

Optical Properties of the Cork of Stems and Trunks of Beech (*Fagus Sylvatica* L.)

J. Pilarski^{1,2*}, K. Tokarz¹, M. Kocurek¹

¹Institute of Plant Physiology, Polish Academy of Sciences, Niezapominajek 21, 30-239 Kraków, Poland

²Institute of Biology, Jan Kochanowski University, Świętokrzyska 15, 25-406 Kielce, Poland

Received: 12 January, 2008

Accepted: 9 June, 2008

Abstract

The investigations were carried out on 1-3- and 10-year-old stems and on the trunks of beech. The optical properties measured were: reflectance, absorption and transmittance of irradiation. The reflectance was measured in the bark and the cork, while absorption and transmittance were measured on isolated cork. Reflectance was measured only on the bark of trunks and the range of the investigations was 400-1100 nm.

The reflectance of irradiation in the stems increased with increasing wavelength and decreased with the age of stems. In the range 400-700 nm it ranged from 18% in 1-year-old stems to 10% in 10-year-old stems, and reflectance in the trunks was equal to 15%. In the range 700-1100 nm, it ranged from 51% in 1-year-old stems to 36% in 10-year-old stems and in the trunks.

Absorption of the cork decreased with increasing wavelength from about 92% in the range 400 nm to about 15% in the range 700 nm, and to 15% in the range 1100 nm. Any distinct influence of stems age on cork absorption was not observed.

Transmittance of irradiation increased with increasing wavelength and the age of the stems. In the range 400 nm it was >1% in all age groups of the stems. In the range 700 nm in 1- and 2-year-old stems, it was equal to approximately 45%, and in the 10-year-old ones it amounted to 60%. In the range 700-750 nm, transmittance decreased to about 38% in the bark of 1-3-year-old stems, to 50% in 10-year-old ones and it remained at this level up to 1100 nm.

Keywords: optical properties, reflectance, absorption, transmittance, stem, bark, cork, beech

Introduction

Although support for leaves, transport and storage are the basic roles of stems [1], the presence of photosynthetic pigments in them indicate their photosynthetic function [2].

One of the main factors that influences the formation of the photosynthetic apparatus is light irradiation. It affects the morphological and anatomical structure of plants, the ultrastructure of chloroplasts, the content of photosynthetic pigments and their quantitative and qualitative composition [2].

Irradiation reaching plants is subjected to physical processes, among which the most important are reflectance, absorption and transmittance. The reflectance of irradiation can be divided into outer and inner reflectance [3, 4]. The outer reflectance is the reflection from the surface [5-8], and the inner reflectance is connected with the reflection of irradiation during its penetration through the cells and reflection from the cellular structures [9-12].

Each of these processes is an important indicator of the current physiological condition of the plant and its adaptation to some specific environment. The optical properties of leaves, stems and fruits change with age, as do the physiological properties and they depend on their location on the plant.

*e-mail: j.pilarski@ifr-pan.krakow.pl

In trees and shrubs, the optical properties of the bark of stems and trunks have a direct influence on the development, content and composition of the photosynthetic pigments in the chlorophyll-containing tissues. These pigments are located mainly in bark and their smaller contents are also present in the xylem and in the pith [13-16]. Reflectance and absorption of irradiation in the cork determine the transmittance of irradiation to the chlorophyll-containing cells in the stem – its amount and spectral composition. In species in which with the stems age a considerable increase in the thickness of cork occurs, its absorption increases and the transmittance of irradiation decreases, which is responsible for the diminishing content of the photosynthetic pigments in the stems and the decay of photosynthetic activity in them. This can be observed for example, in lilac (*Syringa vulgaris* L.) [17-18]. In species where the increase in cork thickness with stem age is rather small, the content of the photosynthetic pigments in the bark decreases slowly [15]. In pine, in the upper parts of the tree, the cork on the branches and trunks peel off, hence it does not accumulate, and in these parts of the tree the photosynthetic pigments are retained for decades. In the lower parts of the pine trunk in which the cork accumulates, the photosynthetic pigments in the peridermis decay.

With the ageing of the stems, the diminishing reflectance can be observed, as can the increasing absorption and diminished transmittance of irradiation to the chlorophyll layer under the cork [1, 2, 19]. Spectral investigations of the optical properties of stems, defining the reflectance, absorption and transmittance, were carried out only on lilac (*Syringa vulgaris* L.) and apple (*Malus domestica*) (*Malus domestica*) trees and only in the PAR range. These investigations have shown that irradiation transmitted by cork in the PAR range is very poor in the range 400 nm, and as the wavelength increases the amount of transmitted irradiation grows. A small amount of irradiation in the blue range and relatively high amount in the red range influences the chloroplast ultrastructure and pigment compositions. Chloroplasts developed in such conditions are similar to shade-adapted leaf chloroplasts and are characterized by the existence of only a few granal stacks, low chl *a/b* ratio and higher amounts of PS I [1, 20].

In species in which the accumulation of cork does not take place because its outer cells peel off, the photosynthetic pigments in cork are present all the time, not only in stems and branches, but also in the trunks and poplar trees belong to these species. They have a characteristic bright-grey colour that slightly glitters in the sunshine. They are frequent objects of physiological investigations [13, 14, 21-24].

There is no literature data available concerning the optical properties of the bark of trees, in which the photosynthetic pigments are present in the bark throughout the life of the tree in the stems and trunks. In the young stems they are present in considerable amounts in all tissues under the cork, also in the pith. In addition, with the ageing of the stems and their increasing thickness, the content of the chlorophyll decreases in deeper situated tissues and in the

trunks they are present only immediately under the cork, in the phelloderm and the cortex of the bark, and in trace amounts in the protophloem [15]. This is evidence of a considerable transmittance of irradiation through the cork. The optical properties of cork are an important parameter determining the presence of the photosynthetic pigments and the photosynthetic activity in the bark over a long time. The results of spectral investigations of the optical properties of stems published so far, report only on the photosynthetically active range in lilac (*Syringa vulgaris* L.) and in apple (*Malus domestica*) trees. Irradiation in the infrared range which is an important factor in the thermal balance of the stems was, not taken into consideration. Hence, the aim of the present study was the examination of the optical properties of the bark of beech, with consideration given to the age of the stems.

Material and Methods

The investigations were carried out on the European beech tree (*Fagus sylvatica* L.). The examined material was the bark of stems of various ages: 1-, 2-, 3- and 10-years-old and the bark of tree trunks, with a diameter between 20-60 cm. The material was collected from approximately 20 m high trees growing in a natural beech forest stand in Kraków neighborhoods. The term “bark” comprises all the tissues, both primary and secondary, outside the cambium [31]. The relative optical properties, in relation to incident irradiation, were determined in a laboratory using a spectroradiometer (LI-1800, LI-COR Lincoln, Nebraska), with an external integrated sphere (S12 LI-COR Lincoln, Nebraska), in photosynthetically active radiation (PAR 400-700 nm) and near infrared radiation (NIR 700-1100 nm). The reflectance (R) and transmittance (T) were determined from direct measurements, and the absorption (A) was calculated according to the formula: $A = 100 - (R + T)$. The measurements of reflectance were conducted on isolated cork and on isolated bark. Isolation was done in laboratory conditions. Bark and cork were isolated using a Cole Palmer binocular.

Firstly, bark was isolated and reflectance was determined, secondly cork from the bark was isolated and reflectance and transmittance were determined. The values obtained on isolated bark represented the values of total reflectance, which was the sum of the outer reflectance in the cork and inner reflectance in the cells situated under the cork, while those obtained on isolated cork represented the value of the outer reflectance. The value of inner reflectance was calculated as the difference between the reflectance in the bark and that in the cork. On the bark of trunks, only the total reflectance was determined because of difficulties connected with the isolation of a sufficiently large surface area of the cork necessary to carry out the measurements.

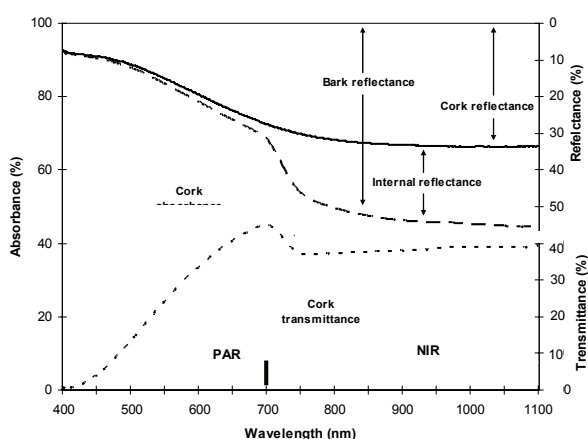
The measurements were carried out in five replicates, on material collected from different trees. The presented results are the arithmetic means with the calculated standard deviation (SD).

Results

The thickness of the cork of 1-3-year-old stems was equal to 0.04-0.05 mm, whilst that of 10-year-old stems was 0.11 mm, and the thickness of the trunk cork was 0.15 mm.

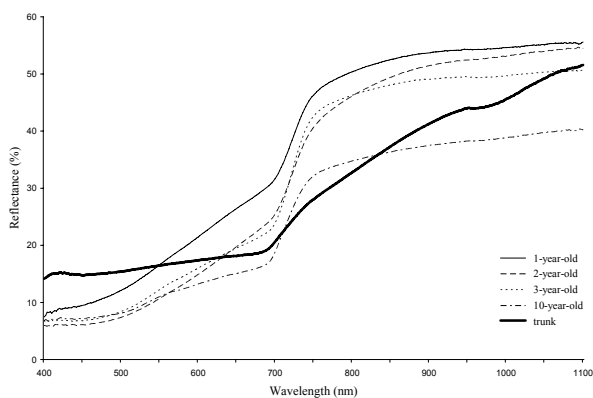
Fig. 1 shows the optical properties of 1-year-old stems and leaf. Leaves' reflectance increased from 6% in 400-500 nm range to almost 19% in 500-600 nm range and decreased to 12% in 600-700 nm range. In PAR range average leaf reactance was a little above 12%. In NIR range leaf reflectance increased to 35.5%. Incident solar radiation absorbed by the leaves in PAR range was 63% with 83% and 61% in 400-500 nm and 600-700 nm, respectively. In NIR range leaves absorption decreased to 4%. Leaf transmittance in PAR range was 25%, with high value 37% in 500-600 nm range and in NIR range transmittance increased to 61%.

Irradiation incident on the stem is subjected to outer reflectance from the cork surface. The outer reflectance increased with increasing wavelength from 7.5% in the range 400 nm to 28% in 700 nm and to 34% in 1100 nm. The outer reflectance in the PAR range amounted to 16% and in the NIR range it was equal to 32%. Irradiation reaching the chlorophyll layer of the bark, after it has been transmitted through the cork, was subjected to partial inner reflectance, which in the PAR range was rather small, being equal to 1.6%, whilst in the NIR range it was greater, amounting to 19%. The inner reflectance in the range 400 nm was equal to zero and it increased with increasing wavelength to 3% in the 700 nm and thereafter increased rapidly up to 17% in 750 nm; after which further increases were rather slow, up to 21% in 1100 nm. The total reflectance in the stem was equal to 17.6% in the PAR range and to 51.5% in the NIR range. Irradiation passing through the cork was absorbed, with the absorption decreasing with an increasing



	400-700 nm	700-1100 nm	400-500 nm	500-600 nm	600-700 nm
1-year-old stems					
Cork reflectance	16.0 ± 1.8	32.4 ± 3.1	9.2 ± 1.2	15.2 ± 2.0	23.8 ± 2.1
Bark reflectance	17.6 ± 4.2	51.5 ± 5.8	9.7 ± 1.2	16.7 ± 2.1	26.5 ± 5.4
Internal reflectance	1.6 ± 0.75	19.1 ± 5.26	0.5 ± 0.3	1.5 ± 0.72	2.7 ± 1.2
Cork absorption	59.3 ± 6.7	10.0 ± 2.1	85.2 ± 1.4	59.1 ± 7.7	33.1 ± 1.8
Cork transmittance	23.1 ± 2.1	38.6 ± 1.8	5.0 ± 1.0	24.1 ± 2.6	40.4 ± 3.0
Leaf reflectance	12.4 ± 0.31	35.5 ± 0.09	6.0 ± 0.08	18.9 ± 0.06	12.3 ± 0.06
Leaf absorption	62.9 ± 0.27	4.3 ± 0.1	83.6 ± 0.13	43.8 ± 0.22	60.9 ± 0.2
Leaf transmittance	24.7 ± 0.31	60.3 ± 0.14	10.3 ± 0.13	37.3 ± 0.23	26.8 ± 0.21

Fig. 1. Characteristic of distribution of irradiation in the 1-year-old stems of beech (n = 5).



Bark reflectance (%)	400 - 700 nm	700 - 1100 nm	400 - 500 nm	500 - 600 nm	600 - 700 nm
1-year-old stems	17.6 ± 2.2	51.5 ± 4.8	9.7 ± 1.2	16.7 ± 2.1	26.5 ± 3.4
2-year-old stems	12.5 ± 2.3	48.6 ± 1.0	6.3 ± 0.4	10.9 ± 1.0	19.9 ± 1.7
3-year-old stems	12.9 ± 2.2	46.8 ± 2.3	7.1 ± 0.8	12.5 ± 1.3	19.6 ± 2.2
10-year-old stems	10.1 ± 1.6	36.1 ± 1.6	7.6 ± 0.9	10.9 ± 0.8	15.2 ± 2.4
Trunks	14.9 ± 2.1	36.8 ± 1.8	13.1 ± 0.2	14.9 ± 2.7	16.7 ± 3.1

Fig. 2. Spectral reflectance of the bark of the different stems age (n = 5).

wavelength. In the 400 nm range it amounted to 92%, in 700 nm - to 33% but it decreased 5% in the 1100 nm range. The mean absorption in the PAR range was equal to 60% and in the NIR range – to 10%. The intensity of irradiation transmitted to the chlorophyll layer increased with the increasing wavelength in the PAR range, decreased in the range 700-750 nm and increased again in the range from 750-1100 nm. In 400 nm, the transmittance of irradiation was almost equal to zero; in 700 nm it was equal to 45%, whilst it decreased to 37% in 750 nm and increased to 40% in 1100 nm. Transmittance of irradiation in the PAR range amounted to 23%, and in the NIR range it was equal to 39%.

The dependence of the reflectance of irradiation on the stem ages is illustrated in Fig. 2. With the age of the stems it becomes reduced, although the changes are rather small and in the PAR range, the difference between 1-year-old and 10-year-old stems amounted to 7%, and in the NIR range the difference increased to 15%. In the whole examined range the reflectance of 1-year-old stems was the greatest, whilst that of the 2- and 3-year-olds was similar. The age of the stems has no influence on the inner reflectance both in the PAR and NIR range (Table 1).

Fig. 2 also shows the reflectance of irradiation in the bark of trunks. It represents the mean from five measurements carried out on the bark of trees of various diameters, from 20-60 cm. The small standard deviation is an indication that the age of the trees had no essential influence on this parameter. In the 400-700 nm range, the reflectance in the trunks increased slowly with increasing wavelength

from 14% in the range 400 nm to 20% for 700 nm. In the NIR range the increase of reflectance was greater and in 1100 nm the reflectance amounted to 51%. The mean value for the PAR range was equal to 15%, and in the NIR range, to 37%.

The results of measurements of the absorption of cork in stems of various ages are presented in Fig. 3. They show that the age of the beech stems had no significant influence on the absorption of cork. In the examined year groups, with increasing wavelength, the absorption in the PAR range decreased rapidly from about 93% in the range 400 nm to about 30% in 700 nm, while in the NIR range the decrease was gradual to 10% in 1100 nm.

The spectral transmittance of irradiation in the cork to the chlorophyll layer of the bark is illustrated in Fig. 4. The curves have a similar progress and differ only in their values. With the increase of the wavelength to 700 nm the transmittance increased almost linearly. Above 700 nm up to 750 nm, the transmittance decreased considerably and a further increase of the wavelength to 1100 nm caused only a small increase in transmittance. In the whole examined range, the cork transmittance was greatest in the case of the 10-year-old stem and the least for a 2-year-old one. In the PAR range, the cork transmittance of a 10-year-old stem was similar to that of a 3-year-old one and 10% greater than that of a 1-year-old stem, and 13% greater than the cork transmittance of a 2-year-old stem. In the NIR range, the transmittance in 1-3-year-old stems was similar – about 38.5%, and that of a 10-year-old stem amounted to 46%.

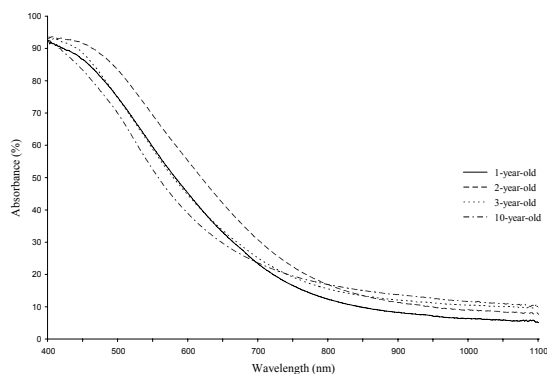


Fig. 3. Spectral absorption of the different stems age cork (n = 5).

Cork absorption (%)	400 – 700 nm	700 – 1100 nm	400 – 500 nm	500 – 600 nm	600 – 700 nm
1-year-old stems	59.3 ± 6.7	10.0 ± 1.7	85.2 ± 1.4	59.1 ± 7.7	33.1 ± 11.8
2-year-old stems	67.3 ± 32.1	13.6 ± 2.3	90.3 ± 0.3	68.6 ± 2.8	41.9 ± 3.2
3-year-old stems	60.0 ± 1.8	13.6 ± 1.6	86.6 ± 1.5	57.8 ± 1.6	34.7 ± 2.2
10-year-old stems	56.2 ± 2.2	17.7 ± 1.0	84.6 ± 2.6	52.6 ± 4.0	29.9 ± 1.5

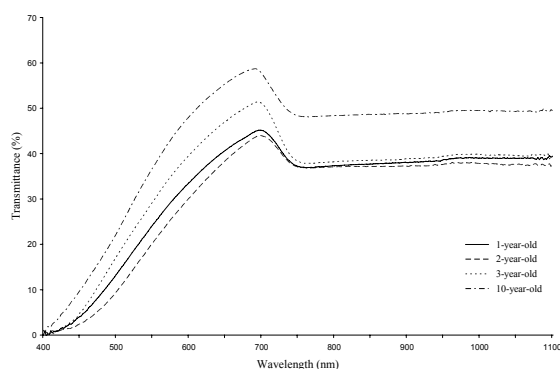


Fig. 4. Spectral transmittance of the cork of the different stems age (n = 5).

Cork transmittance (%)	400 – 700 nm	700 – 1100 nm	400 – 500 nm	500 – 600 nm	600 – 700 nm
1-year-old stems	23.1 ± 2.5	38.5 ± 2.9	5.1 ± 1.6	24.2 ± 2.7	40.4 ± 3.1
2-year-old stems	20.2 ± 2.2	37.8 ± 1.0	3.4 ± 0.4	20.5 ± 1.5	38.2 ± 2.7
3-year-old stems	29.7 ± 2,1	39.6 ± 2,6	6.3 ± 1.0	29.7 ± 1.5	46.7 ± 2.5
10-year-old stems	33.7 ± 2.1	46.2 ± 1.0	7.6 ± 1.1	36.5 ± 1.9	54.9 ± 2.8

Table 1. Internal reflectance of the different stem ages (n = 5).

Internal reflectance	400-700 nm	700-1100 nm	400-500 nm	500-600 nm	600-700 nm
1-year old	1.6	19.1	0.5	1.5	2.7
2-year old	0.9	18.8	0.2	0.8	1.5
3-year old	1.8	17.9	0.4	1.5	3.0
10-year old	1.1	18.2	0.5	1.3	1.4

The presented results indicate that the optical properties of the beech stems do not change greatly with age. A reduction of reflectance in the bark can be observed and the absorption of the cork does not greatly change, whereas the transmittance of cork shows an increase and in 10-year-old stems it was the greatest in the examined year groups of stems. The cork reaches its stable thickness on the trunks and its reflectance does not change with trunk thickness.

Discussion

Distribution of irradiation in the leaves is a frequent object of investigation and there is a lot of information on this subject in the literature. In the PAR range, the reflectance of irradiation in the leaves amounts to 6-20%, the absorption to 50-95% and transmittance to 1-15% [3, 30]. In the leaves, only 1-7% of the absorbed irradiation is chemically bound in the process of photosynthesis [25, 26].

In the process of photosynthesis in stems, the irradiation can be utilized only after it has been transmitted by the cork. It is much weaker and spectrally changed in comparison with incident irradiation as a result of the cork reflectance and absorption. In most species the light conditions in the bark deteriorate with the age of the stems.

The decrease of reflectance with the stems age, similarly as in the case of the beech, has been observed in other plant species e.g. in lilac (*Syringa vulgaris* L.) [1], and apple (*Malus domestica*) tree [2]. It is caused by the bursting of the outer layer of cork as a result of the increasing thickness of the stems, due to the action of cambium and phellogen. The cork surface does not present a smooth surface and it is full of grooves that reduce the reflection of irradiation. Cork cells die soon after formation and in their cell walls waxes, suberin and tannins accumulate, which causes brownish or even dark dyeing of the cork. Grooves in the cork's surface as well as a cork's brownish or dark colour and scattering inside stem tissues influence reflectance decrease and absorption increase. In the case of beech the dead cells of the cork peel off, resulting in an uneven cork surface, whilst the effect is similar to that observed in plant species with the growing thickness of cork.

Investigations carried out in the PAR range on the stems of lilac (*Syringa vulgaris* L.) [1], have shown that in the current year stems, the reflectance was equal to 25%, absorption 59% and transmittance – 17%. With the age of the stems the optical properties changed, and in a 3-year-old

stem the reflectance diminished to 12%, the absorption increased to 79% and transmittance diminished to 10%. During that time the cork thickness tripled and the content of photosynthetic pigments diminished by about 40% [1]. In the apple (*Malus domestica*) tree [2] in the current years stem, the reflectance amounted to 14%, absorption – 55% and transmittance – 30%, and in 3-year-old stems the reflectance diminished to 10%, the absorption increased to 66% and transmittance diminished to 23%. In the apple (*Malus domestica*) tree, the thickness of cork at that time increased by about 80% and the content of the photosynthetic pigments remained relatively unchanged. These results indicate that in the apple (*Malus domestica*) tree, the light conditions for photosynthesis are much more favourable in comparison with lilac (*Syringa vulgaris* L.). In the author's investigations carried out on beech trees over a period of 10 years, the reflectance diminished by about 6%, the absorption of the cork in 1- and 10-year-old stems was similar and transmittance increased with the age of the stems from about 22% in 1- and 2-year-old stems to 34% in 10-year-old ones. In the case of beech, the amount of irradiation reaching the chlorophyll-containing cells of the bark is significantly higher in comparison with the apple (*Malus domestica*) tree.

The inner reflectance in the beech in the PAR range was rather small, which is evidence of its great absorption in the chlorophyll layer of the bark. There is no literature data available concerning the inner reflectance in the stems of lignified plants. In the investigations on the leaves of ilex it was deemed equal to about 15% [3], thus considerably more than in the bark of beech. Increased reflectance in the NIR range prevents excessive warming of the stems. Reflectance and absorption values in NIR range are connected with the amount of live cells, their relative water content and cell walls' colour – the driest cell or tissue the biggest reflectance [3]. Investigations carried out on various tree species have shown that infrared absorption by the bark of a beech tree amounts to 70% and is the highest from among the investigated 17 species of trees in which the mean values of absorption in the range amounted to 40-60% [27]. Similar results have been obtained in the present study when summing up the absorption and transmittance of cork. Investigations carried out on poplar have shown that reflectance in the bark of stems in the PAR range amounted to about 15%, in the range above 700 nm it increased rapidly to 70% in the range 950 nm and to 80% in 1100 nm [28]. In the beech tree the increase of

reflectance above 700 nm was equal to only 19% and above 750 nm the changes of reflectance were small. The age of stems decreased in reflectance, which might be caused by a decrease of live cells and brownish or even dark dye of the cell walls.

In the beech, the increase of the cork thickness with the age of the stems is rather small and this accounts for the small changes of the cork absorption with the age of stems and the cork thickness of the beech trunk is smaller than the cork thickness of 3-year-old stems of lilac (*Syringa vulgaris* L.), and the observed increase of transmittance in 10-year-old stems should be attributed to the fact that the outer dead cells of the cork break off more easily.

The spectral transmittance of cork in the PAR range shows a similar course in various plants. It is very small in the range 400 nm, but increases with increasing wavelength and is the highest at 700 nm [1, 2, 19]. In lilac (*Syringa vulgaris* L.) and in the apple (*Malus domestica*) tree in the range 400 nm, the transmittance in the current year stems amounted to about 5%, decreasing with the age of the stems, and in 3-year-old stem it was equal to about 1%. In the author's investigations on beech, the cork transmittance in 400 nm was close to zero in all examined year groups of stems, and in 700 nm it increased up to 60% in 10-year-old stems. Pfanz and Aschan [19] in 700 nm obtained a transmittance of 40% in the beech and a little above 30% in the poplar tree. In lilac (*Syringa vulgaris* L.) the transmittance amounted to 65% [1] and in the apple (*Malus domestica*) trees in 700 nm the transmittance in the current year stems and 1-3-year-old stems was similar, amounting to 53-56% [2]. Investigations carried out on other species of lignified plants show a decrease of cork transmittance by as much as 50% in 2-year-old stems in comparison with the current year stems [19]. In the apple (*Malus domestica*) tree in the PAR range, the cork transmittance in the current year stems amounted to 30%, and in 3-year-old stems it decreased to 23%. In the author's investigations carried out on beech in the PAR range, the cork transmittance in the 1- and 2-year-old stems amounted to 23-34% and was smaller in comparison with the 10-year-old stems.

In the case of poplar [28] report about the cork transmittance in the blue range amounting to 20-30% and in the red range – to 50-60%. In the author's investigations, the cork transmittance in the range 400-500 nm was equal to 3.4-7.3%; thus it was much smaller in comparison with the results obtained on the poplar tree and in the range 600-700 nm it amounted to 38-50%, which was smaller but closer to the results obtained on poplar.

A comparison of the results obtained by other authors is difficult, because in their investigations the accurate age of the examined stems in most cases was not taken into consideration.

In presented results the optical properties of the bark of the stems and trunks of beech change little with the age of the trees. This accounts for the presence of photosynthetic pigments in the bark of a beech tree under the cork, during the whole life of the tree and the bark is photosynthetically active during the whole life of the tree.

References

- PILARSKI J. Optical properties of bark and leaves of *Syringa vulgaris* L. Bull. Acad. Pol. Sci. Biol. Sci. **37**, 253, **1989**.
- TOKARZ K., PILARSKI J. Optical properties and the content of photosynthetic pigments in the stems and leaves of the apple tree. Acta Physiol. Plant. **27**, 183, **2005**.
- HODANOVA D. Leaf optical properties. In: Z. Šesták (ed). Photosynthesis during leaf development. Academia, Praha: pp. 107–127, **1985**.
- VOGELMANN T. C. Plant tissue optics. Annu. Rev. Plant Physiol. Plant Mol. Biol. **44**, 231, **1993**.
- CLARK J. B., LISTER G. R. Photosynthetic action spectra of trees. II. The relationship of cuticle structure to the visible and ultraviolet spectral properties of needles from four coniferous species. Plant Physiol. **55**, 407, **1975**.
- MARTIN G., JOSSERAND S. A., BORNMAN J. F., VOGELMANN T. C. Epidermal focussing and light microenvironment within leaves of *Medicago sativa*. Physiol. Plant. **76**, 485, **1989**.
- McCLENDON J. H. The microoptics of leaves. I. Patterns of reflection from the epidermis. Amer. J. Bot. **71**, 1391, **1984**.
- REICOSKY D. A., HANOVER J. W. Physiological effects of surface waxes. I. Light reflectance for glaucous and nonglucous *Piceapungens*. Plant Physiol. **62**, 101, **1978**.
- GAUSMAN H. W. Photomicrographic record of light reflected at 50 nanometers by cellular constituents of Zebrina leaf epidermis. Agron. J. **65**, 504, **1973**.
- GAUSMAN H. W. Reflectance, transmittance, and absorption of light by subcellular particles of spinach (*Spinacia oleracea* L.). Agron. J. **64**, 551, **1973**.
- SINCLAIR T. R., SCHREIBER M. M., HOFFER R. M. Diffuse reflectance hypothesis for the pathway of solar radiation through leaves. Agron. J. **65**, 276, **1973**.
- WOOLLEY J. T. Refractive index of soybean leaf cell walls. Plant Physiol. **55**, 172, **1975**.
- LARCHER W., LÜTZ M., NAGELE M., BODNER M. Photosynthetic functioning and ultrastructure of chloroplasts in stem tissues of *Fagus sylvatica*. J. Plant Physiol. **132**, 731, **1988**.
- PFANZ H., ASCHAN G., LANGENFELD-HEYSER R., WITTMAN C., LOOSE M. Ecology and ecophysiology of tree stems corticular and wood photosynthesis. Naturwissenschaften **89**, 147, **2002**.
- PILARSKI J., TOKARZ K. Chlorophyll distribution in the stems and trunk of beech trees. Acta Physiol Plant **28**, 523, **2006**.
- SZUJKO-LACZA J., RAKOVAN J. N., HORVATH G., FEKETE G., FALUDI-DANIEL A. Anatomical, ultrastructural and physiological studies on one-year old *Euonymus europaeus* bark displaying photosynthetic activity. Acta Bot. Acad. Sci. Hung. **20**, 393, **1971**.
- PILARSKI J. Content of chlorophyllous pigments in shoot bark and leaves in *Syringa vulgaris* L. Bul. Acad. Pol. Sci. Ser. Biol. Sci. **32**, 415, **1984**.
- PILARSKI J. Gradient of photosynthetic pigments in the bark and leaves of lilac (*Syringa vulgaris* L.). Acta Physiol. Plant. **21**, 365, **1999**.
- PFANZ H., ASCHAN G. The existence of bark and stem photosynthesis in woody plants and its significance for the overall carbon gain. An eco-physiological and ecological approach. Prog. In Bot. **62**, 477, **2001**.

20. ZOTIKOVA A. P., ZAITSEVA T. A. Effect of white and red light on the pigment content and functional activity in pie chloroplasts. *Russian Journal of Plant Physiology*, **47**, 748, **2000**.
21. BERVEILLER D., KIERZKOWSKI D., DAMESIN C. Interspecific variability of stem photosynthesis among tree species. *Tree Physiol.* **27**, 53, **2007**.
22. CESCHIA E., DAMESIN C., LEBAUBE S., PONTAILLES J-Y., DUFRÊNE E. Spatial and seasonal variations in stem respiration of beech trees (*Fagus sylvatica*). *Ann. For. Sci.* **59**, 801, **2002**.
23. DAMESIN C. Respiration and photosynthesis characteristics of current-year stems of *Fagus sylvatica*: from the seasonal pattern to an annual balance. *New Phytol.* **158**, 465, **2005**.
24. LARCHER W., NAGELE M. Changes in photosynthetic activity of buds and stem tissues of *Fagus sylvatica* during winter. *Trees* **6**, 91, **1992**.
25. NOBEL P. S. *Physicochemical and environmental Plant physiology*, 3rd edn. Elsevier, Academic Press, Amsterdam Boston Heidelberg London New York Oxford Paris San Diego San Francisco Singapore Sydney Tokyo, **2005**.
26. SALLE P.J.M. Net carbon exchange rates of field-grown crops in relation to irradiance and dry weight accumulation. *Aust. J. Plant Physiol.* **7**, 555, **1977**.
27. NICOLAI V. The bark of trees: thermal properties, microclimate and fauna. *Oecologia*, Berlin, **69**, 148, **1986**.
28. KHAROUK V. I. MIDDLETON E. M., SPENCER S. L., ROCK B. N., WILLIAMS D. L. Aspen bark photosynthesis and its significance to remote sensing and carbon budget estimate in the boreal ecosystem. *Water, Air, Soil Pollut.* **82**, 483, **1995**.
29. MANETAS Y., PFANZ H. Spatial heterogeneity of light penetration through periderm and lenticels and concomitant patchy acclimation of corticular photosynthesis. *Trees* **19**, 409, **2005**.
30. PILARSKI J. Optical properties of plants. (in ed) Maria Filek, Jolanta Biesaga-Kościelniak, Izabela Marcińska, Institute of Plant Physiology, Polish Academy of Sciences, Kraków, Poland, pp.143-158, **2004**.
31. ESAU K. *Plant anatomy*. John Wiley & Sons, Inc., New York, **1967**.
32. GAUSMAN H. W. Reflectance of leaf components. *Remote Sens. Environ.* **6**, 1, **1977**.
33. VOGELMANN T. C. Penetration of light into plants, *Photochem. Photobiol.* **50**, 895, **1989**.