trees got leaves. In the laboratory, F_v/F_m recovered within about a week under low irradiance at 20 °C. Rapid recovery of photochemical efficiency of PS2 in the bark may be important to reduce respiratory loss of CO_2 from the stem before the trees get leaves.

Additional key words: chlorophyll fluorescence induction; irradiance; oxygen evolution; phellem; photosystem 2; poplar; quantum yield; seasonal course; tree age.

Introduction

The bark of many trees has photosynthetically active cells beneath the cork cambium. The chlorophyll (Chl) content per unit bark area can be as high as in leaves (Pearson and Lawrence 1958, Solhaug *et al.* 1995). In *P. tremula* the bark contains 17-40 % of the whole tree Chl (Kharouk *et al.* 1995). Although net photosynthetic rate in the bark is negative or close to zero (Kharouk *et al.* 1995, Nilsen 1995), the capacity for gross photosynthesis may be high (Solhaug *et al.* 1995). Bark photosynthesis probably has an ecological function in reducing CO_2-loss from stem respiration (Keller 1973, Foote and Schaedle 1976), and it may be especially important when deciduous trees have lost their leaves during the cold season (Foote and Schaedle 1978) or when tropical trees have lost their leaves during periods of drought (Muthuchelian 1992).

A low Chl *a/b* ratio in bark cells (Larcher *et al.* 1988, Muthuchelian 1992, Solhaug *et al.* 1995) indicates shade adaptation of photosynthesis in the bark (Lichtenthaler *et*

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al. 1981, Anderson 1986). This may be a result of shading by leaves and by the phellem outside the photosynthetically active cells in the bark. In *P. tremula* a large fraction of the bark is often covered by thin phellem that may transmit 35-55 % of incident irradiation (Kharouk *et al.* 1995, Solhaug *et al.* 1995). When the trees have lost their leaves, photosynthetically active cells in the bark of *P. tremula* may therefore receive high irradiances. Exposure to high irradiances especially at low temperatures often results in photoinhibition (Ögren *et al.* 1984, Strand and Öquist 1985, Huner *et al.* 1993).

Photoinhibition is an irradiance dependent reduction of photosynthetic efficiency. Photochemical efficiency of PS2 can be measured by the Chl *a* fluorescence ratio F_v/F_m, and this ratio is often used as an estimate of the degree of photoinhibition. However, factors other than high irradiance, such as heat and frost, may cause reduced F_v/F_m values (Havaux 1992, Robberecht and Junttila 1992, Ranney and Peet 1994). In this study the seasonal variation in F_v/F_m in bark from *P. tremula* exposed to different irradiance was measured using Chl fluorescence. In addition, the capacity for gross photosynthesis (P_G) was estimated by measuring O_2 production from bark disks at high CO_2 concentrations.

Materials and methods

Trees were selected from two stands, one with 10-15 year old trees and another with 30-40 years old trees, in Ås (59°30'N, 10°47'E).

Chl *a* fluorescence was measured with a portable fluorometer (Plant Efficiency Analyser, *PEA, Hansatech,* UK). Stems were taken into the laboratory and fluorescence was measured within 2 h. Bark sections of about 2×5 cm and about 0.5 cm thick were cut from the stem with a knife. Most of the phellem was carefully scraped off with a scalpel before dark adaption for 15 min in a standard leaf clip. Fluorescence induction curves of 5 s duration were recorded during irradiation with 1500 μmol(photon) m^{-2} s^{-1} from light emitting diodes. Recovery of F_v/F_m was studied by placing the lower end of 1 m long stem sections in water in the laboratory. The stems were covered with transparent plastic, and the photon fluence rate (PFR) was about 10 μmol(photon) m^{-2} s^{-1} and temperature was about 20 °C. Fluorescence was measured after about one and two weeks.

Photosynthetic O_2 evolution was measured according to Solhaug *et al.* (1995) on bark disks with intact phellem.

Results and discussion

Seasonal variation in F_v/F_m: There was a rapid decrease in F_v/F_m in early October 1992 at the same time as the trees lost their leaves. F_v/F_m stayed low between 0.4 and 0.6 until it rapidly increased to values above 0.8 during a warm period in late April (Fig. 1). However, the winter 1992/93 was relatively mild, and next year in February 1994 after a cold period F_v/F_m values lower than 0.2 were measured. At that time, apparent quantum yield of photosynthetic O_2 evolution was 0.0135 (Fig. 2) compared with 0.070 in summer 1992.

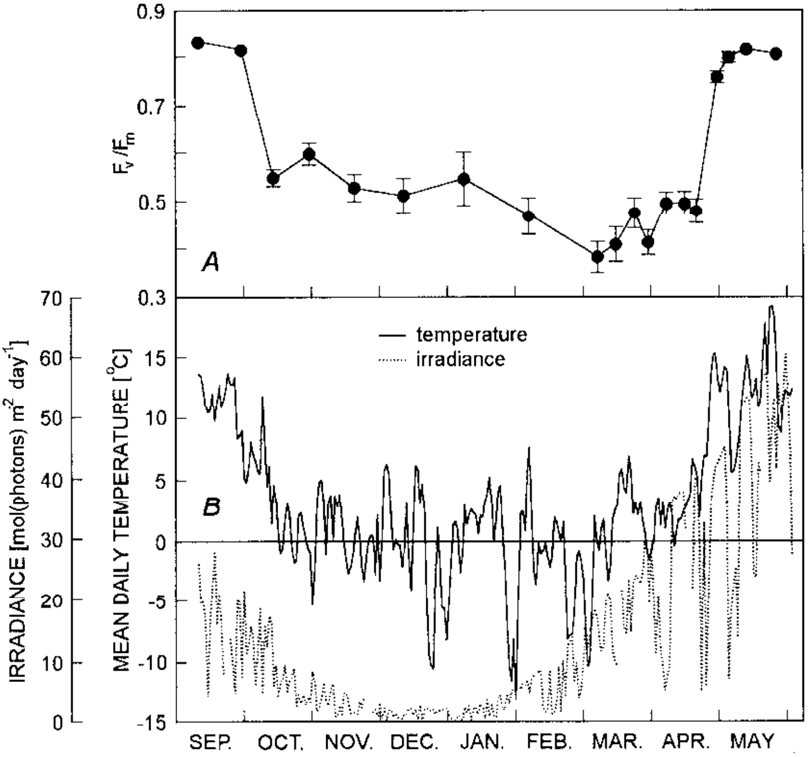

Fig. 1. Seasonal variation in photoinhibition in bark from *P. tremula* measured as F_v/F_m. Mean daily temperature and irradiance (400-700 nm) is shown below.

The lowest values of F_v/F_m were found at the most sun-exposed south-facing side of the stems (Fig. 3). The stand with the youngest trees was mostly exposed to light from south-west and the lowest values of F_v/F_m were found between south and south-west (Fig. 3*A*), while the other stand was mostly exposed to light from south-east and the lowest F_v/F_m was found for bark in the south-east direction (Fig. 3*B*). In addition, the level of F_v/F_m was lower below thin phellem near the top of the trees than below thicker phellem farther down (Fig. 3).

During growing season the photosynthetically active cells in the bark will receive a quite low PFR because these cells are covered with phellem and there is additional shading by leaves. Very low chlorophyll *a/b* ratio in the bark also indicates shade adaptation of bark photosynthesis. However, during the cold season, the bark receives relatively more irradiance because there is no shading by leaves and because of radiation reflection from the snow. In addition, the PFR on the south side of vertical stems will be increased by low sun angle. The phellem may transmit as much as half of PFR (Solhaug *et al.* 1995), and the chloroplasts in the bark may therefore receive relatively high PFR during the winter which combined with low temperatures will result in photoinhibition. There was also a considerable reduction in F_V/F_m on the north side of the stems which are exposed to much lower irradiance.

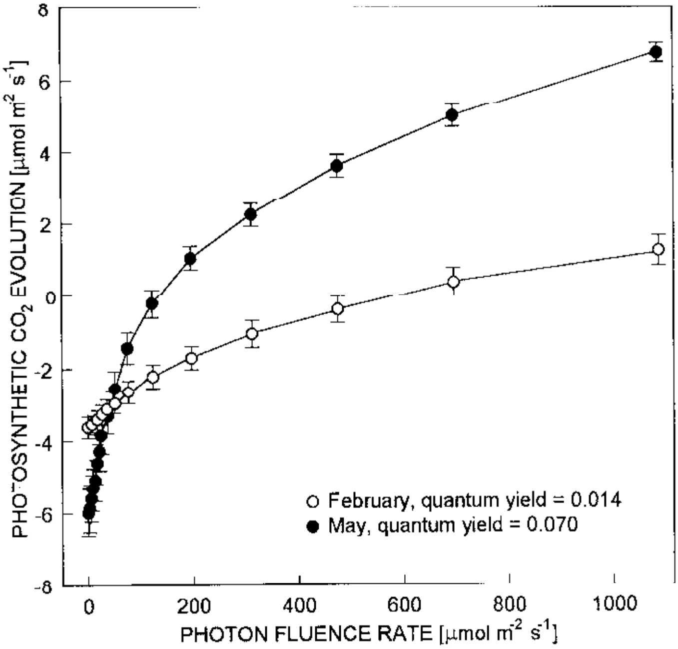

Fig. 2. Photosynthetic O_2 evolution for bark discs from *P. tremula*. Apparent quantum yields are shown above the curves. *n* = 5.

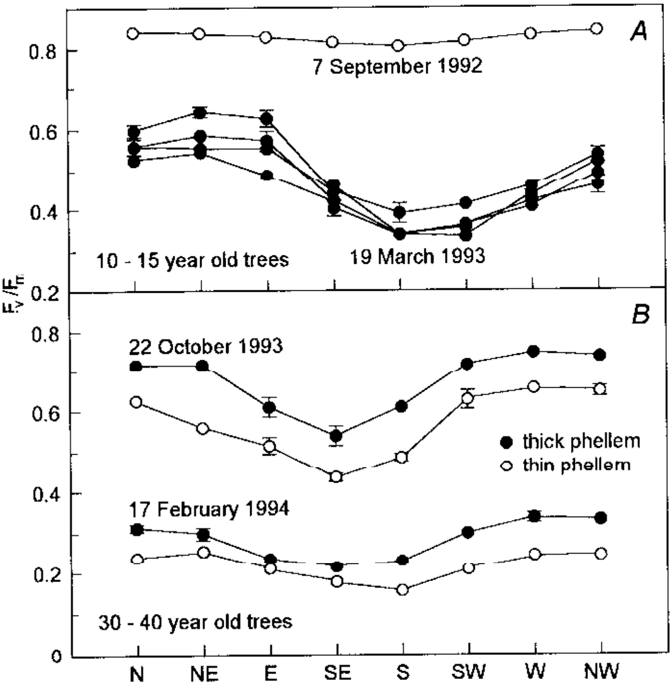

Fig. 3. Photoinhibition in bark of *P. tremula* measured as F_V/F_m at different sides of the stems (*A, B*) and at two different heights with thick phellem at the middle of the stem and thin phellem near the top (*B*). In *A* each curve represent one separate tree, and in *B* one tree with both thin and thick phellem was harvested at each date. N = north, NE = north-east, E = east, SE = south-east, S = south, SW = south-west, W = west, NW = north-west. *n* = 5.

This reduction is probably also partly photoinhibition since low irradiances at low temperatures can result in photoinhibition and reduction in quantum yield similar as in Scots pine needles (Strand and Öquist 1988). In addition, the reduction in F_v/F_m may be a result of other seasonal changes in the photosynthetically active cells and tissues (cf. Šesták and Šiffel 1997). In needles from conifers, there is a seasonal change in chloroplast ultrastucture involving a disorganization and reduction of the membrane system during winter (Senser *et al.* 1975, Martin and Öquist 1979), and there is also a reorganization of the light-harvesting complexes with a decrease in chlorophyll content and an increase in xanthophyll cycle carotenoids during winter (Adams *et al.* 1995, Ottander *et al.* 1995).

Reversible reduction of maximal efficiency of PS2 during winter in evergreens is regarded as a mechanism in which photosynthesis is downregulated so excess energy can be safely dissipated as heat and thereby the photosynthetic apparatus is protected against irreparable damage due to too much radiant energy (Huner *et al.* 1993).

However, it is difficult to separate the effects of different environmental stresses on photosynthesis because they interact and are rather complex (Havaux 1992). The whole reduction in F_v/F_m is therefore not neccessarily a result of photoinhibition, but high irradiance must play a role since the reduction in F_v/F_m was greatest on the south side of the stems and below thin phellem.

Recovery: The photochemical efficiency of PS2 in bark from *P. tremula* recovered in late April. A rapid recovery is probably important for an efficient bark photosynthesis that can reduce respiratory loss of CO_2 when stem respiration increases with temperature in spring.

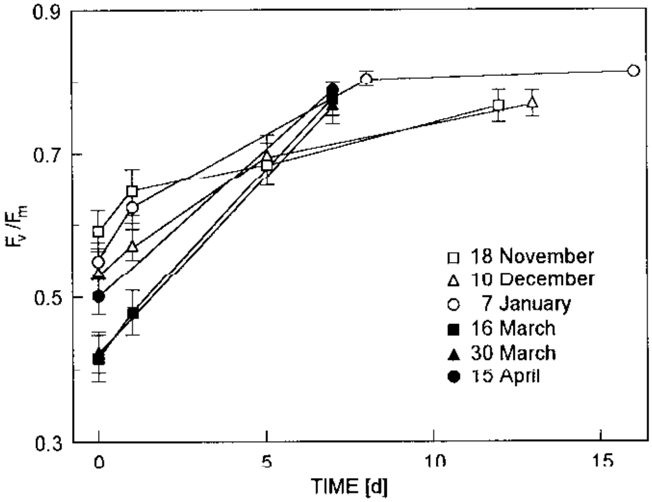

Fig. 4. Time course of recovery from photoinhibition for bark from *P. tremula* on stem sections placed in low irradiance at 20 °C at various days from 18 November to 15 April.

When stem sections were placed in low irradiance at about 20 °C in the laboratory, the bark recovered from photoinhibition within one or two weeks (Fig. 4). The recovery from low F_v/F_m values was slower for stems taken into warm temperatures in November and December than for stems taken later in winter or spring (Fig. 4).

This might indicate some connection with dormancy (*e.g.*, Tranquillini 1979). This recovery from low F_v/F_m was slower than for Scots pine needles that recovered within 2-3 d (Ottander and Öquist 1991). In ivy (*Hedera helix* L.), phenotypic sun leaves recovered from photoinhibition in winter at a faster rate than phenotypic shade leaves (Oberhuber and Bauer 1991). The recovery rate for the phenotypic shade leaves from ivy was about equal to the recovery rate for bark from *P. tremula*.

Photosynthetic capacity of the bark measured as P_G at 1100 μmol(photon) m^{-2} s^{-1} and 5 % CO_2 was about 10 μmol(O_2) m^{-2} s^{-1} in May (Fig. 2) which is about 50 % of the capacity of leaves measured with the same method (Solhaug *et al.* 1995). Therefore, *bark photosynthesis in P. tremula has high capacity to reassimilate CO_2 from stem* and bark respiration. In February the photosynthetic capacity was only 30 % of the capacity in May (Fig. 2). However, the need for reassimilation will be much lower in winter because of low respiration in the low temperatures during winter (Fig. 1).

Conclusion: The photochemical efficiency of PS2 in bark from *P. tremula* was considerably reduced during winter. Since the reduction in F_v/F_m partly depended on the sun exposure and on the phellem thickness, photoinhibition must be partly responsible for the low F_v/F_m values. The photochemical efficiency of PS2 in bark recovered within about a week. Recovery of photochemical efficiency of PS2 in the bark in spring may increase the reassimilation of respiratory CO_2 from the stem and bark in the relatively warm period with high irradiance before the trees get photosynthetically active leaves in late May.

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