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Original Research

Implication of Stem Structures for Photosynthetic Functions in Select Herbaceous Plants

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Abstract

For our investigation two species of herbaceous plants were selected with different morphological and anatomical stem structures: Japanese knotweed and topinambur. The distribution of chlorophyll (chl) in photosynthetically active tissues, divided into younger and older parts of stems, was studied by the use of the chl autofluorescence phenomenon. The content of chl in the stems of the topinambur was lower than in leaves by ca. 40-50%. In the J. knotweed, the quantity of chl was lower by ca. 70% in the young fragments of stems than in leaves, whereas in the older parts it approached the levels found in leaves. The chl *a/b* ratio was generally higher in leaves compared with stems. It was also found that the maximal efficiency of PSII (F_v/F_m) did not differ greatly between leaves and stems in these two plant species. Despite this, the maximal net photosynthetic rates (P_N) in the stems of both species were low and kept to level of 0-0.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Much higher levels of P_N were noted in the leaves of J. knotweed at ca. 10 and ca. 14 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in the topinambur. The stems of herbaceous plants are characterized by high resistance of the epidermis, although they do not have a cork limiting light and transpiration. As a result, similar to lignified, the stems of herbaceus plants use mainly internal CO_2 from respiration in the process of photosynthesis.

Keywords: carbon fixation, carotenoids, chlorophyll content, chlorophyll fluorescence, corticular photosynthesis, conductance, diffusive resistance, Japanese knotweed, stem, topinambur

Introduction

The stem as well as leaves of some chlorophyll-containing flowers and fruits all participate in CO_2 assimilation by plants. The proportion of the stem in trees and shrubs in the overall photosynthesis of the plant is estimated by various authors to be 5-15% [1-3]. The principal factor limiting the intensity of photosynthesis in the stems of lignified plants is believed to be the low availability of photosynthetically active radiation (PAR), caused by high absorption and low transmission by the cork.

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The high absorption of radiation by the cork results in a mere 10-30% of radiation reaching the chl layer of the cork [4, 5], which is the main place where the photosynthetic pigments occur in the stems of lignified plants [6]. Despite this, chl can be distributed across the section of the stem, which testifies to the penetration of the PAR there [7-9].

The stems of woody plants usually contain smaller quantities of photosynthetic pigments compared with leaves [3-6]. In young stems, which have a thin cork layer, the content and composition of chl may be similar to that in leaves, but with the increasing age of the stem and increased thickness of the cork, the proportion in *a/b* ratio decreases. Again, the proportion between chl *a/b* decreases with the distance from the surface of the stem [10].

In herbaceous plants which lack a cork layer, light penetration into the stem is easier than that in lignified plants. The optical properties of stems of herbaceous plants do not differ much from those of leaves, i.e. ca. 80-90% of falling radiation within the scope of 400-700 nm is absorbed by them, which amounts to ca. four times more than in lignified plants [11].

Independent of light conditions on positive net photosynthetic rate (P_N) in stems is rarely to be seen [12, 13]. It seems that the gasometric methods for determination of the proportion do not reflect the real value because of CO_2 reassimilation [14, 15]. The occurrence of the C_4 cycle found in the stems of herbaceous plants can additionally boost the increased proportion of photosynthesis, contributed by the stem to the total for the plant [16, 17].

For this reason, the determination of chl *a* fluorescence provides a more comprehensive picture of the photosynthetic activity of stems. These determinations were applied to plants having a cork layer [18-20], as well as in the stems of herbaceous plants [21].

The maximum quantum efficiency of PS II (F_v/F_m) is a very sensitive indicator of the state of the PS II and, in healthy leaves, usually stands at 0.83 [22, 23]. Still, the value of the parameter may differ depending on the species, and also between various organs of the plant, as they may also vary during the course of vegetation season. In some herbaceous plants, e.g. *Helleborus viridis*, the maximum quantum efficiency of PS II of leaves and green non-leaf organs fell between 0.74 and 0.79 [21], whereas in the stems of lignified plants, this value was lower than that in their leaves and ranged from 0.65 at the beginning of the vegetation season to 0.78 in the summer [19].

The objective of this study was to find whether the photosynthetic activity in the stems of herbaceous plants lacking a cork layer (i.e. with higher penetration by light) may occur with higher intensity than in lignified plants.

Material and Methods

The studies were conducted on two species of herbaceous plants having stems of a different structure; namely: Japanese knotweed (*Reynoutria japonica* Houtt.), which has a smooth-surfaced leaves and stems, with air chambers occupying most of the pith of the stem, and with lenticels in the stem epidermis: and secondly topinambur (*Helianthus tuberosus* L.), with hair-covered stems where the pith is filled with parenchymal cells, and epidermis lacking lenticels. The plants were cultivated in field conditions.

The measurements were taken in early September, before anthesis. The leaves and stems used for measurement were taken from two levels along the height of the plant: at the first node above ground level with healthy leaves (older fragment) and, from the upper part of the plant, at the first node from the top (younger fragment), having a fully developed leaf.

Photosynthetic pigments: chl *a* and *b*, and the sum of carotenoids were measured in 80% acetone using the method described by Wellburn [24]. The content of the pigments was expressed in $mg \cdot dm^{-2}$. The data presented are the arithmetic means of five repetitions. Statistical analyses of the data were made with Statistica 6.0 (Statsoft, Tulsa, OK, USA).

The distribution of chl in stems was determined by using the autofluorescence of chl *a*. Cross-section fragments of stems with a thickness of about 1 mm were soaked in a few drops of polyethylene glycol. The images of fluorescence were recorded with a Bio-Rad MRC 1024 (Bio-Rad Microscience, Herts, UK) confocal microscope equipped with a Nikon Diaphot 300 microscope (Nikon, Amsterdam, NL) and PlanFluor 10 ×, NA 0.3 lens. The autofluorescence in the studied plant tissues was excited by a 488 nm line emitted by a 100 mW argon laser (ILT, USA). The images of square-shaped areas with 1,040 μm-side, were recorded using 512×512 pixels and 8 bits resolution. Fluorescence was recorded within a 515-630 nm range (cell walls) and 640-700 nm range (chl). Also recorded were images in transmitting light. In the combined confocal images, the fluorescence within a 515-630 nm range – representing the cell autofluorescence was – green color, within a 640-700 nm range – autofluorescence of chl – red color, and the images in transmitted light – blue color.

The measurements of gas exchange were conducted in the leaves and stems in natural conditions using a Portable Photosynthesis System LI-6400 (LI-COR Inc., Lincoln, NE, USA). The measurements included: P_N, PAR, air temperature, and total conductance to water vapor (g_{tw}) for leaves and stems.

The diffusive resistance of the leaves and the stems for water vapor was measured on plants growing in field conditions, by means of a porometer MK-3, Delta-T Devices Ltd., Cambridge, UK). The measurements were conducted in 30 replicates and the list of the results presents the arithmetic means with standard deviations. The results were calculated in $s \cdot cm^{-1}$.

The determination of chl *a* fluorescence was conducted using a fluorometer Handy-PEA (Hansatech Instruments Ltd., Norfolk, UK). The measurements were conducted in the laboratory, on leaves and stems. Prior to the measurement-taking, the plants were kept in darkness for 20 minutes. The intensity of excitation was 1,500 $\mu mol \cdot m^{-2} \cdot s^{-1}$, and measurement duration was 1 s. Parameters were determined according to Strasser et al. [25].

Results

Photosynthetic Pigment Content

The results of photosynthetic pigment content measurements obtained for the leaves and stems of J. knotweed are shown in Fig. 1. In older leaves, somewhat higher content of chl *a* and *b*, were found compared with younger leaves. However, the chl *a* content increased, in the older fragments of stem – threefold, and that of chl *b* – fourfold, compared with the younger fragments. At the same time, the chl content in younger fragments of the stem was lower than in leaves, whereas in older fragments – slightly higher than in leaves. The sum of chl in the older fragments of the stem

amounted to ca. 2.8 mg·dm^{-2} and, in leaves at the same height of the plant, 2.3 mg·dm^{-2}. The chl *a/b* ratio in younger parts was higher compared with older fragments: in leaves it was 3.2 and 2.4, whereas in the stems the differences were smaller: 2.1 and 1.7. In the leaves examined, the carotenoids content stayed at the same level (0.43 mg·dm^{-2}), but in the older parts of the stems it was higher by a factor of 2 compared with the younger ones. In the older fragments of leaves and stems, a higher ratio of Chlorophylls/Carotenoids was noted compared with younger ones.

The results obtained for topinambur are illustrated in Fig. 2. In a difference to the case of J. knotweed, the chl content of the stems of topinambur was always lower than in their leaves: with respect to chl *a* by ca. 50% and chl *b* by ca. 30%. The carotenoid content in stems was also lower by ca. 30% compared with leaves. The chl and carotenoid contents in the whole stem were similar. The situation was different in the case of leaves: the upper leaves had a higher chl *a* content and higher *a/b* ratio. The sum of chl in younger leaves was ca. 3 mg·dm^{-2}, in older leaves 2.7 mg·dm^{-2}, and in stems ca. 1.5 mg·dm^{-2}.

Chlorophyll Distribution in Stems

Figs. 3 and 4 illustrate the autofluorescence of younger (A) and older (B) parts of stems.

In the younger part of the J. knotweed stem (Fig. 3 A), chl was present in both epidermis and the bark, as well as in conductive bundles: in phloem, xylem parenchyma, and (as traces) in the pith. The strongest fluorescence was exhibited by cortex as well as phloem and xylem parenchyma. With the increasing thickness of the stem (Fig. 3 B), the cortex and phloem thickness also increased. These tissues manifested intensive fluorescence, thereby marking significant chl content. Thickness increments in other tissues, such as phloem fibres and xylem, show low-intensity fluorescence.

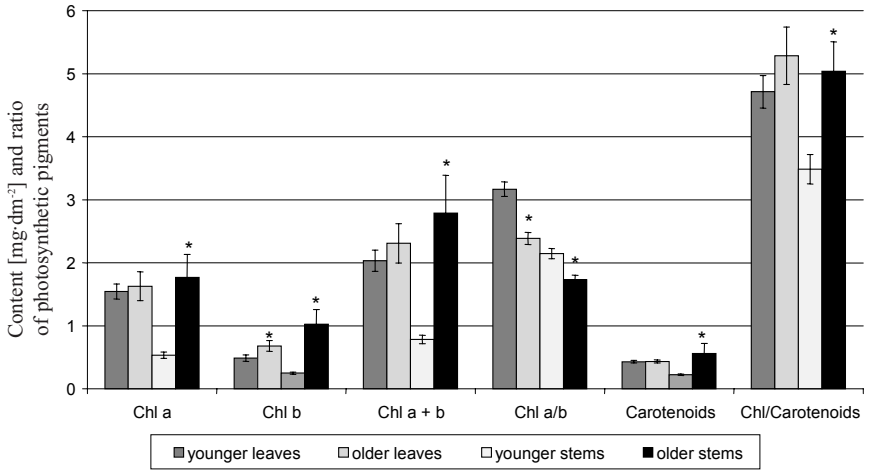

Fig. 1. Photosynthetic pigment content of leaves and stems of Japanese knotweed. Means ± SD. (n=5). T-tests were performed for values of corresponding pairs (younger and older) for leaves and stems separately.
**Significant differences compared to younger parts at p<0.001*.

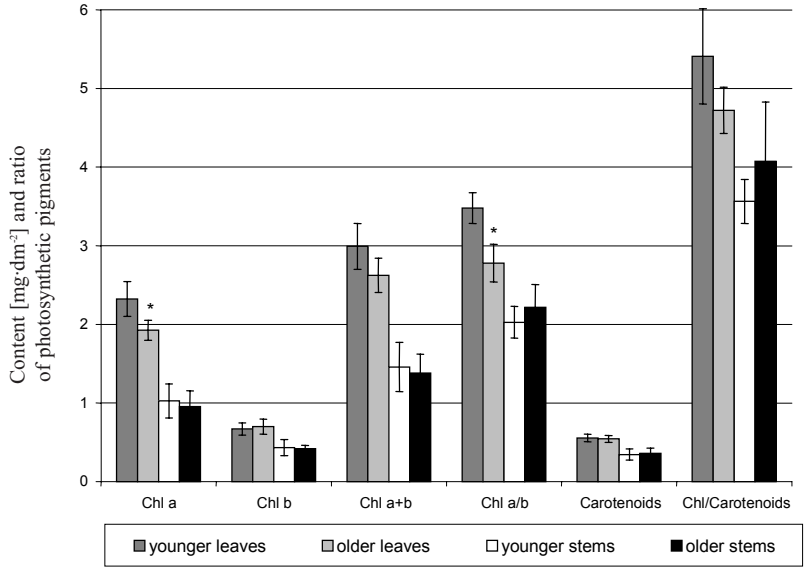

Fig. 2. Photosynthetic pigment content of leaves and stems of topinambur. Means ± SD. (n=5). T-tests were performed for values of coresponding pairs (younger and older) for leaves and stems separately.
**Significant differences compared to younger parts at p < 0.001*

Table 1. The density of stomata on leaves, density of lenticels on stems, and the resistance of leaves and stems.

Variable	Topinambur			Japanese knotweed		
	Leaves		Stems	Leaves		Stems
	Adaxial surface	Abaxial surface		Adaxial surface	Abaxial surface	
Stomatal density [pores mm^{-2}]	18.5±6	148±20	0	0	129±20	0
Lenticel density [pores cm^{-2}]	0	0	0	0	0	12.5±6
Diffusive resistance [$s \cdot cm^{-1}$]	1,350±581	205±45	4,500±417	5,100±1,308	200±32	6,300±2,026

Means±SD, (n=30).

Table 2. Comparison between chlorophyll *a* fluorescence parameters in the leaves and stems of Japanese knotweed and topinambur.

Species		F_o	F_m	F_v	F_v/F_m	Tfm [ms]	Area
Japanese knotweed	Leaves	178.9±13.7	1,055.2±112.8	876.2±104.4	0.830±0.013	514.2± 73.6	36,534± 4,459
	Stems	162.7± 13.5	885.1± 102.4	722.3±95.2	0.815±0.019	615.7±91.6	13,310±1,726
Topinambur	Leaves	197.8±20.3	1,218.4 ±103.5	1,020.6±97.5	0.837±0.018	378.4±99.7	34,234±6,388
	Stems	133.0±21.5	803.4±177.2	670.3±156.1	0.832±0.011	636.4±65.0	14,700±2,984

Means ± SD, (n=30).

In the younger fragment of the topinambur stem (Fig. 4 A), similar to the case of J. knotweed, the strongest fluorescence was observed in the cortex and conductive bundles: both in phloem and xylem, as well as in pith rays, whereas fluorescence in pith was weaker. In the section obtained for an older fragment of internode (Fig. 4 B), the highest chl content can be found in the bark, pith rays, and primary xylem. Considerably less fluorescence can be observed in the phloem and phloem fibres, as well as in the wood parenchyma and (as traces) in the pith.

In both species, chl fluorescence is also observed in the epidermal cells, and also in the hairs of the topinambur. The analysis of the chl location indicates that in young stems, chloroplasts are present in all tissues, with the highest numbers occurring in external tissues of the stems. Furthermore, with increases in thickness the chloroplasts vanish from the tissues situated deeper in the stem.

Diffusive Resistances

In the species under study, the adaxial side of the leaves lacked stomata (as in J. knotweed) or had only a small number thereof (as in the topinambur) (Table 1). The stomata were situated on the abaxial side of leaves and had similar densities – 148 mm^{-2} in the topinambur and 129 mm^{-2} in the J. knotweed. The stems lacked stomata in both species, whereas on the stems of J. knotweed there were ca. 13 lenticels per cm^2, whereas the topinambur stems lacked them altogether.

The results of porometric diffusive resistance measurements for water vapour showed (Table 1) that the stomatal resistance of the abaxial side of leaves was similar in both species (ca. 200 $s \cdot m^{-1}$). The diffusive resistance of the adaxial surface of topinambur leaves with hairs was ca. 1,350 $s \cdot cm^{-1}$ – almost 7 times higher compared with the abaxial side of leaves. In smooth leaves of J. knotweed, the diffusive resistance of the upper side of leaves was ca. 5,100 $s \cdot m^{-1}$ and thus was more than 25 times higher than that of the abaxial, and several times higher compared with the adaxial part of topinambur leaves.

The results of diffusive resistance measurements in stems showed that they were high compared with the abaxial side of leaves, but were more similar to the resistances of the adaxial sides of leaves. The diffusive resistance of hair-covered stems of the topinambur was ca. 4,500 $s \cdot cm^{-1}$, whereas on the smooth stems of J. knotweed it was 6,300 $s \cdot cm^{-1}$.

Gas Exchange

The daily changes in some parameters of gas exchange in leaves are illustrated in Fig 6. In the morning hours the intensity of P_N of the leaves of both plants was increasing together with the increase in PAR intensity, while the temporary descent at noon was connected with the overcast skies. P_N was generally higher in the case of topinambur (up to 14 μmol $m^{-2} \cdot s^{-1}$) in comparison to the J. knotweed, whose P_N wasn't exceeding 10 μmol $m^{-2} \cdot s^{-1}$. Since 5 p.m. a decrease in the intensity of P_N was being noted and since 7 p.m. dark respiration was noted, which in the case of both species was about 0.4 μmol $m^{-2} \cdot s^{-1}$.

G_{tw} daily changes was very similar to P_N. G_{tw} in case of topinambur reached 230 $mmol \cdot m^{-2} \cdot s^{-1}$ during the high intensity of PAR, while in the case of J. knotweed it wasn't exceeding 150 mmol $m^{-2} \cdot s^{-1}$.

In Fig. 6 the parameters of gas exchange of stems of J. knotweed and topinambur were compared. The daily progress of P_N in the stems was different in both plants. In the stems of J. knotweed a little P_N (up to 0.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$) was noted in the morning and afternoon hours, when the stems were in higher irradiance, above 400 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Since 5 p.m. the efflux of CO_2 was being observed.

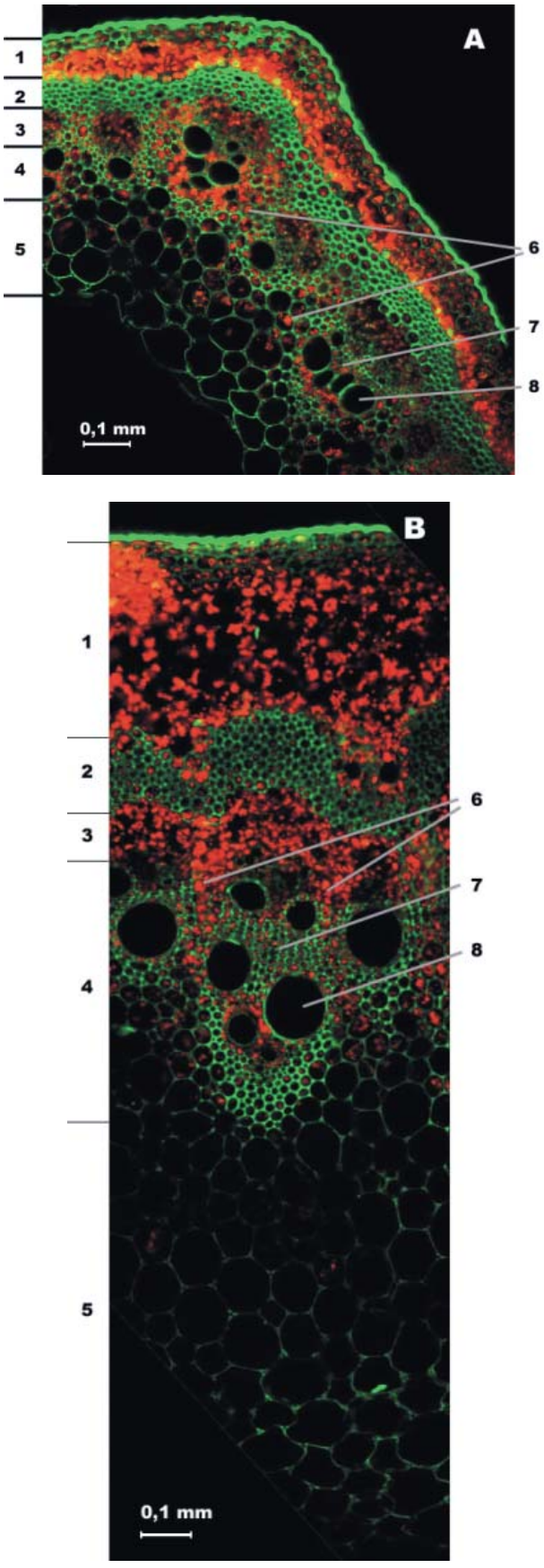

Fig. 3. Cross-section of Japanese knotweed stem: A – younger fragment, B – older fragment. 1 – cortex, 2 – pericyclic sclerenchyma, 3 – phloem, 4 – xylem, 5 – pith, 6 – rays, 7 – xylem parenchyma cells, 8 – vessels. Red – autofluorescence of chlorophyll, green – autofluorescence of cell walls.

As for topinambur, since the beginning of taking measurements until 11 a.m. the P_N was fluctuating about 0 μmol·m^{-2}·s^{-1}, while between 12 a.m. and 2 p.m. the release of about 0.5 μmol·m^{-2}·s^{-1} took place. The highest P_N was noted at 3 p.m. – about 0.25 μmol·m^{-2}·s^{-1}. Since 4 p.m. a release of CO_2 was being noted again; it was gradually increasing and after sunset was equal to 1.5 μmol·m^{-2}·s^{-1}.

The g_{tw} of stems' epidermis was on the level of about 10-20 mmol·m^{-2}·s^{-1} in the case of topinambur and from 1 to 2.3 mmol·m^{-2}·s^{-1} in the case of J. knotweed. In comparison to the leaves, P_N of the stems was very low – in the case of topinambur it was up to 2.5% of the value of P_N in the leaves, in the case of J. knotweed – 10% of it.

Similarly, the g_{tw} of stem epidermis was very low at ca. 1% of the value obtained for the leaves of J. knotweed and ca. 10% for those of topinambur.

Chl *a* Fluorescence Parameters

The results of chl *a* fluorescence measurements in leaves and stems are presented in Table 2. The fluorescence curves in the leaves and stems of J. knotweed differ throughout their course (Fig. 7). The minimal fluorescence (F_o) value for leaves was ca. 10% higher compared with the stems. The values increased with time and reached maximum fluorescence (F_m) sooner in leaves – after 512 ms, and a bit later – after 616 ms – in stems. F_m and variable fluorescence (F_v) of leaves reached values some ca. 20% higher than the stems. These significant differences in F_o, F_m, and F_v between leaves and stems did not, however, translate into a maximum quantum efficiency of PS II (F_v/F_m), which stayed only slightly lower in stems compared with leaves: at 0.815 and 0.830, respectively. The area above the graph signifying the plastoquinone pool was, however, markedly different. In leaves, it was more than 2.5 times higher than in stems.

In topinambur, the differences in the direction of the fluorescence curves of leaves and stems were much greater. The values of F_o in leaves was 50% higher compared with stems. Topinambur leaves reached maximum fluorescence much sooner, after only 378 ms, compared with stems where Tfm was 636 ms. F_m, as well as F_v in leaves, reached values some 50% higher than in the stems. At the same time, the maximum quantum efficiency (F_v/F_m) in leaves (0.837) was not significantly different from that in stems (0.832). The area above the graph for leaves was, however, almost 2.5 times greater compared with stems.

Discussion

Due to the lack of cork, the stems of herbaceous plants can benefit from better light conditions to perform corticular photosynthesis than those of the lignified plants. Photosynthetic assimilation of CO_2 in the stems of herbaceous plants should contribute to improved carbon balance more than in the case of trees or shrubs. It is known that the influence of the environment and more specifically of light

is crucial for developing the photosynthetic apparatus [26, 27]. The leaves that adapt to strong light are characterized by a higher ratio of chlorophyll *a/b* than leaves adapted to shade [28].

Furthermore, the higher the leaves are placed on a plant, the better accessibility to light and the higher the ratio of chlorophyll *a/b* [29]. Increased ratio of chl *a/b* is also characteristic for the leaves that are not fully expanded [30, 31]. Poorer light conditions of the older leaves are reflected in their lowered chl *a/b* ratio that can be seen in the J. knotweed and the topinambur. Stems occupy less favorable position in relation with the light that results in a lower chl *a/b* ratio. A similar relation has been observed both in the knotweed and the topinambur. However, only in the J. knotweed, as in the case of leaves, a lower chl *a/b* ratio have been signalized in the older stems in comparison with the younger parts of the stems. This situation reflects the diversified light conditions in the stem area of the J. knotweed, as it was in the example of lignified plants [32]. In the topinambur, the chl *a/b* ratio was alike in the whole stem area, which can justify a proportionately similar amount of radiation accessing different parts of the stem.

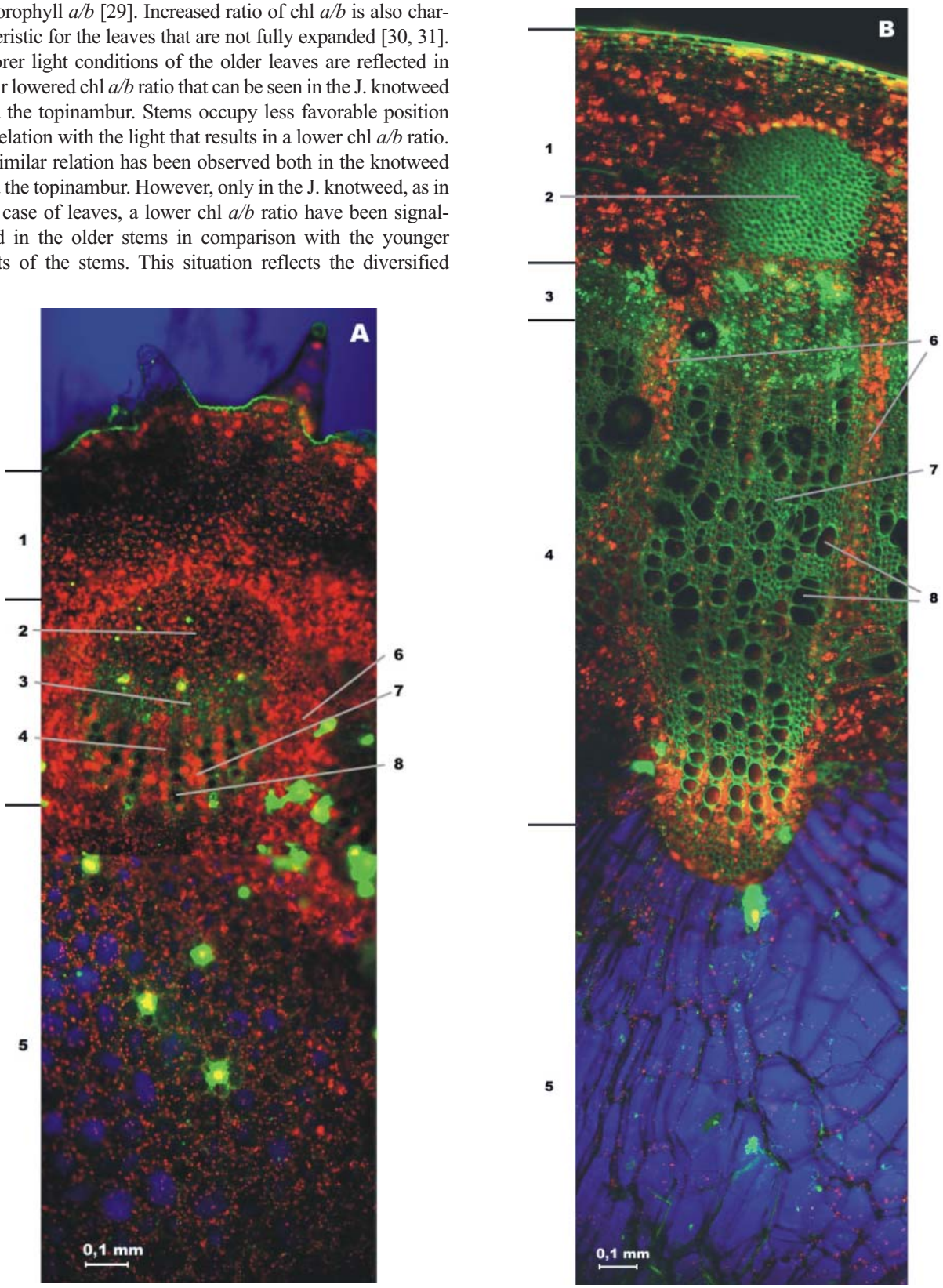

Fig. 4. Cross-section of topinambur stem. A- younger fragment, B – older fragment. 1- cortex, 2 – pericyclic sclerenchyma, 3 – phloem, 4 – xylem, 5 – pith, 6 – rays, 7 – xylem parenchyma cells, 8 – vessels. Colors as in Fig. 3.

The leaves of the plants adapted to lower ratios of irradiance obtain a higher total level of chlorophyll pigment in terms of unit area, thus enabling effective absorption of the radiation [26, 28]. However, the content of chlorophylls in non-leaf organs is usually lower than in leaves, despite the poorer light conditions [12, 33-35]. The level of chlorophylls in the stems of lignified plants usually reaches 50-70% of the level in the leaves [3, 4, 6, 21] and rarely upgrades to 100% [1]. In the J. knotweed, the level of chlorophylls in the older parts of the stems was 3 times higher than in the younger parts, which can be explained by the poorer conditions in the lower parts of the stem. In the topinambur, the level of chl was similar in the overall stem area.

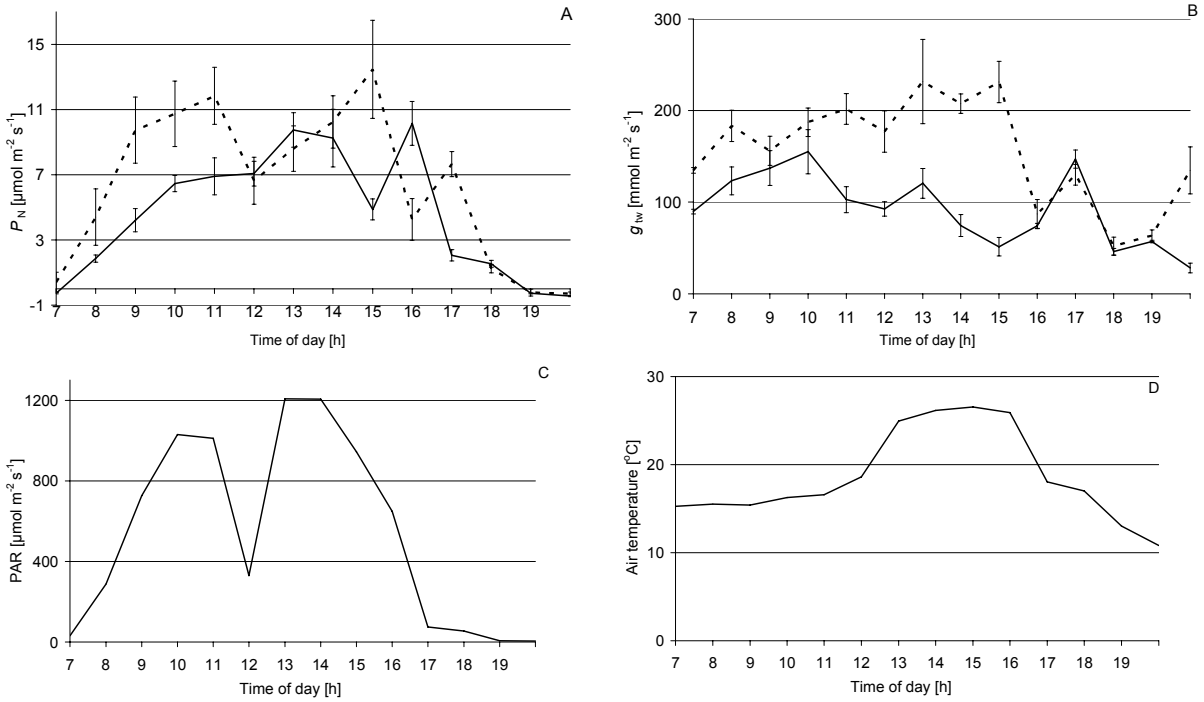

Fig. 5. Daily changes in some parameters in Japanese knotweed (solid line) and topinambur (dotted line) leaves, measured on 02.09.2008. A – net photosynthetic rate (P_N), B – total conductance to water vapor (g_{tw}), C – photosynthetically-active radiation (PAR) on leaf level, D – air temperature. Means±SD. (n=5).

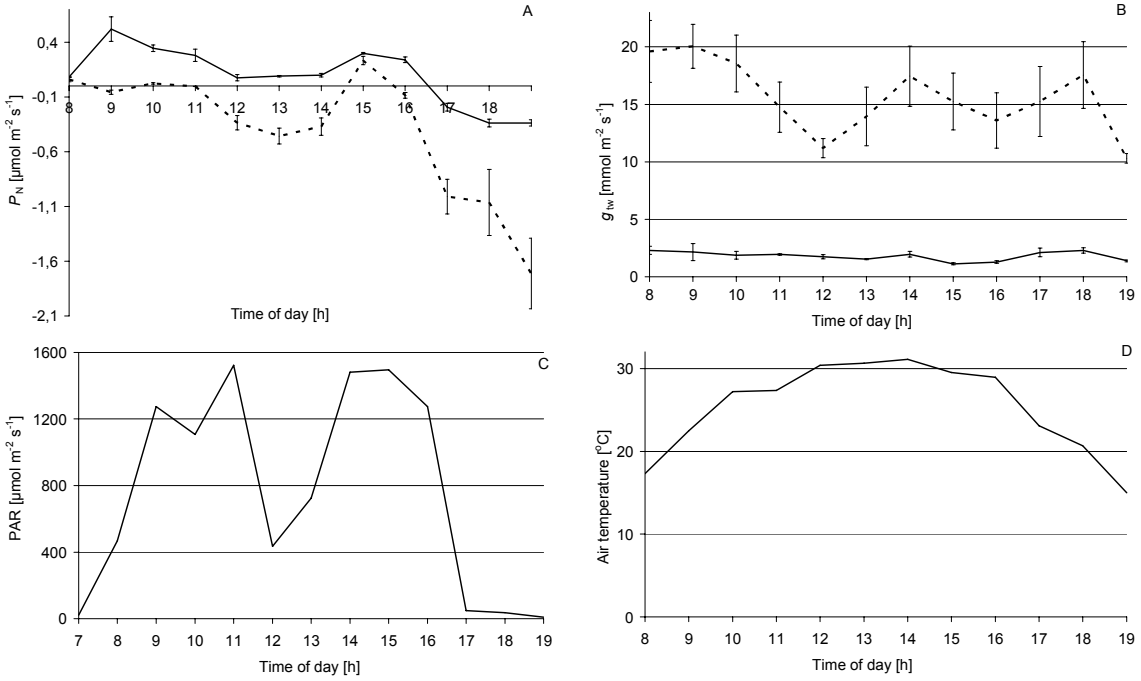

Fig. 6. Daily changes in some parameters in Japanese knotweed (solid line) and topinambur (dotted line) stems, measured on 07.09.2008: A – net photosynthetic rate (P_N), B – total conductance to water vapor (g_{tw}), C – photosynthetically-active radiation (PAR) on stems level, D – air temperature. Means±SD, (n=5).

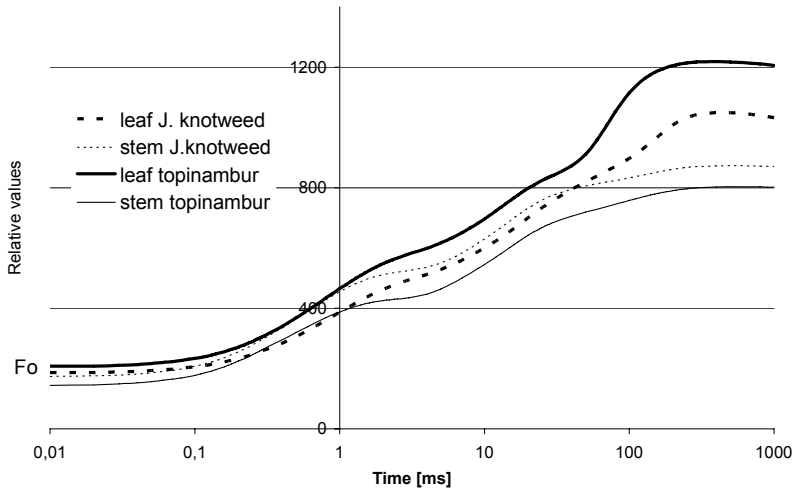

Fig. 7. Chlorophyll *a* fluorescence in stems and leaves of Japanese knotweed and topinambur. Means of 30 repetitions.

There is a lot of information on the distribution of chl in the stems of trees ands shrubs [6, 8, 36], but not a great deal can be found regarding herbaceous plants [35]. The highest quantities of chl in the stems of lignified plants are found in the cortex, as well as in the pith rays and a small quantity in the pith. In lignified plants, with progressing thickness increments, chl remains only in the cortex [36]. In the J. knotweed, when the stem develops, the cortex layer, conducting bundles and near tissues become thicker. In the topinambur, however, the radial growth means principally the increment of wood, elongation of pith rays and disappearance of chl in the pith. This is the reason why, despite the radial growth in the older sections of topinambur stems, the chl content per unit area is similar to that in younger sections of the stems. A different situation occurs in the J. knotweed, where a thicker layer of primary cortex contains more chl.

The chlorenchyma so formed in the stems of both plants shows high photosynthetic activity. The maximum efficiencies of the photosynthetic apparatus adapted to darkness (F_v/F_m), which in the stems of the J. knotweed amount to 0.815 and 0.832 in the topinambur, approach those in leaves (at 0.830 and 0.837, respectively), and do not deviate from the level known from references for healthy leaves – ca. 0.83 [22, 23].

Despite the similar F_v/F_m ratio found in the leaves and stems of the J. knotweed and the topinambur, the values of P_N in stems were low (0-0.5 μmol·m^{-2}·s^{-1}) compared with leaves (10-14 μmol·m^{-2}·s^{-1}), which conformed with the results obtained in lignified plants where fairly low values of P_N, usually below 0.5 μmol·m^{-2}·s^{-1} were found [12, 13].

The differences between the topinambur and the J. knotweed noted in the gas exchange, in response to light, may result from differences in the diffusion resistance of stem epidermis. As in lignified plants, the stems of the herbaceous plants under study also lack stomata, which hampered the gas exchange with the surrounding atmosphere. In the J. knotweed, the diffusion resistance of stem epidermis (having lenticels) resemble that determined on the adaxial side of the leaves (where they lack stomata) of the same plant. In the leaves and stems of the topinambur, trichomes produced by epidermis increase the contact surface with the atmosphere and thereby reduce diffusion resistance.

There is an opinion presented in publications stating that lenticels facilitate gas exchange [2, 37], but the studies on the stem of *Syringa vulgaris* [38] demonstrated similarly high diffusion resistances compared to those obtained by us in herbaceous plants. Again, high CO_2 concentrations inside stems, reaching as much as several percent [15, 39], confirm the difficulties in gas exchange between the stems and the surrounding atmosphere.

The high values of diffusion resistance in stem epidermis are corroborated by independently determined values, of the g_{tw} of the stem in the studied herbaceous species. In the leaves of both species, g_{tw} stayed within the range of 50 to 230 mmol·m^{-2}·s^{-1}, whereas in the topinambur stems it was 5-11 times lower at from 10 to 20 mmol·m^{-2}·s^{-1}. The lowest g_{tw} appeared in the stems of the J. knotweed: 1.5 to 2 mmol·m^{-2}·s^{-1}, which is ca. 10 times lower than in the topinambur. The stems of lignified plants may have an even lower g_{tw} of ca. 1 mmol·m^{-2}·s^{-1}, e.g. as in four-year old stems of *Pinus monticola* (ca. 1 mmol·m^{-2}·s^{-1} [14], or in young stems of *Betula pendula* (1.1 mmol·m^{-2}·s^{-1}) [7].

The other reason why the effect of CO_2 in darkness is so low in the J. knotweed (ca. 0.5 μmol·m^{-2}·s^{-1}) compared with the topinambur (ca. 1.2 μmol·m^{-2}·s^{-1}) is, indeed, the little thickness of the layer of respiring cells in this plant. The thickness of live cells in the stem of the J. knotweed ranged from 0.6 to 1.5 mm, whereas in the topinambur – from 7.5 mm to 11.0 mm.

The lack of stomata in the epidermis of stems, and the absence of an efficient system of intercellular spaces similar to that in leaves, results in major difficulties in the provision of external CO_2 and, subsequently, in low or negative values of P_N compared with leaves. In herbaceous plants, the external part of the primary cortex can use atmospheric CO_2 to drive photosynthesis. The cells situated deeper must use CO_2 released in respiratory processes or dissolved in xylem sap.

Despite the lack of cork, the stems of herbaceous plants have a similar property as the lignified plants: a gas-resistant epidermis that is supposed to limit the transpiration. This is why the stems of herbaceous plants collect small quantities of CO_2 but fully participate in its re-assimilation.

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Abbreviations

Area – area above the fluorescence curve
chl – chlorophyll
F_m – maximal fluorescence
F_o – minimal fluorescence
F_v – variable fluorescence
F_v/F_m – maximal efficiency of PSII
g_{tw} – total conductance to water vapor
PAR – photosynthetically-active radiation
P_N – net photosynthetic rate
PSII – photosystem 2
SD – standard deviation
Tfm – time at which the F_m was reached

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