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Photosynthetic Performance of Twigs and Stems of Trees With and Without Stress

By

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S u m m a r y

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A normal tree leaf is thought to be green (although sometimes reddish in the so-called "blood"-forms or yellowish in the so-called "aurea"-forms). That also stems can appear greenish or even green is not directly evident. Nevertheless, photosynthetic activity is to be measured in the cortical tissues of woody shrubs and trees. The chlorophyll-containing tissue within the stem is able to use the stem-internal CO_2 and the light penetrating the rhytidome to photoassimilate and produce sugars and starch. It is therefore of interest of how much light penetrates the bark of trees and how much carbon dioxide is necessary for a functioning photosynthesis and even more how sensitive this bark photosynthesis responds to acidic or otherwise contaminated rain or mist, soaking the bark of twigs and stems.

I n t r o d u c t i o n

At a certain stage in the life of a tree and at special occasions it is necessary and unavoidable to cessate leaf photosynthesis. This is evident in temperate zones during late autumn. Senescing deciduous and sometimes even coniferous (*Larix*) species get coloured leaves which are then shed within weeks or even days leaving the pure framework of the naked stem, branch and twig system. Analogous events may also occur even during the vegetation period when whole trees are defoliated by insect attacks (e.g. *Cheimatobia* (*Geometra*) *brumata* L.; Frostspanner). In this case the trees can sometimes re-foliate within several weeks if they are able to provide a new leaf generation by the so-called lammas shoot

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(German: Johannis-Trieb). Thirdly, partial defoliation can also occur by the action of high concentrations of air pollutants or heavy drought. In any case, the tree is left without leaves for a certain period. But this total removal of the chlorophyll-containing leaves does not mean a total collapse of the photosynthetic ability of the tree. Directly below the dead part of the outer bark (the rhytidome) a chlorophyll-containing tissue in the inner bark is located; this living tissue the so-called chlorenchyma is able to photosynthetize (LANGENFELD-HEYSER 1989, LARCHER & al. 1988, LARSEN 1939, PILARSKI 1995, NILSEN 1995, SCHAEDLE 1975, ZIEGLER 1957) and to supply sugars to the cortical cells even during fully leafless periods.

Material and Methods

Several tree species were used for the experiments. The different species and their growth conditions were described earlier PFANZ & al. 1998. Photosynthesis was measured using Clark type oxygen electrodes as described in PFANZ 1994 and PFANZ & al. 1998. A defined bark area was held by cutting out bark and chlorenchymal pieces with the use of a calibrated cork-borer and dry weight was determined by weighing the fresh weight, storing the pieces in an oven at 85°C for 36 h and re-weighing. Chlorophyll was extracted in DMSO according to RONEN & GALUN 1984.

Results and Discussion

To get an idea of the amount of chlorophyll found in tree barks, isolated chlorenchyma was extracted and chlorophyll was determined and calculated on a unit dry weight or surface area (Table 1) . In holly (*Ilex aquifolium*) the green bark has roughly 25-30% of the chlorophyll content of leaves when compared on a unit area (SCHMIDT personal commun.; for other species see also GUNDERSEN 1954, LARCHER & al. 1988, PILARSKI 1984, 1993, 1995).

Table 1. Chlorophyll contents of the chlorenchymous part of the bark of twigs of different trees during spring. The tissues had been separated mechanically, weighed and surface-determined; chlorophyll was extracted using DMSO. In this case, only the upper, sun-exposed parts of sun-twigs were analysed. The data are given in mg Chl g^{-1} dry matter or mg Chl cm^{-2} twig area.

Tree species	Surface-related chlorophyll content		Dry weight-related chlorophyll content	
	age of twig		age of twig	
	0- year-old	1-year-old	0- year-old	1-year-old
*Ilex aquifolium**	0.026	0.027	1.83	1.56
Fagus sylvatica	0.01	0.02	0.68	0.67
Betula pendula	0.01	0.02	0.51	0.73
Quercus robur	0.03	0.03	1.38	1.26

* unpublished data by J. SCHMIDT

Is there enough light and carbon dioxide within a stem to allow photosynthesis?

Up to 53% of the light that strikes the outer bark may pass the rhytidome to finally reach the chlorophyll-containing inner bark in 1-year-old twigs of beech; in birch it is only 47% and in poplar and rowan around 30%. The amount of light penetrating the outer bark decrease with increasing age of the twig (which is clearly correlated with bark thickness). This is on a first sight more than enough for a shade-adapted chloroplast for a suffcient photosynthesis.The availability of carbon dioxide might not be a limiting factor as the concentrations that have been measured with several techniques within the stems are in a percent range (up to 26%!; EKLUND 1990, MACDOUGAL & WORKING 1933, ZIEGLER 1957) and this may be rather inhibitory than limiting (cf. CO_2 inhibition of photosynthesis in PFANZ & al. 1998). As also the hydration state of the chlorenchymous cells seems to be nearly optimal, all prerequisites for a functionable photosynthesis are given.

Light response of green cortical cells

When photosynthesis was examined at increasing light regimes in most of the trees studied so far, nearly 1000 $\mu E\ m^{-2}\ s^{-1}$ PhAR were needed for obtaining maximum rates. It has to be mentioned again, that only the upper, sun-exposed sides of sun-twigs were used for the experiments. Results of the different parts and sides of a single twig and differences between shade and sun twig of different species will be published elsewhere.

Acid mist and acid rain effects on bark photosynthesis

To study the effects of potential pH-perturbances on the chlorenchyma brought about by pH-shifting agents and solutions (soaking the bark and permeating into the interior), chlorenchymal tissues were mechanically isolated from twigs and oxygen evolution was studied while pH was steadily varied. Table 2 shows that on a percentage scale cortical photosynthesis of three different tree species was reduced by 50% when pH was lowered to values around 3 or increased to values near 7.5 to 8. But even a pH-change of only pH 1 at both sides of the pH-optimum lead to a drop in photosynthetical activity by up to 30%, depending on the species concerned.

Table 2. Relative photosynthetic performance of bark photosynthesis of three different tree species. Values were obtained with peeled chlorenchyma in an oxygen electrode; twigs were harvested in June. Measurements were performed in buffered aqueous solutions with constant bicarbonate concentrations and a temperature of 20°C.

pH of incubation medium	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0
beech	15	29	74	100	73	41	11	0
aspen	21	48	68	100	98	80	18	0
birch	5	26	47	78	100	100	23	0

Photosynthetic response in the presence of sulfur dioxide, nitrogen oxide or hydrogen fluoride

Experiments were carried out with mechanically isolated chlorenchymal tissues that were incubated in solutions reflecting and simulating the apoplastic fluid (see PFANZ 1994) and different concentrations of air pollutants were added. The situation resembles the normal physical and chemical sequence of steps of the diffusional uptake of gaseous pollutants by tissues where after the diffusional air path, the passage is followed by a solution step and hydration and /or dissociation reactions of the compounds formed (cf PFANZ & HEBER 1989).

To demonstrate the importance of the dead cortical tissues (peridermal tissues), experiments were carried out in the absence or presence of the outer bark during the application of sulfur dioxide. In birch, in the absence of a shielding cortical cover, the amount of sulfur dioxide necessary to inhibit bark photosynthesis by 50% was nearly 10 times lower than in the presence of the shielding bark tissue (data not shown). The trees can thus endure SO_2-concentrations 10 times higher when shielded by a slightly permeable rhytidomal barrier than if directly exposed to the stressor. The probable reason is a reduction in the permeation velocity of the pollutant.

Conclusions

Chlorenchymal photosynthesis can be measured using mechanically isolated tissues. Quantitative calculations on the contribution of cortical photosynthesis on the overall carbon gain of a tree are presently not possible; they depend on the age of the twig, branch or stem, on the chlorophyll content, on the thickness of the overlaying dead bark tissues absorbing the necessary light, and the location of the organ (sun or shade twig), to mention only some.

Like leaf photosynthesis, bark photosynthesis seems to be also very sensitive to very acidic or alkaline solutions.

Similar to leaves, bark photosynthesis can be inhibited or even totally blocked in the presence of air pollutants (NO_2, HF, SO_2) or even CO_2.

Besides the protection of the chlorenchyma against light, high temperatures, fires, and pathogen attacks, the dead bark part is a very effective barrier to penetrating solutions (e.g. acid rain) and other pollutants.

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