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REVIEW ARTICLE

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Ecology and ecophysiology of tree stems: corticular and wood photosynthesis

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Abstract Below the outer peridermal or rhytidomal layers, most stems of woody plants possess greenish tissues. These chlorophyll-containing tissues (the chlorenchymes) within the stems are able to use the stem internal CO_2 and the light penetrating the rhytidome to photoassimilate and produce sugars and starch. Although net photosynthetic uptake of CO_2 is rarely found, stem internal re-fixation of CO_2 in young twigs and branches may compensate for 60–90% of the potential respiratory carbon loss. Isolated chlorenchymal tissues reveal rather high rates of net photosynthesis (being up to 75% of the respective rates for leaf photosynthesis). Corticular photosynthesis is thus thought to be an effective mechanism for recapturing respiratory carbon dioxide before it diffuses out of the stem. Furthermore, chloroplasts of the proper wood or pith fraction also take part in stem internal photosynthesis. Although there has been no strong experimental evidence until now, we suggest that the oxygen evolved during wood or pith photosynthesis may play a decisive role in avoiding/reducing stem internal anaerobiosis.

Introduction

It is well accepted that green leaves are not the only plant organs capable of photo-reducing carbon dioxide. Photosynthesis can be measured in petioles, green flowers, calyces, green fruits, cones, stem tissues and even roots. There is no doubt that photosynthesis of green tissues other than the leaf mesophyll will positively contribute to the overall carbon budget of plants (Weiss et al. 1988; Blanke and Lenz 1989; Hetherington 1997). It is not only herbaceous or gramineous plants which have special greenish tissues; woody species also contain chlorophyll in several plant parts.

During evolution, developing land plants had to face several new problems. The reduction of potential water loss by evapotranspiration and the stabilisation of the upright plant body were the main tasks. The stem evolved to move, hold and support the assimilating tissues in a proper position towards the light. Formerly green cauloids thus ‘changed their colour’ to become brown stems (branches, twigs) because of a changing functional necessity. Although the formerly outer subepidermal chlorenchymes changed their anatomical position (possibly constrained by other tissues), they did not necessarily fully disappear. In most woody species, the outer tissue layers of twigs, branches or stems reveal greenish bark sub-layers (Fig. 1a). C_3 stem photosynthesis (or CAM stem photosynthesis) have been well described separately from corticular photosynthesis (Nilsen 1995).

During unfavourable periods, leaves of woody plants are often shed episodically or transiently to leave a fully leafless stem/branch skeleton. In autumn, in northern temperate zones, decreasing temperature (which often means dry air) and longer nights initiate leaf senescence and abscission in deciduous trees and shrubs. Pests (for instance, phytophagous insects) or fungal (or bacterial/viral) diseases can also lead to a total defoliation of trees. However, defoliation does not necessarily lead to the final death of the tree. Storage carbohydrates, and probably the participation of bark photosynthesis, bridge the phases until leaves have re-developed within the same (lammas shoot, dormant buds) or the next vegetative period. Even during periods when there is a well developed leaf biomass, the chlorenchyma-containing stem segments are able to contribute to the carbon (and oxygen) cycles within a tree.

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Fig. 1 **a** *Sambucus nigra* with peeled peridermal layers to show bark chlorenchyma (*upper part*) and additionally with peeled inner bark to show proper wood (*lower part*); **b** cut twig of *Fraxinus excelsior* showing chlorenchymal bark layer and cylindrical perimedullar halo around pith; **c** chlorenchyma below the peridermal layer of newly formed wound callus in *Quercus ilex*; **d** *Platanus* spp. with rhytidomal islands of different colour and thickness. All photographs by H. Pfanz

Prerequisites for corticular photosynthesis

As bark photosynthesis follows the same rules as leaf photosynthesis, several prerequisites are necessary for a working reductive CO_2 assimilation metabolism. Besides an effective chloroplast structure (Kriedemann and Buttrose 1971; Ames and Tepper 1978; Larcher et al. 1988; Langenfeld-Heyser et al. 1996; see also the section on chloroplast ultrastructure) and the obligatory enzymatic equipment, nutrients, water, light and carbon dioxide are essential to drive photosynthetic carbon reduction. In the following it will be demonstrated that all these factors are present in sufficient amounts and quantities within the chlorenchymal bark tissues of trees.

Chloroplasts and pigments

Chlorophyll inside the stems

The first scientific observations regarding the existence of green bark tissues were published around 1900

Table 1 Chlorophyll contents of stripped bark layers of sun-exposed twigs of deciduous and coniferous trees. Chlorophyll was determined during spring where, due to active growth, the tissue could be peeled directly at the vascular cambium. Numbers in brackets indicate the age of the twigs in years. Area, and dry and fresh-weight relations are given (all data from H. Pfanz, unpublished results)

Tree species	Chlorophyll per unit bark area (mg chl m^{-2})	Chlorophyll per bark fresh weight (mg chl g^{-1} FW)	Chlorophyll per bark dry weight (mg chl g^{-1} DW)
Acer campestre (1–5)	200	0.64–1.49	1.04–0.54
Acer platanoides (1–3)	300	1.79–2.78	0.81–0.66
Acer pseudo-platanus (1–3)	300–400	1.80–2.84	0.87–1.01
Aesculus hippocastanum (1–3)	189–220	1.15–2.03	0.45–0.38
Betula pendula (1–5)	120–237	0.27–1.36	0.51–0.68
Fagus sylvatica (1–3)	100–200	0.39–0.87	0.68–0.64
Fraxinus excelsior (1–3)	500	3.10–3.73	1.38–1.17
Populus tremula (1–3)	332–456	1.36–2.06	0.99–1.17
Quercus robur (1–5)	310–524	0.59–3.97	1.38–0.86
Salix fragilis (1–2)	300	1.26–2.16	0.94–0.96
Sambucus nigra (1)	300	0.96	1.85
Sorbus aucuparia (1–5)	300–500	3.24–3.92	0.76–0.89
Tilia platyphyllos (1–4)	200–300	1.30–2.85	0.56–0.46
Ulmus glabra (1–2)	300	1.95–1.73	1.89–1.23
U. laevis (1–4)	100	0.12–0.81	0.50–0.37
Larix decidua (1–5)	190–434	0.89–6.12	0.41–0.60
Picea abies (1–4)	180–270	0.19–2.40	0.43–0.53
P. pungens (1–3)	211–300	1.73–2.80	0.56–0.45
Pinus nigra (1–4)	140–323	1.17–2.61	0.16–0.13

(Moeller 1882; Ross 1887; Schneider 1903; Cannon 1905, 1908; Scott 1907).

Stem chlorophyll (chl) contents range from 130 mg chl m^{-2} in young twigs of beech (*Fagus sylvatica*) up to 500 mg chl m^{-2} in ash and oak (Table 1). Clearly, chlorophyll content depends on the age of the stem organ and on its exposure to light (Pearson and Lawrence 1958). The sun-exposed upper sides of twigs and branches greatly differ in their content from shaded parts that are hidden deeply in the tree crowns. In experiments with the Eurasian trembling aspen (*Populus tremula*), 1- and 2-year-old twigs had 160 mg chl m^{-2} or 230 mg chl m^{-2}, respectively, when trees were grown under full sunlight and 180 and 430 mg chl m^{-2}, respectively, when trees were kept at 20% of full sunlight (Wittmann et al. 2001). Chlorophyll *a*/*b* ratios in bark tissues range between 1.8 (beech: Larcher et al. 1988) and 2.7 (aspen: Kharouk et al. 1995). Chlorophyll levels showed distinct variation during the leafless season (Kauppi 1991; Schulz 1992). The chlorophyll *a*/*b* ratio in beech varied only slightly with age, ranging from 2.38 in young twigs to 2.24 in 14-year-old twigs (Meyer 1990). These low values resemble those of shade-adapted leaves.

Interestingly, area-related chlorophyll contents of younger twigs can be 50–70% and even more of the contents of adjacent leaves (cf. Table 1 and Pilarski 1984; Kharouk et al. 1995; Solhaug et al. 1995; Schmidt et al. 2000). According to Kharouk et al. (1995) the bark of young aspen contains up to 42% of the total tree chlorophyll.

Coniferous trees also possess chlorenchymal tissues in young twigs and branches (Langenfeld-Heyser 1987; Stärke 1990) and green subcortical layers can be found in evergreens from the subtropical and tropical regions (Table 1; and see Muthuchelian 1992).

When chlorophyll contents of *Fagus* twigs are compared on twig fresh weight (fwt) basis or on the volume of the twig organ, an age-dependent decrease is found with increasing age. Starting with values around 233 µg chl *a* g^{-1}fwt (105 µg chl *b* g^{-1} fwt) in the bark of young twigs, the content decreased gradually to reach around 168 µg chl *a* g^{-1} fwt (70 µg chl *b* g^{-1} fwt) in the bark of 10-year-old twigs. Nevertheless, even in 15 year-old twigs chlorophyll can still be found (Meyer 1990; see also Pfanz and Aschan 2000 for 150-year-old beeches). On a unit surface area, however, bark chlorophyll of beech twigs increased with age; starting from 10 µg chl *a* cm^{-2} (5 µg chl *b* cm^{-2}) in newly formed twigs and increasing to 20 µg chl *a* cm^{-2} (10 µg chl *b* cm^{-2}) in 14-year-old twigs (R. Langenfeld-Heyser et al., unpublished results). In beech twigs the age-dependent decrease in chlorophyll content (on fresh weight or volume basis) in the wood is much steeper than in the bark (Meyer 1990); from 85 µg chl *a* g^{-1} fwt (40 µg chl *b* g^{-1} fwt) in the wood of young twigs it decreased to about 10 µg chl *a* g^{-1} fwt (6 µg chl *b* g^{-1} fwt) in the wood of 10-year-old twigs. When compared on a unit surface area basis, leaves normally have 2–3 times higher chlorophyll contents than twigs, but younger twigs can reach up to 70% of the chlorophyll content of the concomitant leaves (Pilarski 1984; Kharouk et al. 1995; Solhaug et al. 1995; Pfanz and Aschan 2000; Schmidt et al. 2000).

Interestingly, chlorophyll is not only found in the outer layers of stems. Although deeply buried in the centre of twigs and branches, wood and pith tissues may also contain functional chloroplasts (see van Cleve 1993; see also Fig. 1b). The chlorophyll concentrations found in the wood fractions of trees ranged from 25 to 212 µg g^{-1} fresh matter, or from 14–40 mg m^{-2} (bark) surface area (Table 2).

Table 2 Fresh-weight or surface-area related total chlorophyll contents of the wood fraction of different central-European trees (data from Meyer 1990; Schulz 1992; H. Pfanz, unpublished results)

Tree species	Chlorophyll per unit bark area (mg chl m^{-2})	Chlorophyll per bark fresh weight (mg chl g^{-1} FW)
Acer campestre	n.d	55–141
Acer platanoides	n.d	25–110
Acer pseudoplatanus	n.d	91–160
Cornus mas	35–40	
Fagus sylvatica	35–50	159–212
Populus tremula	18–14	
Quercus petraea	24–28	74–91

Chloroplast ultrastructure

The number of chloroplasts per cell is highest in the outer fraction (80 µm) of the stem cortex (*Euonymus europaeus*: Szujko-Lacza et al. 1971); it fairly abruptly decreases with depth, leaving only a few chloroplasts per cell in the phloem area (*Populus tremuloides*: Schaedle et al. 1968).

The chloroplast ultrastructure of the outer stem cortex chlorenchyma resembles that of shade leaves to a large extent (*Euonymus europaeus*: Szujko-Lacza et al. 1971; *Populus deltoides*: Ames and Tepper 1978; *Cercidium floridum*: Price 1969; *Fouquieria splendens*: Nedoff et al. 1985; *Fagus sylvatica*: Larcher et al. 1988; *Picea abies*: Langenfeld-Heyser and Ebrahim-Nesbat 1991). Sun-type leaf chloroplasts contain many plastoglobuli, whereas shade-type chloroplasts of leaves show only few plastoglobuli (Lichtenthaler and Meier 1984). Chloroplasts of outer stem cortex chlorenchyma, however, show a considerable number of plastoglobuli (*Fraxinus excelsior*: Fig. 2a; *Picea abies*: R. Langenfeld-Heyser and F. Ebrahim-Nesbat, unpublished results; *Fagus sylvatica*: Larcher et al. 1988).

In several tree species, chloroplasts with grana thylakoids were not only reported in the cortex but also in deeper stem tissues such as ray cells, the perimedullary region and pith. In *Fagus sylvatica* stems, Larcher et al. (1988) could not find ultrastructural differences in chloroplasts from cortex, wood and pith. However, a gradient of ultrastructure from outer stem chloroplasts to those of the pith was observed in *Taxus baccata* (Buns et al. 1993), *Picea abies* (Langenfeld-Heyser and Ebrahim-Nesbat 1991) and *Fraxinus excelsior* (R. Langenfeld-Heyser, unpublished results; Fig. 2a–c). In *Fraxinus excelsior*, height and density of grana stacks increases from phelloderm to collenchymatous outer cortex (Fig. 2a) and then diminishes towards the middle (Fig. 2b) and inner cortex chlorenchyma and the wood. Grana stacks become broader with tissue depth. This is also shown by the electron micrographs of chloroplasts of different stem tissues of *Fagus sylvatica* L. published by Larcher et al. (1988). In the perimedullary region of young *Fraxinus excelsior* stems (Fig. 2c) chloroplasts show slightly more and higher grana stacks than those of the wood rays. In *Taxus baccata* (Buns et al. 1993) and *Vitis vinifera* (Kriedemann and Buttrose 1971), plastids of the pith or perimedullary region show only stacking of stromal thylakoid sheets.

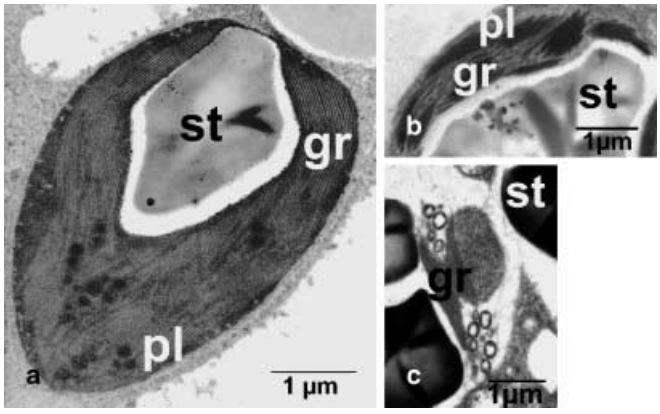

Fig. 2 **a** Ultrastructure of a chloroplast from the collenchymatous outer cortex chlorenchyma (near phelloderm) of a 1-year-old *Fraxinus excelsior* L. stem in midsummer. Note the high density and height of the grana stacks. The starch covers between one-quarter and one-third of the cross-sectional plane of the chloroplast. The chloroplasts show an extremely negative staining effect which has already been described for outer stem chloroplasts of *Fagus sylvatica* (Larcher et al. 1988); this often occurs in tissues containing tannins in vacuoles (Olesen 1978); *marker bar* 1 µm. **b** Ultrastructure of a chloroplast from thin-walled middle cortex chlorenchyma of a 1-year-old *Fraxinus excelsior* L. stem in midsummer. Density and height of the grana stacks are lower than in the outer cortex (see Fig. 2a). Starch grain covers only about six-seventh to seven-eighths of the cross-sectional plane of the chloroplast; *marker bar* 1 µm. **c** Ultrastructure of a chloroplast from the perimedullary region of a 1-year-old *Fraxinus excelsior* L. stem in midsummer. Starch covers most of the cross-sectional plane of the amylo-chloroplast. However, a few grana stacks of considerable height can be detected; *marker bar* 1µm. Starch (*st*), granum (*gr*), plastoglobulus (*pl*). All photographs by R. Langenfeld-Heyser

In young stems of *Fraxinus excelsior* L. (R. Langenfeld-Heyser, unpublished results) and *Picea abies* (Langenfeld-Heyser and Ebrahim-Nesbat 1991) there is an anti-parallel gradient in size of starch grains from cortex to pith, the size of the starch grains increasing from outer cortex to the wood. Such a gradient in size of starch grains has also been observed in young stems of *Populus tremuloides* (Ames and Tepper 1978), *Euonymus europaeus* (Szujko-Lacza et al. 1971), *Fouquieria splendens* (Nedoff et al. 1985) and stems of nonsucculent green-stemmed dicotyledoneous desert perennials (Gibson 1983; Nobuchi and Harada 1985).

Unlike the stem cortex chloroplasts described above, shade-type chloroplasts of leaves contain little or no starch, in contrast to sun-type chloroplasts of leaves

where large starch grains are observed (Lichtenthaler and Meier 1984). Hardly any starch was detected in cortex chloroplasts of young stems of small diameter from *Cercidium floridum* (Adams and Strain 1969; Price 1969); here starch deposition begins with a stem diameter of 6–10 mm. As thylakoid frequency and stacking degree in cortex chloroplasts resemble that of shade leaves, we assume that starch in stem chlorenchyma, especially of chlorenchyma cells situated deeper in the stem interior, could derive from radial transport of leaf assimilates and/or assimilates from the outer cortex chlorenchyma cells (Nelson and Dickson 1981; Langenfeld-Heyser 1987, 1989). As chloroplasts and leucoplasts are evolutionarily seen as two 'varieties' (with gradual transitions) of the same procaryotic origin, varying extents of starch formation and storage in bark chloroplasts appear plausible.

Both gradients – density and height of grana stacks and size of starch grains – indicate a higher photosynthetic capacity in phelloderm and outer cortex than in the chloroplasts of more inwardly situated cells. This has already been verified by microautoradiographic studies with stem slices of *Picea abies* (Langenfeld-Heyser 1989). Despite the chloroplast ultrastructure and starch grain size, photosynthetic activity of chloroplasts in wood and pith has been demonstrated by several methods (^{14}C uptake: Wiebe et al. 1974; Wiebe 1975; chlorofluorometric measurement: *Fagus sylvatica*, Larcher et al. 1988; Larcher and Nagele 1992; microautoradiography: *Picea abies*, Langenfeld-Heyser 1989; immunocytochemistry: *Taxus baccata*, Buns et al. 1993 and *Populus* × *canadensis*, van Cleve et. al. 1993; polarography: several species, Pfanz and Aschan 2000).

Principles and pathways of light penetration

The chlorenchymal tissue of the stem bark is hidden behind epidermal, peridermal or even rhytidomal layers. For photosynthesis to occur, enough photosynthetically active radiation has to pass through these layers to reach the light-harvesting complexes in the thylakoid membranes of the chlorenchymal chloroplasts. It is likely that light transmission through the living epidermal cells of green stems is higher than through the dead periderm or rhytidome. Gibson (1983) found in green-stemmed non-succulent perennial dicotyledoneous plants of North American deserts a chlorenchyma of consistently 80–150 µm depth, mostly with palisade-like chlorenchyma cells directly beneath the epidermis; the thickness of the chlorenchyma is assumed to be correlated to light transmission. Light transmission by the periderm varies, depending on the tree species and the age of the stem. In young stems, peridermal transmission of 5–15% has been reported (*Atriplex confertifolia*: Wiebe et al. 1974; *Populus tremuloides*: Strain and Johnson 1963; *Betula pubescens*: Kauppi 1991); light transmission through the phellem of 1-year-old twigs was 10% (*Fraxinus ornus*: Szujko-Lacza et al. 1970), 50% (*Fraxinus excelsior*: R. Langenfeld-Heyser, unpublished results) or even 60% (*Quercus pubescens*: Szujko-Lacza et al. 1970). Light transmission through the phellem decreases with the age of the stem (*Fraxinus ornus*: 1 year – 10%, 55 years – 1%; *Quercus pubescens*: 1 year – 60%, 10 years – 3%, 13 years – 0%, Szujko-Lacza et al. 1970; *Betula pubescens*: 1 year – 20% 665 nm light, 20 years – 9% 665 nm light, Kauppi 1991). It can be assumed that light transmission depends on the species-specific thickness and cellular composition of the outer bark, its internal and external coloration, its surface structure and its wettability. As a rule, the older the bark, the higher the absorption and/or reflection of the penetrating light, the lower the transmitted portion (Kharouk et al. 1995; Pfanz and Aschan 2000; for an exception see Aschan et al. 2001).

A moist outer bark shows a higher light transmission than a dry one (Solhaug et al. 1995). Epiphytic cryptogams inhabiting the surface of the bark reduce light transmission through the phellem or rhytidome; a cover of crustose *Lecanora* lichens reduced transmission through the phellem of *Populus tremula* stems from 35–55% to 10% of incident radiation (Solhaug et al. 1995).

Light can pass directly through the peridermal or rhytidomal layer; the thicker these layers, the lower the light transmitted. However, sunlight can also use natural openings in the outer bark, the lenticels (or in younger stems even the stomata) (Langenfeld-Heyser et. al. 1996; Langenfeld-Heyser 1997). A third entrance for light into the stem are bark valleys or cracks; e.g. in 7-year-old stems of *Fouquieria splendens*, light transmission through the phellem of the leaf base was zero whereas transmission through the furrow cork was still 40% (Nedoff et al. 1985).

Photon flux density is not equally reduced at all wavelengths. Selective absorption of different wavelengths is due to different colours of the outer bark layers and the penetration behaviour of the different wavelengths. In general, the longer the wavelength (e.g. red light), and thus the lower the inherent energy, the better the light is transmitted through the bark. Within the photosynthetically active radiation, blue light is highly absorbed in the outer bark fractions whereas red light penetrates much further (see Kharouk et al. 1995; Solhaug et al. 1995; Pfanz and Aschan 2000). In *Betula pubescens*, transmission of red light of 725 nm was better than that of 665 nm (Kauppi 1991).

Interestingly, light penetration is not stopped at the inner bark level. Some light penetrates even further to reach the wood or even the pith fraction within twigs and branches. However, light intensities reaching the wood are not high; maximal values of 0.2–5% of incident light have been measured (Wiebe et al. 1974; Pfanz and Aschan 2000). For *Atriplex confertifolia* stems of 6 mm diameter, light transmission to different depths of the stem interior was measured (Wiebe et al. 1974): 5–1% passed the periderm and outer bark parts, 1–0.2% passed through phellem and cortex chlorenchyma, 0.2–0.01% reached the outer xylem and none reached the centre of

the stem. In 1-year-old *Fraxinus excelsior* stems of 6 mm diameter, 50% of the incident photosynthetically active red light (665 nm) passed the periderm, 33% passed the periderm plus outer cortex chlorenchyma, 6% reached the phloem, 2% reached the cambium and 0.4% the pith [R. Langenfeld-Heyser, unpublished results: measurement with a cooled slow scan CCD (charge-coupled device) camera]. Red light (665 nm) attentuation is highest in cortex chlorenchyma, the tissue with the highest density of chlorenchyma cells and the most elaborate chloroplasts (Fig. 2a, b); it is assumed that most of the 665 nm light is absorbed there for photosynthesis. In *Fagus sylvatica* stems of different age and diameter, transmission of 665 nm light reaching the pith was measured with a cooled slow scan CCD camera with exposure times greater than 30 s. To the centre of a 1-year-old stem (radius 2.3 mm) about 0.01% of the incident red light (660 nm) was radially passed, to the centre of a 5-year-old stem (radius 6.8 mm) about 0.000003%, and to the centre of a 16-year-old stem (30 mm radius) only about 10^{-8}%. Transmission of far-red light (735 nm) was 10 times higher (R. Langenfeld-Heyser, unpublished results).

Carbon dioxide – the necessary substrate of corticular photosynthesis

Within a stem the parenchyma cells of the living bark, the ray cells inside the wood and the tissue of the pith are actively respiring in order to keep up with the tree's vital need for energy. Respiration leads to the liberation of CO_2, which normally leaves the plant body following the concentration gradient as described by Fick's law of diffusion. The outer bark layers of the stems consist of peridermal or rhytidomal tissues with a rather low permeability to gaseous diffusion (Waisel 1995; for anatomical details see Pfanz and Aschan 2000). As a consequence, CO_2 accumulates inside the stems, reaching concentrations that are rather high compared with those of other plant organs. Published values for CO_2 concentrations in the intercellular air spaces vary considerably, but are without exception in the percentage range (1–26%: see McDougal and Working 1933; Jensen 1969; Carrodus and Triffett 1975; Pfanz and Aschan 2000) and are thus 500–800 times higher than in ordinary plant organs or ambient air. So, in contrast to normal leaf photosynthesis, CO_2 is not a minor factor but eventually becomes a potential acidification threat to respiring or photosynthesising cells (Wagner 1990; Pfanz 1994).

Stem internal CO_2 concentrations are not constant and may change diurnally and with the time of year. In *Picea abies* CO_2 ranges from below 1% in spring to 10% in early summer (Eklund 1990). In addition, oxygen varies, being low around midsummer (5%) and increasing until autumn to reach atmospheric concentrations (21%) (Ziegler 1957; Carrodus and Triffett 1975; Levy et al. 1999). The stem internal variation in CO_2 may also be influenced by the flow velocity of the xylem sap, which in turn may exert an effect on leaf photosynthesis and/or respiration.

Nano-climate inside the stem

Besides being a protective barrier against pathogens, the bark of trees is also a perfect shield for extremes in irradiance, temperature and forest fires (cf. also pyrophytes: Gill 1995). Furthermore, the outer bark also plays a predominant role in the conduction of lightning (Stahl 1912).

The bark temperature regime

The temperature regime of outer tissues of stems is mainly influenced by environmental factors such as air temperature, solar irradiance, wind velocity, water vapour pressure deficit as well as site-specific conditions (e.g. exposure, height above ground, trunk diameter) and bark properties [e.g. water content, structure, boundary layer conductance, colour (Huber 1935; Aichele 1950; Lieberum 1961; Nicolai 1986)].

The high heat-insulating ability of barks can be demonstrated by the sharp drops in temperature occurring below their surfaces (e.g. Costa et al. 1991); this is caused by the tiny air spaces in the cork cell tissue (Cooke 1948). The influence of air temperature on bark and stem temperatures increases with decreasing trunk diameter; e.g. in small twigs or slender stems it is much higher than in older, thicker trunks.

In a trunk with a diameter of 13.5 cm, the winter bark temperature on the sun-exposed south side can reach 20–35°C above ambient (0 to –5°C: Sakai 1966). Kiese (1972) measured only slightly higher bark temperatures (2–3°C) for beech stems within a closed stand. Higher bark surface temperatures only occurred near the soil level, where heat transfer is reduced due to a lowered air movement. However, for a sun-exposed beech tree at an artificially created forest edge, Nicolai (1986) reported a strong bark overheating of about 15°C above the air temperature in spring. Furthermore, species with smooth barks show strong overheating indicated by high cambial temperatures that may reach up to 40°C. On days with high solar irradiance, exposed individuals (e.g. *Fagus sylvatica* after a clear-cut) are affected by strong overheating; their bark will be irreversibly damaged (sunburn) and finally lost by cracking off (Nicolai 1986; Butin 1996). In many publications there is consensus that the vascular cambium of trees will be destroyed at temperatures exceeding 60°C (Hare 1961; Hengst and Dawson 1994).

Besides environmental factors and site-specific conditions, the stem temperature regime is distinctly affected by the specific bark type and structure. Trees with smooth and thin barks or periderms (e.g. *Fagus sylvatica*) reveal only minor thermal gradients between the

bark surface and the cambium, whereas species with fissured, thicker barks (e.g. *Quercus robur, Alnus glutinosa*) show large temperature differences resulting from effective thermal insolation. Even within such a structured 'bark-(micro)landscape', strong temperature gradients between bark hills and valleys are generated. These trees also avoid overheating of their sensitive cambial tissues by shading the inner bark parts and reducing the irradiance inside a bark valley up to almost 100% (Nicolai 1986). The colour of the bark also influences the bark nano-climate, as pale or whitish surfaces reflect greater proportions of the incident solar radiation (e.g. *Betula pendula, Populus tremula*). The thermal properties of several bark types guarantee an effective stem internal carbon re-fixation, taking into account that the optimum temperature for photosynthetic CO_2 re-fixation is between 20 and 30°C (e.g. aspen: Brayman and Schaedle 1982).

The corticular water regime

The steep gradient of water vapour potential between plants and the surrounding atmosphere is the driving force for water movement from plant to air. To prevent excessive water loss, the aerial parts of higher terrestrial plants require protective layers. The periderms and rhytidomes that replace the ruptured epidermal layers of the growing primary plant organs provide protection against water loss. The rhytidome is composed of successive layers of non-living periderm. The outermost layer of each periderm is a hydrophobic cork tissue (phellem), which consists of cells whose walls contain suberin, a polyester linked to a phenolic matrix, and wax lamellae. The efficiency of protection obviously depends on the thickness of the peridermal and rhytidomal layers as well as on their structure and composition. It is well accepted that the partly suberised phellem of non-lenticellular periderm constitutes an efficient barrier to water vapour diffusion.

Thus, rhytidomal transpiration in comparison with leaf or crown transpiration is rather small; estimates range from about 1/5000 (*Populus tremula*: Geurten 1950) to 1/1000 (Huber 1956) of the respective leaf or canopy rates. Permeability coefficients for peridermal water vapour diffusion resemble those of cuticles (Schönherr and Ziegler 1980). Maximum transpiration values ranging from 30 to 120 µmol m^{-2} s^{-1} clearly depend on the species-specific bark structure. Trees with smooth, dense periderms/rhytidomes (*Fagus, Betula*) transpire about one third of the amounts of species with fissured rhytidomal layers (*Quercus, Populus*). Also seasonal differences in stem transpiration have been observed, with maximal rates occurring between June and August (Geurten 1950). A large proportion of stem transpiration proceeds via bud scales and leaf scars. Although leaf scars cover only 2% of the total twig surface of *Tilia cordata*, sealing them reduced transpiration by about 50% (Huber 1956).

Stem internal carbon release and re-fixation

As in other plant organs, a steady consumption/production of oxygen and carbon dioxide takes place inside the stem. Respirational CO_2 is freed inside the stem during the oxidation of carbohydrates. Mitochondria inside the living tissues of the inner bark, the wood parenchyma and the pith perform this respiration. For mitochondrial dark respiration, oxygen is essential. Thus the oxygen concentration is lowered whereas the CO_2 concentration is increased inside the stem. Stem internal photosynthesis has the potential to partially compensate this contrarotating effect, by reducing the concentration of CO_2 and, in parallel, increasing the oxygen partial pressure.

Besides the well-known fixation of CO_2 during illumination (for a recent review see Pfanz and Aschan 2000), CO_2 can also be fixed in the dark. PEP-carboxylase, an enzyme present in nearly all cells, is able to fix CO_2 (actually bicarbonate HCO_3^-) in quite high amounts (Müller et al. 1991). Besides an obvious function in the normal cellular pH-stat, important anaplerotic functions of PEPcase (e.g. the production of oxalo-acetate) have been suggested which are of relevance, in particular, under the impact of energy-demanding stress (Wiskich and Dry 1985; Saurer et al. 1995). Dark fixation capacities of tissues can be stimulated in the presence of nitrate and ammonium (Müller et al. 1991; Vuorinen and Kaiser 1997). The highest re-fixation rates have been recorded under elevated CO_2 concentrations, although PEPcase is known to have a relatively low K_m (for bicarbonate). The extremely elevated stem internal CO_2 concentrations may (surprisingly) therefore be ideal prerequisites for PEPcase-driven dark CO_2 fixation within the stems of woody plants. Höll (1973, 1974) was probably the first to describe dark CO_2-fixation in the bark and wood of *Robinia pseudoacacia*.

Stem respiration

A large portion of the carbohydrates assimilated during the daytime are directly consumed in respiration. Respiration is needed to produce energy and carbon skeletons to sustain plant growth, maintenance, transport, and nutrient assimilation processes (e.g. Amthor 1994).

Dark respiration in forest ecosystems can amount to more than 50% of carbon fixed during photosynthesis (Kira 1975; Ryan et al. 1997; Law et al. 1999). Respiration is therefore regarded as a main factor in the regulation of forest productivity and carbon storage (Ryan et al. 1997). Stem respiration has been measured for several decades at a single-tree level (Geurten 1950; Möller et al. 1954; Ziegler 1957; Matyssek and Schulze 1988) and even at the habitat or ecosystem level (Tranquillini and Schütz 1970; Bossard and Rejmanek 1992; Kharouk et al. 1995; Law et al. 1999). For calculations of daily, monthly or annual carbon fluxes of woody plants, stem or bark respiration has frequently been determined separately from respiration and photosynthesis of leaves

(Negisi 1972, 1974, 1978, 1982; Oohata and Shidei 1972; Kakubari 1988; Sprugel and Benecke 1991; Grossman and Dejong 1994a, b).

On an annual basis, maintenance respiration of aboveground stem tissues of conifers consumes up to 13% of net daytime carbon assimilation (Ryan et al. 1995). Taking into account the fact that maintenance respiration may be as high as 50–60% of total stem respiration (Edwards and Hanson 1995), it is assumed that total stem respiration consumes at least 20% of the tree's net carbon assimilation in temperate forests. In mature forests, the CO_2-efflux from standing woody tissue may equal or even exceed foliar respiration by a factor of more than 2.5 (Edwards and Hanson 1995). Measured in a boreal forest ecosystem, mean wood and also mean leaf respiration were almost identical (0.2–1 µmol m^{-2} s^{-1}: Ryan et al. 1997). For balsam fir (*Abies balsamea*) stands, average respiration rates between 0.8 and 1.8 µmol m^{-2} s^{-1} per unit stem area were reported (Lavigne et al. 1996).

Stem and branch maintenance respiration remain relatively constant through forest succession, whereas growth respiration and therefore forest productivity declines in late succession (Gower et al. 1996). Wood respiration is strongly seasonal, with higher rates in midsummer coinciding with wood growth (Matyssek and Schulze 1988; Ryan et al. 1997; Wieser 1997). Cambial activity and tissue temperatures may account for 60–80% of the variation in stem and branch respiration (Maier et al. 1998). Generally, respiration increases exponentially with temperature (Ryan et al. 1995). Additionally, a reasonably good relationship between annual maintenance respiration and sapwood volume (per unit stem surface area) has been found (Ryan et al. 1995; Lavigne and Ryan 1997). Nutritional status of the tree also strongly affects stem or branch respiration (Maier et al. 1998; Stockfors and Linder 1998).

Within all stem parts, dark respiration rates sharply decrease with an increasing age of the organs (*Fagus crenata, Quercus acutissima*: Han and Suzaki 1981). Smaller, and thus younger, twigs of *Pinus densiflora* show obviously higher respiration rates (5–10 mg CO_2 dm^{-2} h^{-1}) than branches with a diameter of 10 cm (2–5 mg CO_2 dm^{-2} h^{-1}). The reason for this decrease in respiration is mainly the reduced ratio of bark to wood mass (Negisi 1974) and also a generally higher resource turnover in younger plant parts.

Therefore, branches in the upper canopy (and small diameter coarse roots) were found to have the highest respiration rates (*Pinus radiata*: Ryan et al. 1996). The age-dependent dark respiration within current-year twigs of aspen showed a decrease from the youngest to the oldest internodes from values around 11 µmol CO_2 m^{-2} s^{-1} to 3 µmol CO_2 m^{-2} s^{-1} (Aschan et al. 2001). Thus, the ability to effectively re-fix stem internal respiratory carbon is of greater importance in younger, still-growing and metabolically highly active parts of the crown and of minor importance in the older stem fractions (see Foote and Schaedle 1976a, b; Cernusak and Marshall 2000; Pfanz and Aschan 2000; Wittmann et al. 2001).

Corticular photosynthesis is mainly CO_2 re-fixation

The first observations of the existence of photosynthesis in the inner bark of trees were probably those of Schneider (1903), Scott (1907) and Cannon (1905, 1908) at the beginning of the nineteenth century. Several attempts have been made to qualitatively prove its existence or even quantify rates of carbon assimilation (Larsen 1939; Geurten 1950; Ziegler 1957; Pearson and Lawrence 1958; Strain and Johnson 1963; Kriedemann and Buttrose 1971; Perry 1971; Schaedle 1975; Foote and Schaedle 1976a, b, 1978). Since then great efforts have been made to understand bark photosynthesis from an ecophysiological point of view as well (Pilarski 1984, 1990, 1993; Larcher et al. 1988; Langenfeld-Heyser 1989; Kharouk et al. 1995; Solhaug et al. 1995; Pfanz and Wobus 1998; Pfanz et al. 1998, 2001; Pfanz 1999; Cernusak and Marshall 2000; Pfanz and Aschan 2000; Schmidt et al. 2000). It is meanwhile well accepted that corticular photosynthesis very rarely leads to a net carbon gain (but see Wittmann et al. 2001). Rather, the ideally strategic anatomical location (often cylindrically just below the outer bark ring) suggests the function of recapturing respiratory CO_2 which would otherwise be lost to the surrounding air (for details see later).

The response of corticular chlorenchyma to light

As already demonstrated for the chlorophyll contents and for the cytological characteristics of bark chloro-plasts, corticular photosynthesis shows nearly ideal shade adaptation. When photosynthesis of twigs, branches and the main stem of holly (*Ilex aquifolium*) was examined under an increasing light regime, only 250–300 µmol photons m^{-2} s^{-1} were needed for obtaining maximum rates, irrespective of whether isolated leaf material or peeled chlorenchymes from young twigs were used (Schmidt et al. 2000). Although holly is a clearly shade-adapted understorey tree or shrub, some differences were detected between shade and more sun-exposed branches (Fig. 3). In separated tissue fractions, chlorenchymal rates of maximum net photosynthesis (1.2–1.0 µmol O_2 m^{-2} s^{-1}) were about half as high as in comparable leaves (2.5–3.0 µmol O_2 m^{-2} s^{-1}). When fully shade-adapted twigs and leaves were examined, a photo-inhibitory reduction of net photosynthesis was found when light was increased over a threshold of 100–130 µE photons m^{-2} s^{-1}. Higher light-adapted organs did not show this inhibition (Fig. 3). Similar results were obtained by quantifying the CO_2 gas exchange of twigs of European beech (*Fagus sylvatica*: Wittmann et al. 2001). According to Larcher (1994), light saturation of deciduous shade leaves is around 200–500 µE m^{-2} s^{-1}; chlorenchymal photosynthesis is thus performed by extremely shade adapted chloroplasts (which is also indicated by a low chlorophyll *a*/*b* ratio). This fact is underlined when photosynthesis of chloroplasts of still more shade-adapted stem internal tissues such as pith or wood are studied.

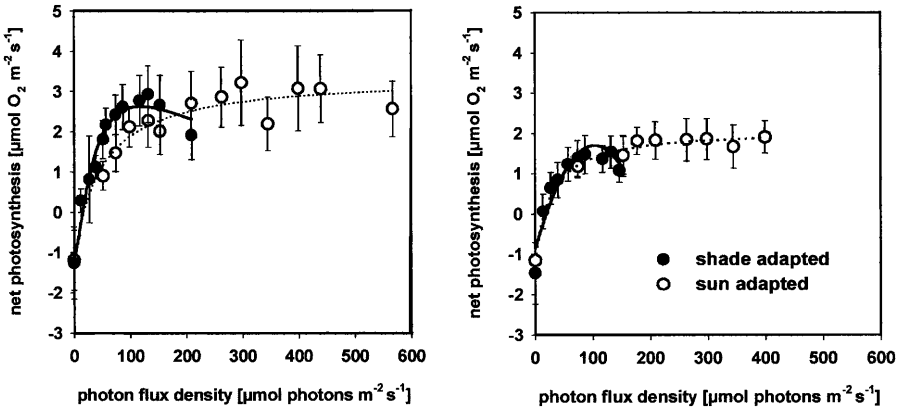

Fig. 3 Light dependencies of surface-related net photosynthesis of leaves (*left panel*) and peeled peridermal and bark layers of young twigs of *Ilex aquifolium* (*right panel*) as measured with an oxygen electrode under optimum conditions. The wood and pith fractions of the twigs had been carefully removed prior to the experiment. The *open circles* indicate samples taken from sun-adapted parts of the canopy; *solid circles* indicate shade-adapted organs (data from Schmidt et al. 2000, with permission)

Table 3 O_2 concentrations as measured in intact tree stems and in detached stem, twig and branch segments. Data are given in percentage w/v where 1% *w*/v = 1,000 Pa = 10,000 µmol mol^{-1} = 10,000 ppm (*w* winter, *s* summer)

Tree species	Stem internal oxygen concentration	Authors
Juglans major	8–15%	McDougal and Working (1933)
Parkinsonia microphylla	5.5–22.3%	McDougal and Working (1933)
Picea abies	2 to 5% (s) – 20% (w)	Eklund (1990)
Pinus strobus	3% (s) – 11% (w)	Chase (1934)
Populus deltoides	1% (s) – 5% (w)	Chase (1934)
Populus tremuloides	0–21.2%	McDougal and Working (1933)
P. macdougalii		
Quercus agrifolia	11.3–18.5%	McDougal and Working (1933)
Quercus borealis	12% (s) – 14% (w)	Chase (1934)
Quercus rubra	0.4–0.9%	Jensen (1967)
Quercus rubra	<2% (sound trees), 1–4%	Jensen (1969)
Q. coccinea	(decayed trees)	
Q. velutina		
Salix lasiolepis	8–14%	McDougal and Working (1933)
Sequoia sempervirens	8.5–17.4%	McDougal and Working (1933)
Ulmus americana	3% (s) – 6% (w)	Chase (1934)

Wood photosynthesis – CO_2-fixation under extreme conditions

Quite interestingly, besides the photosynthesis of bark tissues, green tissues can also be found behind the inner bark layers of woody plants. In several trees, chloroplast-containing cells have been described in the ray cells of the wood, and as ring-shaped halos around the pith (perimedullary region; see Fig. 1b, Table 2) or inside the pith itself (Wiebe 1975; Herrmann 1987; Langenfeld-Heyser 1987, 1989; Buschmann 1989; Langenberg 1990; Stärke 1990; Buns et al. 1993; van Cleve et al. 1993; Pfanz and Aschan 2000).

Carbon re-fixation within wood and pith

Using radioactively labelled carbon dioxide ($^{14}CO_2$), Wiebe (1975) was probably one of the first researchers to directly demonstrate the ability of wood chlorenchyma to photo-reduce CO_2. In addition, Höll (1974) measured an incorporation of CO_2 into organic matter within the wood tissues, but this effect was ascribed to dark CO_2 fixation via PEP-carboxylase (see Müller et al. 1991; Vuorinen and Kaiser 1997). Meanwhile several authors have shown that many tree species are able to perform photosynthesis inside their wood or pith parenchyma (Larcher et al. 1988; Langenfeld-Heyser 1989; Larcher and Nagele 1992; Buns et al. 1993; van Cleve et al. 1993; Pfanz and Aschan 2000). Compared to rates of bark photosynthesis, wood or pith photosynthesis is rather low. This raises the question whether this special photosynthesis serves other purposes than pure CO_2 re-fixation.

Avoiding hypoxia

According to Carrodus and Triffett (1975) and Eklund (1990) the stem internal oxygen concentrations fluctuate strongly in diurnal as well as annual cycles (see also Ziegler 1957; Shain and Mackay 1973; Levy et al. 1999). In contrast to the extraordinarily high CO_2 concentrations measured inside the stem organs (see above), oxygen concentrations are usually much lower than in ambient air (see Table 3). Oxygen consumption in the bark of young stems is high, being 80% of the whole stem consumption (Ziegler 1957; Langenfeld-Heyser 1997). Although oxygen concentrations vary with species, mode of sampling and analytic techniques, average

endogenous oxygen concentrations within tree stems generally range far below optimal levels (e.g. Carrodus and Triffett 1975). As respiration clearly depends on the presence of O_2 and may be more or less reduced below a certain threshold, there is the danger of stem internal hypoxia (Amthor 1976; Bouma et al. 1997; Jahnke 2000). Below a certain O_2 concentration anaerobic fermentation may even occur. Fermentation would produce ethanol and/or lactic acid, which would have deleterious effects on cellular membranes and enzymes and on cellular pH-stat (see McManmon and Crawford 1971; Pfanz and Heber 1989). Low oxygen or even anoxia would probably have negative effects on heartwood formation, as coloured heartwood seems to be produced only in the presence of oxygen (Frey-Wyssling and Bosshard 1959; Yazawa et al. 1967). On the other hand, a high CO_2 content within the heartwood–sapwood interface is thought to induce flavonoid and polyphenol formation (Jensen 1967; Carrodus 1971; Iqbal 1995).

In experiments with isolated wood segments of young, 1–5-year-old twigs of *Fraxinus excelsior* (wood ring around pith) and *Fagus sylvatica* (wood), an oxygen production of 2.5–3.0 µmol O_2 m^{-2} s^{-1} was determined (measured under optimum light, CO_2 and pH conditions: H. Pfanz, unpublished results). The rates had been calculated on a unit wood surface which was oriented rectangularly to the twig radius.

Evolutionary considerations

Chlorenchymal photosynthesis – an ancient technique and its modern application

Algae have always been able to perform photosynthesis using their whole cells or thalli as a photosynthetically active light collector. But when plants 'stepped' onto land, part of the thallus/cormus had to undergo a functional change and successively serve as support and positioning skeleton for the evolving leafy assimilation organs (e.g. *Psilotum*, *Tmesiptersis* or *Rhynia*). Rigid sclerenchyma, water-impermeable surface structures, and water-transducing tissues had to be formed in the newly evolving upright standing stems. This led to unavoidable changes in the inner and outer anatomy of the stems. The formerly photosynthesising outer chlorenchymal (epi- and hypodermal) layers had to give way to tissues protective against an unwanted loss of water. Evapotranspiration had to be reduced in this highly evaporative environment and thus water-impermeable layers – the peridermal and rhytidomal tissues – were formed. Unregulated water loss of the stems was consequently reduced but, as a consequence, light became minimal to the stem-inward-shifted chlorenchymal layers. It is intriguing to speculate whether the sub-rhytidomal or corticular photosynthesising tissues may be regarded as a remnant of ancient stem photosynthesis which still retains the useful ability to affect the carbon balance of recent woody plants, or as a highly evolved and specialised characteristic. Furthermore, besides corticular photosynthesis, stem photosynthesis also still occurs in several species of modern woody plants. Broom (*Genista* spp.), *Ephedra*, *Cytisus*, *Viscum* and *Ulex* species even today demonstrate the ancient capability (or 're-invention'/'convergent development') of stems to assimilate airborne CO_2. Possessing functional stomata, the chlorenchymal tissues show an anatomy reminiscent of leaf palisades and spongy mesophyll (see Gibson 1983; Comstock and Ehleringer 1988; Nilsen 1995).

Ecological aspects

Carbon recycling and stem internal re-fixation – a profitable operation?

Maximum re-fixation rates of various woody species seem to depend mainly on the age of the respective twig or stem segment (Table 4). According to Linder and Troeng (1981) the re-fixation rate of *Pinus sylvestris* decreases with advancing age from 45% (2-year-old twig) to 5% (12-year-old branch). We are able to demonstrate the age-dependency of CO_2 exchange even within current-year aspen twigs: along these twigs the efficiency of recycling dropped from 80% to 50–60% (Aschan et al. 2001). Several other studies have verified that branches and stems have a substantial photosynthetic activity at ages of about 10 up to 60 years (e.g. Steinborn et al. 1997; Kaipiainen et al. 1998). One reason for this age-dependency is the strong correlation between re-fixation rates and mitochondrial dark respiration. A proportional decrease in respiration and re-fixation with twig or stem segment age has been observed in deciduous trees (*Fagus crenata*: Han and Suzaki 1981; *Populus tremuloides*: Brayman and Schaedle 1982; *Alnus glutinosa*: Steinborn et al. 1997) as well as in coniferous tree species (*Pinus sylvestris*: Linder and Troeng 1981; *Pinus monticola*: Cernusak and Marshall 2000).

Dark respiration and photosynthesis are strongly influenced by tissue temperatures (see above). Stem internal re-fixation thus follows a seasonal pattern similar to that of mitochondrial respiration, with highest rates in summer and lowest in winter (e.g. Foote and Schaedle 1976a).

For the entire year, bark photosynthesis in 5- to 7-year-old aspen trees reduced the stem respiratory CO_2 loss by 16–18% (24-hour basis) or 29% (daytime basis) (Foote and Schaedle 1976a). During summer (June to August), aspen bark tissue assimilated 59% of the annual total CO_2 respired (Foote and Schaedle 1978). Kharouk et al. (1995) estimated the average bark input to whole tree C balance as 10–15% during the midsummer vegetative period, and suggested that a larger, undetermined fraction might be attributed to bark under environmental or phenological conditions where leaf contributions are limited. For young beech trees Gansert (1994) found annual respiratory re-fixation rates about 24%.

Re-fixation may influence productivity up to stand level by increasing the carbon-use efficiency (CUE), the

Table 4 Maximum stem internal CO_2 re-fixation rates for various woody species

Species	Maximum re-fixation rate (% of dark respiration)	Age (years)	Authors
28 various species	77±10		Comstock and Ehleringer (1990)
Acer rubrum	31 (winter)	0–1	Coe and McLaughlin (1980)
Cornus florida	79 (winter)	0–1	Coe and McLaughlin (1980)
Fagus crenata	56–98	5	Han and Suzaki (1981)
Fagus sylvatica	80–90	0–1	Wittmann et al. (2001)
Alnus glutinosa	45	10	Steinborn et al. (1997)
Guiera senegalensis	75		Levy and Jarvis (1998)
Pinus monticola	76±3	3–4	Cernusak and Marshall (2000)
Pinus sylvestris	45	2	Linder and Troeng (1981)
	5	12	
Pinus sylvestris	54	55–60	Kaipiainen et al. (1998)
Populus tremula	60–80	0–1	Wittmann et al. (2001)
Populus tremuloides	85–90 (winter) 90–92 (summer)	6–8	Foote and Schaedle (1976a)

ratio of net primary production to production plus respiration. Ryan et al. (1997) estimated about 50% higher (above-ground) CUE for boreal forest stands dominated by *Populus tremuloides* than in conifer stands of *Picea* or *Pinus*. As a main reason for the offset in respiratory losses the effective recycling of respired CO_2 through re-fixation within aspen bark is mentioned.

Ageing aspects – a comparison between leaves and twigs

According to Larcher (1994), maximum net photosynthetic activity in leaves is achieved when they are fully developed and mature (4–6 weeks after bud break in deciduous leaves and sometimes 3–4 months after sprouting in coniferous trees). The behaviour of the corticular assimilatory tissue is somewhat different. Corticular photosynthesis of young twigs and branches reveals highest activities in the young, developing state and its effectiveness is reduced to some extent during ageing (mainly due to the development of thicker, light-reducing outer bark layers). The younger twigs and branches could thus contribute to a more positive twig carbon balance, whereas older branch parts would have more structural functions (without necessarily losing their capability to re-assimilate respirational carbon). It seems therefore as if trees and shrubs have to provide a sufficient area of young (and thus green) parts in the canopy to maintain an efficient energy and carbon budget.

Bark senescence and rhytidomal peeling

In addition to what has been said on the age-dependent effectiveness of bark photosynthesis, indirect hints about the importance or necessity of bark photosynthesis may be gathered by the observation of bark renewal in different tree species. In some tree species, thick and light-limiting rhytidomal layers are never (e.g. *Fagus sylvatica*) or only transiently formed, or thicker bark islands are regularly shed at distinct intervals (*Acer* spp., *Betula* spp.). In *Platanus* a patchy network of rhytidomal islands can be seen (see Fig. 1d). Up to six different coloured and gradually thicker rhytidomal stages can be determined. Preliminary results indicate a light transmittance ranging from almost zero in the oldest (thickest) rhytidomal islands up to 60% and more in the young (green) stages (H. Pfanz, unpublished results). It would be intriguing to determine whether a distinct portion of a tree stem has to be photosynthetically active (possessing a highly light-transmitting rhytidome) in order to allow an effective stem internal carbon acquisition.

Logistic short cuts

Tree stems reveal a longitudinal and radial stem growth (dilatation growth); they have to regulate bud burst, sprouting and flourishing and for these functions they need (local) energy. Apical and vascular-cambial meristems exhibit an annual cycle of activity and dormancy (rest and quiescence) (Little and Pharis 1995). In most trees and shrubs, cambia have to be active before mature leaves can provide these regions with photosynthates. Such behaviour may be obligatory, in particular, in ring-porous trees which initiate early-wood formation in parallel or prior to bud break. Furthermore, the developmental stage of plants and the seasonal (phenological) aspects such as bud break in early spring raise the question of the importance of an additional energy supply by the cortex. Quite a few shrubs and trees flower in early spring in the leafless state (e.g. some cherries, *Forsythia*, *Cornus mas*, *Prunus spinosa*). If most of the energy reserves stored in autumn are already nearly depleted in spring (Eschrich 1995; Sauter and Witt 1995), an additional supply of carbohydrates via corticular photosynthesis might be of importance (*Fraxinus excelsior*: Langenfeld-Heyser et al. 2001). A supply of soluble sugars is vital also in the autumnal adaptation to the cold winter season. As has been shown for leaves, bark and wood parenchyma also metabolise insoluble starch to produce osmotically active soluble sugars functioning as cryoprotective solutes in frost-resistant tissues (Sauter and van Cleve 1991). Callus formation and wound heal-

ing may also be partly regulated and energised by the living bark tissue. Lignification and suberinisation as primary processes following wounding are costly, as are ethylene and phytoalexin production (Biggs 1985; Sutherland 1991; Gottstein and Gross 1992). In all young meristematic callus tissue studied so far, a green sub-peridermal layer has been found (see Fig. 1c).

In defence reactions against pathogenic fungal or bacterial invaders, the biosynthesis of several toxins or defence chemicals acting as biochemical barriers consumes energy and would ideally be performed close to the affected region. Tannins (e.g. gallic acid), phenols or even extracellular enzymes (chitinases, β-1.3-glucanases) are synthesised before or during fungal attacks (Wargo 1975; Woodward and Pearce 1988; Mauch and Stählin 1989; Scalbert 1991). Furthermore, bark exudates including terpenoids, gums (polysaccharides), latex (poly-isoprenes), and kino (proanthocyanidins) have to be synthesised and transported to their secretion loci (Hillis 1987). Even here, an energy source close to the infected area could be of high logistic value.

Water-use efficiency – a comparison between bark and leaf

Compared with leaf photosynthesis, corticular photosynthesis seems to be an 'intelligent' method of carbon (re)-fixation without a great water loss. There is a fundamental difference between photosynthesis in leaves and bark: in order to take up CO_2, leaves have to open their stomata, thus exposing drought-sensitive mesophyll tissues to the ambient atmospheric water-vapour conditions. Bark chlorenchyma, on the other hand, are supplied with CO_2 endogenously respired by the surrounding heterotrophic stem tissues. Water-use efficiency in leaves (WUE_{leaf}) is typically defined as the ratio of net photosynthetic assimilation to transpiration (mmol CO_2 mol^{-1} H_2O). As bark photosynthesis rarely reaches positive net values, WUE_{bark} itself is usually negative. However, bark photosynthesis will improve whole tree WUE, because it increases net C fixation at the whole-plant level by reducing CO_2 evolution from the stem. Therefore, it seems to be appropriate to define WUE_{bark} as the ratio of stem internal CO_2 refixation or 'gross photosynthesis' to transpiration. Estimations for *Pinus* bark revealed WUE values of about 130 mmol CO_2 mol^{-1} H_2O, a value that is 50 times higher than in the corresponding foliage (Cernusak and Marshall 2000).

Corticular photosynthesis and symbiosis

Many plants with proper stem photosynthesis possessing rather small or sometimes even no leaves seem to rely on N_2-fixing microorganisms (Harvey 1972; Nilsen et al. 1989, 1993; Bossard and Rejmanek 1992). However, the root nodules require a constant supply of reduced C in order to remain functional. During leafless times, the nutritional C supply of the symbiotic bacteria is only guaranteed through photosynthesising stems. Also most central-European trees have fungal partners to form a root–fungus interrelationship – known as mycorrhizal symbiosis. Whether the ability of the inner bark to recapture respired CO_2 influences the induction of the mycorrhiza, or enhances the growth of the fungal mycelium or even induces the formation of the fungal fruit bodies, has not been studied so far.

The bark as habitat or food source for animals and plants

Ecologically, the surface of a tree trunk is a microcosm par excellence. The rhytidome or cortisphere (cortiplane) forms an excellent ecological niche for epiphytic (epi- and pericortical) plants and animals. Airborne algae (e.g. *Chlorella*, *Chlorococcum*: Wylie and Schlichting 1973), mosses (e.g. *Leucodon sciuroides*, *Hypnum cupressiforme* f. *filiforme*: Jahns 1995) and lichens (e.g. *Lobaria pulmonaria*, *Parmelia* spp., *Hypogymnia physodes*: Wirth 1995) typically colonise tree bark in ecosystems all over the world. Furthermore, myriads of insects live or feed on the outer or inner cortex of tree stems.

Mining and dwelling insects

Bark beetles (Family Scolytidae: *Ips* spp., *Scolytus* spp., *Tomicus* spp.) are one guild of insects that selectively live on, or more accurately in, tree bark or wood (Nüsslein 1905). They seem to grow better when feeding on the soft, protein- and starch-containing bast tissue than when feeding on rhytidomal or woody tissue fractions (see Ayres et al. 2000). These beetles often grow phyto-pathogenic fungi within their bore holes. The fungi have easy access to the cell wall material and digest the tissue, finally being partially eaten up by the beetles' larvae as ambrosia. An extreme adaptation to the narrow space between the rhytidome and the wood can be seen with the beetle *Mormolyce* spp. (Carabidae); the fiddle beetle is heavily compressed from top to bottom and is thus optimally adapted to hunt insects below the rhytidome of dying or decaying trees.

Browsing

Many browsing animals use bark as well as leaves to feed on. Apart from the larvae of various species of butterflies and beetles, mammals play a dominant role in bark damage. During winter or drought periods, rodents such as lemmings, voles and mice, as well as hares and rabbits, are feeding on bark. Larger herbivores including deer, elk and musk-oxen do not scorn the protein and carbohydrate rich tissues of the inner living bark either. The specialised feeding of the beaver (*Castor fiber*) on the carbohydrate resources of alder (*Alnus glutinosa*, *A. incana*), aspen (*Populus tremula*), willow (*Salix* spp.)

and beech (*Fagus*) bark (Soppa 1985) is also well known. In nearly all ecosystems (boreal forest, tropical rainforest, shrub tundra, subtropical savanna), browsing animals seem to prefer fast-growing and thus productive specimens, rich in protein and carbohydrates and will avoid eating stems of slowly growing specimens which are characteristic of unproductive habitats (Bryant and Raffa 1995).

Concluding remarks

With a few exceptions, nearly all the trees and shrubs examined have been found to possess a greenish sub-layer within the cortex of the stems, at least in young twigs. As long as this tissue is able to positively contribute to the tree's carbon budget it will be kept alive and functioning. In evergreen conifer trees, needles are shed at a more or less defined age. Nevertheless, if shaded by competitors or higher branches of its own crown, needles will become net carbon consumers rather than photo-assimilating carbohydrate producers. Within a relatively short time, the purely carbon-consuming needles will be aborted (Matyssek and Schulze 1988). The assimilating tissue in the stems of woody plants may be treated similarly as part of a modular system (Stitt and Schulze 1994) and it is thus only preserved if a positive net carbon balance is established. Internal feedback loops may also be able to compare gross and net contributions at an organ or even at the tissue (or cell) level. As long as stem internal carbon recycling reduces the respirational loss of CO_2 or as long as the oxygen production during photosynthesis helps to avoid the danger of anaerobiosis (or as long as light is available), chlorenchymal tissues within a stem will probably be kept functioning. On the other hand, if the establishment or the maintenance of light-transducing channels (or the supply with water) is too costly, the function of these tissues will inevitably be changed.

During stress phases (e.g. under whole-plant N-limitation) corticular photosynthesis is much less reduced than leaf photosynthesis and consequently the proportional importance of stem to canopy CO_2 gain increases (Nilsen 1992). As photosynthesis creates oxygen, the balanced ratio of $CO_2$to O_2 might also be used for an effective defence against phyto-pathogenic fungi (Jensen 1969). During undisturbed metabolic phases and also during growth periods of enhanced biotic and abiotic stresses, corticular photosynthesis may positively contribute to the plant's synchronised reactions. Whether corticular photosynthesis represents an evolutionary relict, a botanical atavism, or an evolutionary necessity which is indispensable for most modern woody plants' carbon balance, remains an open question.

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