Light-modulation of bark photosynthesis in birch (*Betula pendula* Roth.)

Christiane WITTMANN and Hardy PFANZ *

Institute of Applied Botany, University of Duisburg-Essen, FRG

*Corresponding address:
Univ.-Prof. Dr. H. Pfanz, Institut für Angewandte Botanik, Universität Essen, Universitätsstr. 5
D-45117 Essen; Tel.: 0201-183-2153; Fax: 0201-183-4219; e-mail: hardy.pfanz@uni-essen.de

Abstract. Bark photosynthesis has been shown to be an effective mechanism for stem-internal refixation of respiratory CO_2. In young birch trees (*Betula pendula* Roth.) this function is clearly modulated by the prevailing light intensity regime. Although positive net photosynthesis was not found in intact birch twigs, apparent twig respiration was reduced upon illumination by 65 % in high-light grown birches and even more in shade grown trees (81 %). Compared on a unit area basis the bark chlorenchyma contained up to 55% of the chlorophyll of the concomitant leaves when grown under 100 % sunlight and even 66 % when trees were grown under low-light (20 % of full sunlight). Light penetration through the periderm of birch twigs and branches is age-dependent and ranges in control trees from roughly 24 % of the incident sunlight in recent-year twigs to 1–3 % in 5-year-old main stems. Peridermal light transmittance was also changed by the light intensity regime. An additional light-reducing peridermal layer present in control trees was not found in shade-grown birches. It was shown that CO_2-refixation is not limited to the light-exposed outer parts of tree crowns. Our results show that also inner branches of trees are well adapted to function as a rather efficient system to prevent respiratory carbon loss.

Key words: *Betula*, bark photosynthesis, light intensity, carbon fluxes, CO_2-refixation

Introduction

In nearly all trees, woody shrubs and bushes chlorophyll-containing tissues can be found in the inner bark layers. These chlorenchymes are able to photosynthetically reduce the flux of respiratory CO_2 to the atmosphere and in parallel to evolve thylakoid-borne O_2 (PFANZ et al. 2002, PFANZ & ASCHAN 2000), a process that has been termed „CO_2-refixation" or alternatively „corticular photosynthesis" (SPRUGEL & BENECKE 1991, NILSEN 1995, PILARSKI 1995).

Plant productivity depends on the balance between photosynthetic carbon assimilation and the expenditure of fixed carbon by respiration (EDWARDS ET al. 1981, WARING & RUNNING 1998). Equivalent gains in whole plant carbon assimilation can be made by increasing the rate of carbon uptake from

the atmosphere (i.e by the stimulation of leaf photosynthesis) or by decreasing respiratory carbon losses (i.e through bark photosynthesis; CERNUSAK & MARSHALL 2000). In different deciduous trees (e.g. *Fagus sylvatica*, *Populus tremula*) stem-internal refixation of CO_2 in young twigs and branches may compensate for 60–90 % of the potential respiratory carbon loss (PILARSKI 1995, WITTMANN ET AL. 2001, ASCHAN ET AL. 2001). The light-driven stem-internal refixation of carbon dioxide may therefore be an important measure to optimize carbon fluxes at the whole-tree (or even whole-canopy) level.

Light is one of the major environmental factors regulating plant productivity. There is plenty of knowledge on the effects of different light on the carbon gain of leaves, but information on the light-dependency of bark photosynthesis or on the carbon budgets of twigs and branches is still scarce. To illuminate the influence of the light environment on the photosynthetic activity of the inner bark cells we grew young birch trees (6-year-old) in distinct light environments (20 % and 100 % of full sunlight) and studied the effectiveness and the probable adaptive light dependency of stem-internal carbon refixation as well as related morphological and cyto-chemical parameters.

Materials and Methods

Plant material
Six-years-old birch trees (*Betula pendula* L.) were grown outside in 20 l plastic containers under sufficient nutrition (Einheitserde Typ T, Balster, Germany) and water supply, realised by periodic fertilisation with Osmocote (Bayer, Germany) and daily irrigation. In early spring 1999, 20 trees were shaded with a tentlike construction, covered with a light-reducing net tissue (light permeability about 20 % of incident sunlight); the other cluster (control, 100 %) was exposed to natural sunlight conditions. The net structure of the shading tissue as well as the open front and back of the tent enabled permanent air circulation, avoiding overheating during hot summer days.

PFD transmittance
The quantity and quality of light (photon flux density ; PFD) transmitted through the peridermal layers of birch twigs were studied in 2001. According to PFANZ (1999) tissues were removed with a cork borer and placed for 5 min in isotonic solution. The wet bark samples were sandwiched between two microscopy slides and tightly adjusted over an opening in a black plastic plate towards a quantum sensor (model LI-190SA, Li-Cor) connected with a quantum radiometer (Li-250, Li-Cor, Lincoln, Neb., USA). PFD transmission was measured by illuminating it with a 100 W quartz halogen lamp (Xenophot HLX 64625, Osram, Germany) equipped with an infrared filter (NIR filter ST 931619/KB, Balzers, Lichtenstein) to avoid warming the samples and producing approximately 1000 µmol m^{-2} s^{-1} (see Pfanz 1999). Relative PFD transmission was calculated as a percentage of the incident PFD directly above the sample surface.

Photosynthetic pigment determination
Disks from leaves or from bark were removed by a calibrated cork borer (5 mm in diameter) and placed in 80 % (v/v) dimethyl sulfoxide (DMSO). Pigment extraction required approximately 2 h at 65°C in the dark. To avoid acidification and a concomitant phaeophytinisation of the chlorophylls, 20 mg $Mg_2(OH)_2CO_3$ was added. Finally, extract absorbances were measured with a spectrophotometer (UV 160, Shimadzu, Japan) and pigment contents calculated according to standard equations (Wellburn 1994).

Gas-exchange measurement

Photosynthetic performance of intact twigs and leaves was studied with a portable gas-exchange system (model LI-6400, Li-Cor Inc., Lincoln, USA). To avoid possible wound respiration only intact twig internodes or single mature leaves still attached to the twigs were selected for the gas-exchange measurements. Dark respiration was measured after a 30-min shading period of the respective plant parts within the cuvette. Subsequent light response curves were conducted under constant climatic conditions (20°C, 50-55% relative humidity) and a controlled CO_2 supply (350 ppm). High-irradiance CO_2–exchange rates were first measured after a 30-min period of light exposure to 2000 µmol photons $m^{-2} s^{-1}$. At least ten independent light response curves were assessed for each type of leaf or twig internode.

Curve fittings and calculations of all parameters were done using Sigma Plot 5.0 (SPSS Science Software). Light saturation of CO_2-assimilation was defined at 90% of maximum photosynthetic rate (e.g. von WILLERT ET AL. 1995). Stem internal CO_2-re-fixation rates were calculated as the difference between high-irradiance maximum CO_2-exchange rate and dark respiration.

Results and Discussion

PFD transmittance

Transmittance of light (qualitatively and quantitatively) through the periderm clearly depends on thickness, cellular structure and optical properties of the outer bark layers (VOGELMANN 1993, PFANZ & ASCHAN 2000). With advancing age of the twigs the thickness of the peridermal layers increases; as a result peridermal PFD transmission is reduced.

Light penetration through the periderm of birch twigs ranged from ca. 24 % in recent-year twigs to 1-3 % in 5-year-old main stems. Growth under limiting light conditions greatly influenced peridermal PFD transmittance. A normally formed additional peridermal layer was not found under low light growth conditions. Thus, the peridermal layers of birch twigs permit a relatively higher light flux under shaded conditions.

Pigment content

Compared on a unit area basis the bark chlorenchyma contained up to 55 % of the chlorophyll content of concomitant leaves in high-light grown trees and even 66 % in trees grown under low-light conditions. It is well known that shade-leaves optimise the effectiveness of light absorption by an increased pigment density per unit leaf area and this strategy holds also for twigs.

The chlorophyll a/b ratio in birch chlorenchyma ranged between 2.1 and 2.7. These results are in good agreement with those described for other deciduous species, such as *Fagus sylvatica* (1.8, LARCHER ET AL. 1988), *Populus tremuloides* (2.7, KHAROUK ET AL. 1955), *Syringa vulgaris* (PILARSKI 1999), and *Betula pendula* (KAUPPI 1991). In general, shade adapted cells within a leaf have a lower chlorophyll a/b ratio than cells adapted to high light (e.g. LICHTENTHALER ET AL. 1981, ANDERSON &

OSMOND 1987; THERASHIMA & HIKOSAKA 1995). The lower chlorophyll a/b ratio of the bark chlorenchyma (as compared to the leaves) is easily explained by the hidden location behind the cork layers.

Table 1: Cardinal points of the light response curves of *Betula pendula* twigs cultivated under different growth light regimes (n = 10; +/- SD)

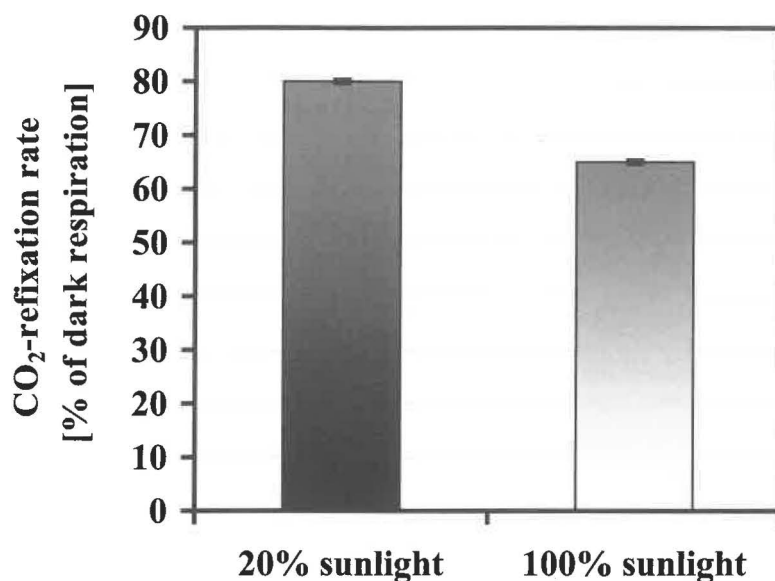| relative light during cultivation [% sunlight]	20 %	100 %
Age of the twig organ	current-year	current-year
max. net photosynthesis rate [μmol CO_2 m^{-2} s^{-1}]	-0.27 ± 0.05	-0.98 ± 0.12
stem-internal photosynthesis [1] [μmol CO_2 m^{-2} s^{-1}]	1.07 ± 0.05	1.79 ± 0.12
saturated PFD [2] [μmol photons m^{-2} s^{-1}]	250	339
dark respiration rate [μmol CO_2 m^{-2} s^{-1}]	-1.34 ± 0.04	-2.77 ± 0.10
Age of the twig organ	1-year-old	1-year-old
max. net photosynthesis rate [μmol CO_2 m^{-2} s^{-1}]	-0.16 ± 0.04	-0.44 ± 0.10
stem-internal photosynthesis [1] [μmol CO_2 m^{-2} s^{-1}]	0.69 ± 0.04	0.98 ± 0.10
saturated PFD [2] [μmol photons m^{-2} s^{-1}]	250	334
dark respiration rate [μmol CO_2 m^{-2} s^{-1}]	-0.85 ± 0.04	-1.42 ± 0.09

[1] stem-internal or "hidden" photosynthesis (Wittmann et al. 2001) was calculated as the difference between high-irradiance maximum CO_2-exchange rate and dark respiration.

[2] saturated PFD [μmol photons m^{-2} s^{-1}] was defined at 90 % of maximum photosynthetic rate (e.g. von Willert et al. 1995); calculations were done using Sigma Plot 5.0 (SPSS Science Software).

CO_2-exchange of twigs and leaves

Birches revealed typical hyperbolic light response curves for both, mature leaves and intact twig segments.

The measured cardinal points of the light response curves of leaf and twig photosynthesis are given in Tab. 1. Besides changes in net photosynthetic rates and apparent dark respiration, distinct changes in stem-internal photosynthesis were observed (cf. WITTMANN ET AL. 2001). Stem-internal CO_2-refixation was calculated as the difference between the maximum CO_2-fixation rate and dark respiration. Furthermore, the light saturation of twig photosynthesis clearly differed, being around 340 μmol photons m^{-2} s^{-1} in high-light-grown twigs and 250 μmol photons m^{-2} s^{-1} in the shade-grown variant (Tab.1). According to LARCHER ET AL. (1994), light saturation of deciduous shade leaves is around 200–500 μE m^{-2} s^{-1}; cortical photosynthesis is thus performed by extremly shade adapted chloroplasts (as indicated above by the low chl a/b ratios). This fact is even more corroborated when photosynthesis of chloroplasts of the tree's pith or wood is studied (PFANZ ET AL. 2002).

Figure 1: CO_2-refixation rates of *Betula pendula* twigs (current- and 1-year-old) cultivated under different light intensity regimes (means with SE, n = 10).

Preliminary calculations revealed that in birch grown under full sunlight around 65 % of the respired CO_2 can be refixed within the twigs. With 81 % corticular photosynthesis is even more pronounced under shaded conditions (Fig.1).

Conclusions

Although twig and branch photosynthesis rarely result in positive net CO_2-fixation, quite a high portion of the respired mitochondrial carbon dioxide is immediately re-used within the tree skeleton and thus contributes substantially to the overall carbon balance and productivity of trees. In young twigs of tree crowns the respiratory CO_2 losses are more efficiently reduced than in older branch parts. Yet, CO_2-refixation is not restricted to the light-exposed outer parts of the canopy. Our results show that the light use efficiency of inner branches is relatively higher. More morphometrical data are needed to elucidate the quantitative effect of bark photosynthesis on the C-budget of trees.

Acknowledgements

Literature

ANDERSON J.M., OSMOND C.B. 1987: Shade-sun responses: compromises between acclimation and photoinhibition. In: Kyle D.J., Osmond C.B., Arntzen C.J. (eds.) Photoinhibition. Elsevier, Amsterdam, pp 1–38.

ASCHAN G., WITTMANN C., PFANZ H. 2001: Age-dependent bark photosynthesis of aspen twigs. Trees 15: 431–437.

CERNUSAK L.A., MARSHALL J.D. 2000: Photosynthetic refixation in branches of western white pine. Funct. Ecol. 14: 300–311.

KAUPPI A. 1991: Seasonal fluctuations in chlorophyll content in birch stems with special reference to bark thickness and light transmission, a comparison between sprouts and seedlings. Flora 185: 107–125.

KHAROUK V.I., MIDDLETON E.M., SPENCER S.L., ROCK B.N., WILLIAMS D.L. 1995: Aspen bark photosynthesis and ist significance to remote sensing and carbon budget estimate in the boreal ecosystem. Water Air Soil Pollut. 82: 483–497.

LARCHER W. 1994: Ökophysiologie der Pflanzen: Leben, Leistung und Stressbewältigung der Pflanzen in ihrer Umwelt. 5th edn. Ulmer, Stuttgart, Germany.

LARCHER W., LÜTZ C., NAGELE M., BODNER M. 1988: Photosynthetic functioning and ultrastructure od chloroplasts in stem tissue of *Fagus sylvatica*. J. Plant. Physiol. 132: 731–737.

LICHTENTHALER H.K., BUSCHMANN C., DÖLL M., FIETZ H.-J., BACH T., KOZEL U., MEIER D., RAHMSDORF U. 1981: Photosynthetic activity, chloroplast ultrastructure, and leaf characteristics of high-light and low-light plants and of sun and shade leaves. Photosynthesis Res. 2: 115–41.

NILSEN E.T. 1995: Stem photosynthesis - extent, patterns and role in plant carbon economy. In: Gartner B. (ed.) Plant stems: physiology and functional morphology. Academic Press, San Diego, pp. 223–240.

PFANZ H. 1999: Photosynthetic performance of twigs and stems of trees with and without stress. Phyton 39: 29–33.

PFANZ H., ASCHAN G. 2000: The existence of bark and stem photosynthesis and its significance for the overall carbon gain: an eco-physiological and ecological approach. Progress in Botany 62: 477–510.

PFANZ H., ASCHAN G., LANGENFELD-HEYSER R., WITTMANN C., LOOSE M. 2002: Ecology and ecophysiology of tree stems – corticular and wood photosynthesis. Naturwissenschaften 89, 147–162.

PILARSKI J. 1995: Participation of stems and leaves in photosynthetic assimilation of CO_2 in lilac (*Syringa vulgaris* L.). Photosynthetica 31: 585–592.

PILARSKI J. 1999: Gradient of photosynthetic pigments in the bark and leaves of lilac (*Syringa vulgaris* L.). Acta Physiologicae Plantarum 21: 365–373.

SPRUGEL D.G., BENECKE U. 1991: Measuring woody-tissue respiration and photosynthesis. In: LASSOIE J.P., HINCKLEY T.M. (eds.) Techniques and approaches in forest tree ecophysiology. CRC, Boca Raton, pp. 329–355.

TERASHIMA I., HIKOSAKA K. 1995: Comparative ecophysiology of leaf and canopy photosynthesis. Plant Cell Environ 18: 1111–1128.

VOGELMANN 1993: Plant tissue optics. Annu. Rev. Plant Physiol. Mol. Biol. 44: 231–251.

WARING R.H. & RUNNING S.W. 1998: Forest Ecosystems: Analysis at multiple scales. Academic Press, San Diego, CA.

WELLBURN A.R. 1994: The spectral determination of chlorophylls *a* and *b*, as well as total carotenoids, using various solvents with spectrophotometers of different resolution. J. Plant. Physiol. 144: 307–313.

WITTMANN C., ASCHAN G., PFANZ H. 2001: Leaf and twig photosynthesis of young beech (*Fagus sylvatica*) and aspen (*Populus tremula*) trees grown under different light intensity regimes. Basic Appl. Ecol. 2: 145–154.

VON WILLERT D.J., MATYSSEK R., HERPPICH W. 1995: Experimentelle Pflanzenökologie. – Georg Thieme Verlag, Stuttgart, New York.