DOI: 10.1007/s11099-014-0004-2 PHOTOSYNTHETICA 52 (1): 3-15, 2014

REVIEW

Contribution of stem CO_2 fixation to whole-plant carbon balance in nonsucculent species

E. ÁVILA+, A. HERRERA, and W. TEZARA

Centro de Botánica Tropical, Instituto de Biología Experimental, Universidad Central de Venezuela, Caracas 1040, Venezuela

Abstract

In many plant species that remain leafless part of the year, CO_2 fixation occurring in green stems represents an important carbon gain. Traditionally, a distinction has been made between stem photosynthesis and corticular photosynthesis. All stem photosynthesis is, *sensu stricto*, cortical, since it is carried out largely by the stem cortex. We proposed the following nomenclature: stem net photosynthesis (SNP), which includes net CO_2 fixation by stems with stomata in the epidermis and net corticular CO_2 fixation in suberized stems, and stem recycling photosynthesis (SRP), which defines CO_2 recycling in suberized stems. The proposed terms should reflect differences in anatomical and physiological traits. SNP takes place in the chlorenchyma below the epidermis with stomata, where the net CO_2 uptake occurs, and it resembles leaf photosynthesis in many characteristics. SRP is found in species where the chlorenchyma is beneath a well-developed stomata-free periderm and where reassimilation of internally respired CO_2 occurs. SNP is common in plants from desert ecosystems, rates reaching up to 60% of the leaf photosynthetic rate. SRP has been demonstrated in trees from temperate forests and it offsets partially a carbon loss by respiration of stem nonphotosynthetic tissues. Reassimilation can vary between 7 and 123% of respired CO_2, the latter figure implying net CO_2 uptake from the atmosphere. Both types of stem photosynthesis contribute positively to the carbon economy of the species, in which they occur; they are advantageous to the plant because they allow the maintenance of physiological activity during stress, an increase of integrated water use efficiency, and they provide the carbon source used in the production of new organs.

Additional key words: carbon balance; CO_2 reassimilation; green stem; stem net photosynthesis; stem photosynthesis; stem recycling photosynthesis.

Introduction

Leaves are dominant photosynthetic organs in most C_3 and C_4 plants; however, in some species from arid and semiarid ecosystems, which remain leafless most of the year, a green stem (considered photosynthetic) contributes significantly to the maintenance of plant physiological activities (Nilsen 1995). Clearly, the green stems of herbaceous and crassulacean acid metabolism (CAM) plants are photosynthetic; nevertheless, the significance of the chloroplast presence in woody stems has only recently become clearer.

In desert and Mediterranean climate ecosystems, it is common to find a wide range of plant species with photosynthetic stems (Nilsen and Sharifi 1997). Internal CO_2 reassimilation in stem tissues is considered the important strategy in the whole-plant carbon economy (Aschan and Pfanz 2003, Aschan *et al.* 2005). A specific

Received 30 January 2013, *accepted* 9 July 2013.
+Corresponding author; e-mail: eleinis.avila@gmail.com
Abbreviations: CAM – crassulacean acid metabolism; CE – carboxylation efficiency; Chl – chlorophyll, C_i – intercellular CO_2 concentration; F_v/F_m – maximum quantum yield of PSII; g_s – stomatal conductance; P_N – photosynthetic rate; $P_{N\text{-leaf}}$ – leaf net P_N; $P_{N\text{-recycling}}$ – stem recycling P_N; $P_{N\text{-stem}}$ – stem net P_N; PEP – phospho*enol*pyruvate; PEPCK – phospho*enol*pyruvate carboxykinase; PPFD – photosynthetic photon flux density; R_D – dark-respiration rate; R_L – light-respiration rate; Rubisco – ribulose-1,5-carboxylase/oxygenase; T – temperature; SNP – stem net photosynthesis; SRP – stem recycling photosynthesis; VPD – vapor pressure deficit; WUE – water-use efficiency; $\delta^{13}C$ – isotopic carbon composition; Φ_{PSII} – effective quantum yield of PSII.
Acknowledgements. We thank Ilsa Coronel for critical reading of the manuscript and Consejo de Desarrollo Científico y Humanístico (CDCH, Venezuela) for financial support to WT (Grant PI 03-7458-2009).

question is what a contribution do they have in the entire-plant carbon balance, specifically, what is the cost-benefit ratio in keeping these green organs under extreme environmental conditions, such as prolonged periods of drought, high temperature (T), and high photosynthetic photon flux density (PPFD). Optimizing carbon gain through the activity of photosynthetic stems is a major adaptation of xerophytic species to long periods of drought (Adams *et al.* 1967, Aschan and Pfanz 2003).

Types of CO_2 assimilation in the stem: a question of nomenclature

Nilsen (1995) and Aschan and Pfanz (2003) distinguished between two types of CO_2 assimilation performed by green stems: stem photosynthesis (SP) and corticular photosynthesis. In this review, we did not discuss CAM photosynthesis in stem-suculent plants. Chlorophyll (Chl) in stems is mainly located in the cortex, hence, the term of corticular photosynthesis was used. Moreover, since Chl is also present in the ray cells of wood and even in the pith, Saveyn *et al.* (2010) used the more general term of woody tissue photosynthesis, which better conveys the concept of CO_2 assimilation by the entire stem.

All stem photosynthesis is, *sensu stricto*, cortical (improperly termed corticular)**,** since it is carried out largely by the stem cortex. Nevertheless, it has become customary to distinguish between stem photosynthesis and cortical photosynthesis on the basis of whether the epidermis with stomata is present or not, respectively. During stem photosynthesis, a net uptake of atmospheric CO_2 is realized due to stomata present in the epidermis (Comstock and Ehleringer 1990, Nilsen *et al.* 1993, Nilsen 1995). Cortical photosynthesis is characteristic for stems with a low stomata density or with periderm; generally, but not always, no net CO_2 assimilation occurs there, while internal reassimilation of CO_2 released by respiration of nonphotosynthetic tissues exists (Nilsen and Sharifi 1994, Nilsen 1995, Aschan and Pfanz 2003). In stem photosynthesis, CO_2 reassimilation should be also expected to take place.

In view of various definitions of photosynthesis carried out by stems in nonsucculent plants, and of reported data, we proposed that the use of the following nomenclature should be considered: (*1*) the stem net photosynthesis (SNP), which would include the net CO_2 fixation by stems with stomata in the epidermis (what has been called stem photosynthesis so far) and the net CO_2 fixation in suberized stems; (*2*) the stem recycling photosynthesis (SRP), which would define CO_2 recycling in suberized stems and include all what has been called corticular photosynthesis so far. The proposed terms would reflect differences in anatomical as well as physiological traits.

Many extensive and up-to-date reviews on the subject of stem photosynthesis have been published (*e.g.*, Nilsen 1995, Pfanz, *et al*. 2002, Aschan and Pfanz 2003). In the present one, we aimed to unify some concepts and to compare SNP and SRP from the structural, functional, and ecological viewpoints with highlighting the adaptive advantages of these forms of photosynthesis and drawing attention to gaps in our knowledge of these processes. We did a thorough revision of published results that should allow to evaluate the net photosynthetic rate (P_N), percentage of reassimilation, and other photosynthetic characteristics.

SNP: structural and functional characteristics

One of the first measurements of stem net P_N ($P_{N\text{-stem}}$) was made by $^{14}CO_2$ fixation in *Cercidium floridum* (Fabaceae) (Adams *et al.* 1967). In this species, contrary to what was found later in other species, $P_{N\text{-stem}}$ was similar to leaf P_N ($P_{N\text{-leaf}}$): 1.96 and 2.55 MBq m^{-2} s^{-1}**,** respectively (Adams *et al.* 1967). A comparison between $P_{N\text{-leaf}}$ and $P_{N\text{-stem}}$ in several desert species is shown in Table 1.

The SNP exhibits properties similar to leaf photosynthesis, such as C_3 metabolism, numerous stomata in the epidermis, and similar response curves of P_N to environmental variables, such as PPFD, intercellular CO_2 concentration (C_i), temperature, and leaf-air vapor pressure deficit (VPD) (Osmond *et al.* 1987, Nilsen *et al.* 1989, Nilsen and Sharifi 1994, Aschan and Pfanz 2003). However, in cells surrounding the vascular bundles of stems and petioles of tobacco, high activity was found for C_4 metabolism enzymes, such as NAD- and NADP-malic enzyme, and phospho*enol*pyruvate (PEP) carboxykinase (PEPCK), that allow decarboxylation of four-carbon compounds present in the xylem and phloem and the resulting reassimilation of the released CO_2 by the stem chlorenchyma (Hibberd and Quick 2002). In stems of nine tree species in a temperate forest, the high PEPCK activity suggests a potential reassimilation of respired CO_2 (Berveiller and Damesin 2008).

Generally, the species with SNP correspond to early successional legumes (Allen and Allen 1981). This functional group, within pioneer species, have several physiological advantages compared to late successional species, including greater shoot nitrogen content, high activity of nitrate reductase, high maximum $P_{N\text{-leaf}}$, and high relative growth rate (Aidar *et al*. 2003). The occurrence of SNP in these species suggests that its main role is to contribute to the input of additional carbon needed for the nodulation process and subsequent maintenance of nodules, which is considered an advantage in habitats with stressful climatic conditions

Table 1. Maximum photosynthetic rate (P_N) and chlorophyll (Chl) content of leaves and stems of different species with stem net photosynthesis. Maximum P_N was estimated at saturating photosynthetic photon flux density and ambient CO_2 concentration. Values are mean ± SE when SE was available. *Cut stem: flat section of one-side stem. SD – Sonoran Desert; MD – Mohave Desert; A – Arizona; C – California.

Species	Family	Location	Maximum P_N [μmol(CO_2) m^{-2} s^{-1}]		Chl content [mg m^{-2}]		Reference
			stem	leaf	stem	leaf	
Bebbia juncea	Asteraceae	SD	10.7	20.7			Ehleringer *et al.* (1987)
Chrysothamnus paniculatus	Asteraceae	SD	15.2	23.6			
Dyssodia porophylloides	Asteraceae	SD	5.4	6.5			
Gutierrezia microcephala	Asteraceae	SD	17.9	21.1			
G. sarothrae	Asteraceae	SD	4.4	16.7			
Hymenoclea salsola	Asteraceae	SD	16.6	24.8			
Lepidium fremontii	Brassicaceae	SD	8.8	12.6			
Porophyllum gracile	Asteraceae	SD	23.9	37.7			
Psilostrophe cooperi	Asteraceae	SD	12.9	12.8			
Salazaria mexicana	Lammiaceae	SD	16.7	15.1			
Senecio douglasii	Asteraceae	SD	1.5	26.0			
Sphaeralcea parviflora	Malvaceae	SD	13.7	22.3			
Stephanomeria paucifolia	Asteraceae	SD	23.3	22.3			
Thamnosma montana	Rutaceae	SD	10.5	21.7			
Eriogonum inflatum	Polygonaceae	MD	10*	20	330	540	Osmond *et al*. (1987)
Hymenoclea salsola	Asteraceae	A	18	30			Comstock and Ehleringer (1988)
Psorothamnus spinosus	Fabaceae	SD	7.8 ± 0.5	-		-	Nilsen *et al*. (1989)
Spartium junceum	Fabaceae	C	6.5	17	200	450	Nilsen and Bao (1990)
Cytisus scoparius	Fabaceae	C	1.7–11.6		1,300 ± 20		Bossard and Rejmanek (1992)
Caesalpinia virgata	Fabaceae	SD	7.8				Nilsen and Sharifi (1994)
Senna armata	Fabaceae	MD	5.8				
Justicia californica	Acantaceae	SD	20.9 ± 2.8	16.2 ± 1.2	230	280	Tinoco–Ojanguren (2008)
Median			10.7	20.49	280	450	

(Bossard and Rejmanek 1992, Nilsen 1992).

In contrast to leaves, stems are not obviously specialized for photosynthesis. Their surface to volume ratio is low alike light transmittance through the bark layer (Pfanz *et al.* 2002). Although seemingly unfavorable to photosynthesis, these conditions do not prevent Chl synthesis and carbon assimilation in stems (Berveiller *et al.* 2007). $P_{N\text{-leaf}}$ is positively correlated to leaf nitrogen content because proteins of the Calvin-Benson cycle and of thylakoids represent the major part of leaf nitrogen (Evans 1989). This relationship has also been observed for $P_{N\text{-stem}}$ (Nilsen 1992).

Maximum $P_{N\text{-stem}}$ lies between 1.7 and 20.9 μmol(CO_2) m^{-2} s^{-1} (Table 1). In general, $P_{N\text{-stem}}$ is lower than $P_{N\text{-leaf}}$, representing between 16 and 60% of the latter, although both rates were similar in some species (Ehleringer *et al*. 1987). Lower maximum $P_{N\text{-stem}}$ than maximum $P_{N\text{-leaf}}$ was associated with low mesophyll conductance in *Spartium junceum*, probably due to the low nitrogen content in the stem chlorenchyma (Nilsen 1992). $P_{N\text{-stem}}$ rarely exceeds $P_{N\text{-leaf}}$, an exception are plants of *Justicia californica*, where $P_{N\text{-stem}}$ was 1.3 times greater than $P_{N\text{-leaf}}$, probably due to better light-use efficiency by stems and similar Chl content in both organs (Tinoco-Ojanguren 2008).

Chl content is generally lower in stems and ranges between 30 and 70% of that in adjacent leaves, making this trait a limitation of SNP. In contrast, Chl content per unit area was higher in stems than in leaves (410 *vs.* 340 mg m^{-2}) in *C. floridum* in spite of similar $P_{N\text{-stem}}$ and $P_{N\text{-leaf}}$ (Adams *et al.* 1967). This indicates that the content of Chl might not be the only factor governing the stem photosynthetic capacity. The quality of light that gets through the outer cortex of the stems, as well as the amount and/or activity of ribulose-1,5-carboxylase/oxygenase (Rubisco) could be important factors in determining stem photosynthetic capacity. The lower $P_{N\text{-stem}}$ could also be related to the lower nitrogen content in stems compared to leaves (Nilsen 1992); nevertheless, in *J. californica*, where both organs have the same Chl content and very similar values of N, $P_{N\text{-stem}}$ was higher than $P_{N\text{-leaf}}$ (Tinoco-Ojanguren 2008). This result supports the hypothesis of higher light-use efficiency in the stems of this species.

Species with SNP showed a high stomata density and stomatal conductance (g_s) in the stem epidermis. In *S. junceum*, the stem stomata density was similar to that

of leaves (both types of epidermis), although the daytime stem g_s was always lower than that of leaf g_s (Nilsen and Bao 1990). Similarly, stem g_s was lower than that of leaf g_s under a wide range of environmental conditions in *Eriogonum inflatum* (Smith and Osmond 1987). Moreover, although stem g_s of *Glycine max* (Fabaceae) was higher than that of *S. junceum*, the stem of the former showed no net assimilation or respiration rate (Nilsen and Bao 1990).

Most photosynthetic stems possess sunken stomata, which may be interpreted as an adaptation to protect guard cells from direct exposure to dry air and the consequent stomata closure; rather, the sunken stomata could be an adaptation to increase stem CO_2 uptake due to a lower VPD above the stomatal pore that would prevent stomata closure (Gibson 1998).

Stems with high $P_{N\text{-stem}}$ and g_s should have lower instantaneous water use efficiency (WUE) than leaves. However, in *E. inflatum*, WUE was slightly higher in the stem than that in the leaf in a wide range of VPD, although stem g_s was more sensitive to temperature and to very high VPD (Osmond *et al.* 1987). SP increases long-term plant integrated WUE, as estimated from isotopic carbon composition ($\delta^{13}C$) data (Nilsen and Sharifi 1997). Integrated WUE was found to be higher in stems than in leaves in a number of green-stemmed, desert species (Ehleringer *et al.* 1987). The higher WUE found in stems compared to leaves of *E. inflatum* was attributed to a better water use pattern and the vertical orientation of the stem, allowing the stems to remain photosynthetically active during drought (Smith and Osmond 1987).

In several C_3 plant species, heterotrophic tissues tend to be enriched in ^{13}C compared with leaves (Cernusak *et al*. 2009); the higher $\delta^{13}C$ found in stems should not only indicate a higher WUE but also possibly a differential use of day *vs*. night sucrose between leaves and sink tissues (Cernusak *et al*. 2009). Besides, it must be taken into account whether the stems are photosynthetic; if they are, the carbon of stem structural carbohydrates was probably assimilated by the stem chlorenchyma, while if they are not, the stem is a sink and the leaves supply them with assimilates.

SNP represents a contribution to the whole-plant carbon gain that may change among seasons, depending on environmental conditions. In *S. junceum*, the stem carbon gain represented 38% of the total gain under optimal water conditions and it increased to 47% under conditions of water deficit (Nilsen and Bao 1990). Similar contributions have been found in other species: 40% in *C. floridum* (Adams and Strain 1968) and 50% in *E. inflatum* (Smith and Osmond 1987). In contrast, the stem contribution did not exceed 23% in *J. californica* (Tinoco-Ojanguren 2008). However, in the latter species, the stem is the only photosynthetic organ present for at least seven months (Tinoco-Ojanguren 2008); it shows the importance of SNP during the leafless period. In *Psorothamnus spinosus*, a leafless species, the whole-plant carbon balance is necessarily dependent exclusively on SNP (Nilsen *et al.* 1989).

Factors affecting SNP

Besides determining the magnitude of the stem contribution to the whole-plant carbon balance, it is important to acquire knowledge on the seasonal acclimation and the influence of water deficit on SNP. For example, the water deficit affected less $P_{N\text{-stem}}$ than $P_{N\text{-leaf}}$ in *S. junceum* and *J. californica* (Nilsen and Bao 1990, Tinoco-Ojanguren 2008), contrary to *E. inflatum*, where $P_{N\text{-stem}}$ appears to be more sensitive to drought at very low values of water potential (Osmond *et al.* 1987). In other species, such as *Caesalpinia virgata* and *Senna armata*, changes in $P_{N\text{-stem}}$ between the spring and the summer were not related to changes in either water potential or nitrogen content, contrary to what is generally found in leaves of different species (Nilsen and Sharifi 1994).

Table 2 summarizes some parameters of the response curves of $P_{N\text{-leaf}}$ and $P_{N\text{-stem}}$ to PPFD, C_i, and T of the stem and leaves of several species. Responses of $P_{N\text{-stem}}$ to environmental variables were similar to those typically found in leaves. Leaves had higher C_i-saturated P_N and carboxylation efficiency than stems, indicating that the photosynthetic capacity in the stems is limited by the amount and activity of Rubisco, which is consistent with lower nitrogen content and lower Chl content than that in leaves (Osmond *et al.* 1987). PPFD-saturated P_N was lower in stems than in leaves and no difference was found in the apparent quantum efficiency between organs (Osmond *et al.* 1987). $P_{N\text{-leaf}}$ was more sensitive to T than $P_{N\text{-stem}}$ because leaf g_s strongly decreased with increasing T and VPD (Osmond *et al.* 1987).

In *C. virgata* and *S. armata*, T and VPD were the main environmental factors, which regulated $P_{N\text{-leaf}}$ and $P_{N\text{-stem}}$, and seasonal acclimation to T (an increase of the compensation point) but not to VPD took place (Nilsen and Sharifi 1994). Under conditions of limited resources, as in the case of nitrogen, $P_{N\text{-stem}}$ of *S. junceum* was less reduced than $P_{N\text{-leaf}}$, resulting in the increase of the stem contribution to the daily carbon gain compared to a decline in leaves (Nilsen 1992). In this case, the importance of $P_{N\text{-stem}}$ increased in the carbon balance of the plant, even though $P_{N\text{-stem}}$ was lower than $P_{N\text{-leaf}}$.

The stem age is an important factor determining the contribution of stems to the whole-plant carbon balance, because both, $P_{N\text{-leaf}}$ and $P_{N\text{-stem}}$, vary with the age of the tissue. In *P. spinosus*, young branches (less than 6-months-old) showed $P_{N\text{-stem}}$ values 30 to 40% higher together with higher values of g_s compared with mature branches (Nilsen *et al.* 1989). The difference between $P_{N\text{-stem}}$ in the young and mature branches was caused

Table 2. Photosynthetic rate at saturating photosynthetic photon flux density (PPFD-sat P_N), saturating photosynthetic photon flux density (PPFD), photosynthetic rate at saturating CO_2 concentration (CO_2-sat P_N), saturating CO_2 internal concentration (C_i), photosynthetic rate at optimal temperature (P_N at T_{opt}) and optimal temperature (T_{opt}) of leaves and stems of species with stem net photosynthesis. Values are mean ± SE when SE was available.

Species	Organ	PPFD-sat P_N [μmol(CO_2) m^{-2} s^{-1}]	PPFD [μmol(photon) m^{-2} s^{-1}]	CO_2-sat P_N [μmol(CO_2) m^{-2} s^{-1}]	saturating C_i [μmol mol^{-1}]	P_N at T_{opt} [μmol(CO_2) m^{-2} s^{-1}]	T_{opt} [°C]	Reference
E. inflatum	leaf	23	1,500	55	700	25	20–30	Osmond *et al*. (1987)
	stem	10		20	800	15	15–25	
P. spinosus	young stem	8	2,000	10.5–15.5	250–350	10	39	Nilsen *et al*. (1989)
	mature stem	4	1,600	5–8	300–350	4	36	
C. virgata	stem - spring	8.2	1,500	8	500–600	6	18–30	Nilsen and Sharifi (1994)
	stem - summer	4.1		10		4		
S. armata	stem - spring	3.2	1,500	8	500–600	5	10–25	
	stem - summer	6.1	1,500	12		4		
J. californica	leaf	12.3	1,500					Tinoco-Ojanguren (2008)
	stem	12.3						
Median	leaf	17.7	1,500	55	700	25	20–30	
	stem	7.1	1,500	10	500	5	25	

mainly by the loss of the epidermis with stomata as a result of a periderm formation, which also limited the passage of light and thus photosynthesis. In some species, a delay occurs in the formation of the periderm (Gibson 1983) and this provides a longer period when $P_{N\text{-stem}}$ can be maintained high. There are few plants, where the epidermis is able to adapt to secondary growth by tangential expansion of cells. In such cases, the epidermis persists for a long time or even the lifetime of the plant and the stem remains green (Lindorf *et al*. 2006).

In deciduous plants, SNP plays an important role in the maintenance of the physiological activities and is the sole carbon source available for the production of new foliage (Mooney and Strain 1964). This may have an important effect on the reproduction of *J. californica,* as flowers and fruits develop during the dry season, when the stem is the only photosynthetic organ present (Tinoco-Ojanguren 2008). In addition, a vertical orientation of the stem might diminish the photoinhibitory damage, since all day lower PPFD reaches this organ, which makes it less vulnerable to photoinhibition during drought (Ehleringer and Cooper 1992). Based on these results, it seems that deciduous species can survive in arid environments at least partly due to the presence of SNP.

The adaptive advantages of SNP

The wide distribution of species with the photosynthetic stem in habitats with stressful climatic conditions shows the importance of this organ for plants (Nilsen and Sharifi 1997). In these species, various benefits of SNP have been proposed: (*1*) the carbon gain during drought in C_3 species, which remain part of the year leafless or without functional leaves and the stem is the only organ responsible for CO_2 assimilation (Osmond *et al.* 1987, Nilsen *et al.* 1989, Nilsen and Bao 1990); (*2*) the increase of the whole-plant WUE, since stems have a higher WUE than leaves and they are the sole green organs present for at least one season of the year (Nilsen and Sharifi 1997); (*3*) the sole source of carbon used in the production of leaves, flowers, and fruits in deciduous species during and after drought (Tinoco-Ojanguren 2008).

SRP: structural and functional characteristics

Stem recycling P_N ($P_{N\text{-recycling}}$), also called internal reassimilation rate, is calculated as the difference between the stem light-respiration rate (R_L) and the stem dark-respiration rate (R_D) and may be expressed as a percentage of the R_D [$(P_{N\text{-recycling}}/R_D) \times 100$ = % reassimilation] (Cernusak and Marshall 2000, Aschan *et al.* 2001, Damesin 2003). $P_{N\text{-recycling}}$ generally reaches values lower than $P_{N\text{-stem}}$, varying between 0.5 and 3.7 $\mu mol(CO_2)\ m^{-2}\ s^{-1}$.

Calculations of the percentage of reassimilation are needed to compare the quantity of reassimilated carbon among species with different $P_{N\text{-recycling}}$. The reassimilation in young branches of different species can offset between 7 and 90% of the respiratory carbon loss. It can even exceed 100% when there is the net CO_2 assimilation and in this case SRP contributes to the whole-plant carbon gain. Values of the reassimilation higher than 100% have been associated with the presence of lenticels in the stem periderm that facilitate CO_2 diffusion from the atmosphere to the chlorenchyma (Berveiller *et al.* 2007).

SNP is present in desert species, while in others, such as those from temperate forests, SRP is common (Table 3). Both types of ecosystems are subjected to periods of water or low temperature stress. These stresses limit photosynthesis, therefore the plant growth (Chaves and Pereira 1992) and a survival, mainly in terrestrial ecosystems (Schulze *et al.* 1987). Hence, the stem contribution to the whole-plant carbon balance is important for desert species, either through a net gain or a decrease in the carbon loss.

It is widely accepted that the respiration of stem inner tissues is the CO_2 source for SRP; however, labeled carbon transported upward by a xylem sap from roots to leaves is fixed in photosynthetic cells of petioles and stems of tobacco and celery (Hibberd and Quick 2002) and in branches of *Platanus occidentalis* (McGuire *et al.* 2009). In detached branches of *Populus deltoides* fed with ^{13}C, wood tissue labeling depended on the transpiration rate and CO_2 concentration in the xylem sap (Bloemen *et al.* 2013). This suggests strongly that CO_2 recycled by SNP or SRP may come also from the roots.

Both R_L and R_D have been estimated from measurements of stem CO_2 efflux. CO_2 dissolved in the xylem sap can move upward in the transpirational stream and can be up to three orders of magnitude higher than the atmospheric concentration (Teskey and McGuire 2002). Since the respired CO_2 can be released into the cortex at any other location of the tree, the stem respiration can be overestimated in some tissues and underestimated in others (Teskey and McGuire 2002). McGuire and Teskey (2004) have suggested a mass balance approach to estimate the stem respiration; they took into account not only the CO_2 efflux but also the CO_2 transport in the xylem and its possible accumulation over time. This approach has been used since then to estimate the stem respiration in several tree species (McGuire *et al.* 2007, Teskey and McGuire 2007, Saveyn *et al.* 2008).

In most plants with SRP, the chlorenchyma is a part of the stem outer cortex (Francino *et al.* 2006, Yiotis *et al.* 2006). In other species, however, chloroplasts can be found in the secondary xylem of the stem (specifically

Table 3. Light-respiration rate (R_L), dark-respiration rate (R_D), stem recycling photosynthetic rate ($P_{N\text{-recycling}}$), and reassimilation percentage of different species. Values are mean ± SE when SE was available. *First value, measurements made in the summer; second value, measurements made in the winter.

Species	Family	R_L [μmol(CO_2) m^{-2} s^{-1}]	R_D	$P_{N\text{-recycling}}$	Reassimilation [%]	Reference
Populus tremuloides	Salicaceae		3.8	3.3	87	Foote and Scheadle (1976)
Pinus monticola	Pinaceae		0–3.5	0–1.5	76	Cernusak and Marshall (2000)
Populus tremula	Salicaceae	1–2	2–11	1–9	50–80	Aschan *et al*. (2001)
Fagus sylvatica	Fagaceae	0.2–1.2	1.9–2.1	0.7–1.9	40–90	Wittmann *et al*. (2001)
Fagus sylvatica	Fagaceae			1–5	50–110	Damesin (2003)
Alnus glutinosa	Betulaceae	0.89 ± 0.05	4.62 ± 0.26	3.73	81	Berveiller *et al*. (2007)*
		–0.35 ± 0.11	1.57 ± 0.44	1.92	122	
Betula pendula	Betulaceae	0.69 ± 0.11	3.04 ± 0.53	2.35	77	
		–0.47 ± 0.03	2.06 ± 0.15	2.53	123	
Fraxinus excelsior	Fagaceae	0.38 ± 0.13	1.44 ± 0.34	1.06	74	
		–0.22 ± 0.01	0.86 ± 0.24	1.08	126	
Ginkgo biloba	Ginkgoacea	0.54 ± 0.10	1.65 ± 0.16	0.53	32	
		0.53 ± 0.43	1.24 ± 0.40	0.71	57	
Picea abies	Pinaceae	1.12 ± 0.10	3.44 ± 0.34	2.32	67	
		1.09 ± 0.55	2.18 ± 0.46	1.09	50	
Pinus sylvestris	Pinaceae	1.16 ± 0.12	4.04 ± 0.53	2.88	71	
		1.91 ± 0.33	4.22 ± 0.15	2.31	55	
Quercus robur	Fagaceae	1.18 ± 0.37	3.75 ± 0.64	2.57	69	
		0.81 ± 0.33	2.87 ± 0.34	2.06	72	
Tilia cordata	Malvaceae	0.68 ± 0.10	2.10 ± 0.19	1.42	68	
		0.51 ± 0.05	2.06 ± 0.20	1.55	75	
Fagus sylvatica	Fagaceae		1–4	0.5–3.5	50–88	Berveiller and Damesin (2008)
Eucalyptus globulus	Myrtaceae		0.5–4.7		7	Cerasoli *et al*. (2009)
Median		0.81	2.14	1.9	72	

in the xylem rays and the interfascicular parenchyma) and even in the pith of the stems (Dima *et al.* 2006, Berveiller *et al.* 2007, Rentzou and Psaras 2008). The stem chlorenchyma of the SRP species lies always below one or more layers of the periderm, a tissue with a high resistance to gas diffusion, thus, CO_2 produced by the internal stem tissue respiration accumulates inside the stem and reaches concentrations between 0.1 and 25.2% (Teskey *et al*. 2008), well above the atmospheric CO_2 concentration (0.04%).

The positive correlation between $P_{N\text{-recycling}}$ and R_D has been reported (Foote and Schaedle 1976, Cernusak and Marshall 2000, Aschan *et al.* 2001, Berveiller *et al.* 2010, Berveiller *et al.* 2007, Wittmann and Pfanz 2008). This occurs because factors affecting R_D, such as T or stem ontogeny, directly affect the amount of CO_2 available for SRP (Foote and Schaedle 1976). Based on this, it has been suggested that, at least in young branches, R_D may be an indicator of potential photosynthesis (Berveiller *et al.* 2007) and such a correlation can be used to estimate $P_{N\text{-corticular}}$ from values of R_D.

SRP is related, as in leaf photosynthesis, to different structural and functional traits, such as Chl content, nitrogen content, and the area/mass ratio of the stem cortex (Cernusak and Marshall 2000, Berveiller *et al.* 2007); based on this, it has been suggested that the selection of the photosynthetic features in both organs occurred under similar evolutionary forces (Berveiller *et al.* 2007).

Chl content in leaves and stems of different SRP species is shown in Table 4. Chl concentration in the stem (72–480 mg m^{-2}) is lower than that in leaves (383–996 mg m^{-2}); it should be reflected in the lower photochemical activity of the stem.

Cernusak *et al.* (2001) developed and tested a model describing carbon isotope discrimination during photosynthetic refixation in the bark of two woody trees. They found that SRP discriminates against ^{13}C and creates the photosynthate pool isotopically lighter than that of the dark respiratory pool. SRP was proved experimentally to contribute during four years to 11% of wood construction in the smooth-barked branches of *E. miniata* trees growing in the field (Cernusak and Hutley 2011).

Factors affecting SRP

Besides being highly resistant to the diffusion of gases, the periderm is a barrier for light. In young branches of *Populus tremula*, PPFD absorbed by the same branch decreased from 17% in the youngest internode up to 8%

Table 4. Total chlorophyll content (Chl *a*+*b*) of leaves and stem barks of species with stem recycling photosynthesis. Values are mean ± SE.

Species	Organ	Chl *a*+*b* [mg g^{-1}(DM)]	[mg m^{-2}]	Reference
Populus tremula	leaf		460 ± 60	Aschan *et al*. (2001)
	stem		120 ± 50	
Populus tremula	leaf		620 ± 60	Wittmann *et al*. (2001)
	stem		230 ± 40	
Fagus sylvatica	leaf		360 ± 10	
	stem		130 ± 10	
Prunus persica	stem		330 ± 10	Alessio *et al*. (2005)
Helleborus viridis	leaf		383 ± 60	Aschan *et al*. (2005)
	stem		72 ± 20	
Alnus glutinosa	stem - summer	0.96 ± 0.03		Berveiller *et al*. (2007)
	stem - winter	0.60 ± 0.00		
Betula pendula	stem - summer	0.66 ± 0.07		
	stem - winter	0.44 ± 0.31		
Fraxinus excelsior	stem - summer	0.46 ± 0.02		
	stem - winter	0.29 ± 0.01		
Ginkgo biloba	stem - summer	0.64 ± 0.05		
	stem - winter	0.22 ± 0.02		
Picea abies	stem - summer	0.43 ± 0.04		
	stem - winter	0.34 ± 0.03		
Pinus sylvestris	stem - summer	0.53 ± 0.07		
	stem - winter	0.56 ± 0.02		
Quercus robur	stem - summer	0.66 ± 0.03		
	stem - winter	0.43 ± 0.06		
Tilia cordata	stem - summer	0.59 ± 0.09		
	stem - winter	0.34 ± 0.24		
Fagus sylvatica	leaf	5.38 ± 0.98		Berveiller and Damesin (2008)
	stem	0.42 ± 0.02		
Calicotome villosa	leaf		996 ± 150	Yiotis *et al*. (2008)
	stem		480 ± 40	

in the oldest one; this was associated with the development of the periderm, thereby causing a reduction in $P_{N\text{-recycling}}$ from 8.9 to 1.6 μmol(CO_2) m^{-2} s^{-1} (Aschan *et al.* 2001). Furthermore, absorbed PPFD and $P_{N\text{-recycling}}$ decreased with the branch age in *Fagus sylvatica* (Wittmann *et al.* 2001), suggesting that $P_{N\text{-recycling}}$ contributes differently to the whole-plant carbon balance and the degree of CO_2 reassimilation is dependent on the branch age.

The attenuation of light by the periderm is not equal for all wavelengths. This selective absorption has been associated with the coloration of the outer bark and with different patterns of light penetration according to the wavelength (Pfanz *et al.* 2002). Generally, the periderm is capable of absorbing light of the short wavelengths (blue) and transmitting light of the long wavelengths (red) (Kauppi 1991, Manetas 2004), thus the magnitude of PPFD reaching the chlorenchyma is enriched in red and far red radiation.

The observation that a small percentage of the incident PPFD on the stem reaches the photosynthetic tissue could explain some adaptations to shade found in several species with photosynthetic stems. The low Chl *a/b* ratio in branches compared to leaves belongs to such adaptations (Cernusak and Marshall 2000, Aschan *et al.* 2001, Wittmann *et al.* 2001, Damesin 2003, Yiotis *et al.* 2008). The shade might not be the only factor that influences pigment contents and their ratios in stems. It has been suggested that other micro-environmental conditions (hypoxia, increased red to blue photon ratios, and extremely high CO_2 concentrations) within twigs determine the carotenoid (Car) composition of the stems (Levizou *et al.* 2004). In species of trees from temperate forests, the Car/Chl ratio was higher in stems than in leaves, indicating a response to low PPFD at blue wavelengths, or an adaptation to increase photoprotection, given the extremely high concentration of CO_2 within the stems (Levizou and Manetas 2007). When CO_2

concentration around twigs was changed experimentally, nonphotochemical quenching was higher at high CO_2 than at low CO_2 (Manetas 2004) and this was associated with the higher Car/Chl ratio in twigs relative to leaves (Levizou and Manetas 2007).

It was thought that light can penetrate lenticels and reach the chlorenchyma below the periderm or rhytidomal layers (Langenfeld-Heyser 1989, Pfanz *et al.* 2002). However, transmittance of the isolated periderms from ten tree species was higher in the regions without lenticels than that of the regions with lenticels (Manetas and Pfanz 2005). Besides, a patchy acclimation of SRP was found. The chlorenchymatous regions below lenticels were found to show the shade acclimation, characterized by a lower effective quantum yield of photosystem (PS) II (Φ_{PSII}), lower nonphotochemical quenching, and possibly a higher risk of photoinhibition (Manetas and Pfanz 2005).

SRP has been evaluated indirectly by studying *in vivo* Chl fluorescence in young branches, which allows estimating the photochemical activity by determining the quantum yield of PSII. Values of the maximum quantum yield of PSII (F_v/F_m) and Φ_{PSII} of leaves and stems of several species in different seasons are shown in Table 5.

In *F. sylvatica*, stems and leaves have similar seasonal patterns of F_v/F_m when leaves are present, with slightly lower values in stems than in leaves (Damesin 2003). Stems of several species show the F_v/F_m ratios from 0.71 to 0.81, close to the maximum value (0.83) of healthy leaves under optimal conditions (Björkman and Demmig 1987). In most species, the stem F_v/F_m ratio decreased to values lower than 0.5 during the winter, suggesting the PSII photoinhibition at low temperatures (Damesin 2003, Berveiller *et al.* 2007, Levizou and Manetas 2008).

Fire diminished CO_2 stem efflux in four species from a north Australian tropical savanna; this was thought to be the result of reduced availability of carbon substrates for the respiration (due to the reduced canopy photosynthesis) and the allocation of fixed carbon to reconstruct the new canopy (Cernusak *et al.* 2006). Refixation by the photosynthetic bark of *Eucalyptus miniata* reduces the respiratory carbon cost of sapwood construction and maintenance, hence, the cost of delivering water to leaves. At the ecosystem level, the estimated reduction of the aboveground carbon loss was 7.4% (Cernusak *et al.* 2006).

More research should be done on environmental variables affecting SRP. The portion of the net contribution of CO_2 fixed through SRP to total biomass must be also assessed accurately in the individual plant by measurements of gas exchange, fluorescence, and carbon isotope discrimination.

The adaptive advantages of SRP

The first advantage, which comes to mind when dealing with SRP, is the respiratory cost balance. When branches are leafless, SRP can compensate the high percentage of carbon lost by the respiration that may even increase during unfavorable periods (Smith and Nobel 1986, Pfanz *et al.* 2002).

The high CO_2 concentration in the stems may be advantageous for the plant, mainly for two reasons: (*1*) atmospheric CO_2 for photosynthesis is not required and thus water loss is diminished, and (*2*) the photorespiration is lower due to the higher CO_2/O_2 ratio. In spite of this, the extremely high CO_2 concentration in *Prunus cerasus* combined with high PPFD (~500 μmol m^{-2} s^{-1} for this species) had a negative effect on the electron transport rate due to the acidification of the stroma, thus the electron transport rate decreased and the risk of the photoinhibition increased due to the lower efficiency of excess energy dissipation (Manetas 2004).

Even though the majority of plants have high CO_2 concentrations in the stems, O_2 concentration can vary widely, but it is usually lower than the atmospheric concentration (Pfanz *et al.* 2002). Since O_2 is consumed during the mitochondrial respiration, the concentration of this gas can greatly decrease within the stem, with a possible occurrence of hypoxia or even anoxia in extreme cases (Pfanz *et al.* 2002). When this takes place, SRP plays an important role in the production of O_2 and the prevention of hypoxia within the stems.

A recent finding of a novel tube system within the photosynthetic cortex of *Olea europaea* stems, with a secondary growth but no rhytidoma, indicates a possible way of a diffusion and gas exchange (CO_2 and H_2O) between the cortex and the atmosphere through the lenticels (Kyriakis and Fasseas 2010).

SRP, although generally not large enough to completely compensate and overcome the respiratory carbon loss from internal tissues of the stem, has an important advantage compared to SNP, since it occurs with lower or no water loss. Therefore, one would expect that stem WUE (calculated as $P_{N\text{-recycling}}$/transpiration rate) in SRP species should be higher than that corresponding to SNP and even higher than in leaves. Stem WUE of *Pinus monticula* was 50 times higher than leaf WUE (Cernusak and Marshall 2000).

Possible advantages of SRP are highlighted in several studies. In *Populus tremuloides*, SRP compensated substantially the respiratory carbon loss, with the reuptake of 29% of CO_2 respired annually (Foote and Schaedle 1976). Woody photosynthesis contributed to the stem and the bud biomass in defoliated plants, as evidenced by the organ growth and ^{13}C enrichment of new tissues (Saveyn *et al*. 2010). In *Myrica cerifera*, together with symbiotic nitrogen fixation and evergreen leaves, an improvement in the carbon use efficiency and WUE due to SRP explains the rapid expansion of this shrub into grassy swales of coastal environments (Vick and Young 2009).

Table 5. Maximum quantum yield of PSII photochemistry (F_v/F_m), relative quantum yield of PSII photochemistry (Φ_{PSII}) at the photosynthetic photon flux density (PPFD) of species with stem recycling photosynthesis. Values are mean ± SE when SE was available.

Species	Organ	F_v/F_m	Φ_{PSII}	PPFD [μmol(photon) m^{-2} s^{-1}]	Reference
Fagus sylvatica	leaf	0.81			Damesin (2003)
	stem - spring	0.78			
	stem - winter	0.25			
Prunus cerasus	leaf	0.833 ± 0.004	0.3	1,500	Manetas (2004)
	stem	0.546 ± 0.042	0.15	1,500	
Arbutus unedo	leaf	0.788 ± 0.009	0.15	1,500	
	stem	0.615 ± 0.021	0.1	1,500	
Pistacia lentiscus	leaf	0.809 ± 0.013	0.2	1,500	
	stem	0.709 ± 0.024	0.1	1,500	
Populus deltoides	leaf	0.856 ± 0.002	0.35	1,500	
	stem	0.662 ± 0.023	0.1	1,500	
Quercus coccifera	leaf	0.811 ± 0.003	0.3	1,500	
	stem	0.654 ± 0.028	0.1	1,500	
Prunus persica	stem	0.77 ± 0.02	0.42 ± 0.07	330	Alessio *et al*. (2005)
Helleborus viridis	leaf	0.77 ± 0.04	0.34 ± 0.04	850	Aschan *et al.* (2005)
	stem	0.75 ± 0.03	0.21 ± 0.03	850	
Alnus glutinosa	stem - summer	0.82			Berveiller *et al*. (2007)
	stem - winter	0.57			
Betula pendula	stem - summer	0.75			
	stem - winter	0.53			
Fraxinus excelsior	stem - summer	0.82			
	stem - winter	0.57			
Ginkgo biloba	stem - summer	0.75			
	stem - winter	0.31			
Picea abies	stem - summer	0.75			
	stem - winter	0.75			
Pinus sylvestris	stem - summer	0.82			
	stem - winter	0.80			
Quercus robur	stem - summer	0.80			
	stem - winter	0.55			
Tilia cordata	stem - summer	0.80			
	stem - winter	0.31			
Olea europaea	leaf	0.847	0.105 ± 0.004	1,500	Filippou *et al*. (2007)
	young stem	0.687	0.097 ± 0.004	1,150	
	mature stem	0.809	0.075 ± 0.008	1,150	
Calicotome villosa	leaf	0.79	0.35		Yiotis *et al.* (2008)
	stem - spring	0.79	0.3		
	stem - summer	0.73	0.15		
Median	leaf	0.81	0.30		
	stem	0.69	0.10		
	stem - spring	0.78			
	stem - summer	0.80			
	stem - winter	0.55			

A critique of methods used to determine SNP and SRP

Various methods used cause many difficulties when assessing and comparing values of $P_{N\text{-stem}}$ and $P_{N\text{-recycling}}$. One of these methods, ^{14}C-labeling, yields information on the short-term gross rather than the net CO_2 fixation. The

use of strips from the stem outer layers may affect results in an uncontrolled manner, given the change in a tissue water status and gas diffusion as compared with those of the intact stem. Measurements of O_2 evolution using O_2 electrodes involve submerging bark strips in a solution, which eliminates the natural diffusive barriers and presumably also internal air spaces, no matter how small. The use of Chl fluorescence, while providing comparative values of potential P_N, does not give information on actual $P_{N\text{-recycling}}$ or $P_{N\text{-stem}}$. A technique implemented for measuring $P_{N\text{-stem}}$ in cacti, where the measuring part of the gas-exchange leaf chamber is gas-tight appressed to the stem (Bronson *et al.* 2011), seems to be promising for obtaining actual values of $P_{N\text{-stem}}$ and $P_{N\text{-recycling}}$ in trees.

Conclusions and future perspectives

It becomes apparent from the above that SNP as well as SRP has many roles in the physiology and ecophysiology of a whole plant. These roles include: (*1*) maintaining physiological activity under a water deficit, when most species are leafless and the stem is the only organ responsible for CO_2 assimilation; (*2*) being the sole source of carbon used in the production of leaves, flowers, and fruits in deciduous species during drought; (*3*) reducing the amount of carbon released by nonphotosynthetic tissues due to internal CO_2 reassimilation, which may even increase during unfavorable periods; and (*4*) improving plant long-term integrated WUE because of the lesser effect of the water deficit on the stem than that in leaves. In summary, the presence of SNP and SRP allows plants to respond better to different environmental stresses, which probably influences the wide distribution of species exhibiting these types of photosynthesis.

Most of the studies on the contribution of the stem CO_2 assimilation to the total carbon gain have been conducted in deserts and Mediterranean habitats; there are very few studies in arid and semiarid tropical areas, indicating that more studies should be done in the tropics in this interesting field of research. Although a powerful tool for evaluating potential P_N, Chl *a* fluorescence has been applied to stems only rarely. The field SNP and SRP evaluation through seasonal daily courses is highly necessary for the assessment on the ecological context of the real contribution of these processes to the whole-plant carbon balance.

References

Adams, M.S., Strain, B.R.: Photosynthesis in stems and leaves of *Cercidium floridum*: spring and summer diurnal field response and relation to temperature. – Oecolog. Plantar. **3**: 285-297, 1968.

Adams, M.S., Strain, B.R., Ting, I.P.: Photosynthesis in chlorophyllous stem tissue and leaves of *Cercidium floridium*: Accumulation and distribution of ^{14}C from $^{14}CO_2$. – Plant Physiol. **42**: 1797-1799, 1967.

Aidar, M.P.M., Schmidt, S., Moss, G., *et al.*: Nitrogen use strategies of neotropical rainforest trees in threatened Atlantic Forest. – Plant Cell Environ. **26**: 389-399, 2003.

Alessio, G.A., Pietrini, F., Brilli, F., Loreto, F.: Characteristics of CO_2 exchange between peach stems and the atmosphere. – Funct. Plant. Biol. **32**: 787-795, 2005.

Allen, O.N., Allen, E.K. The Leguminosae: A Source Book of Characteristics, Uses, and Nodulation. – Univ. Wisconsin Press, Madison 1981.

Aschan, G., Pfanz, H.: Non-foliar photosynthesis – a strategy of additional carbon acquisition. – Flora **198**: 81-97, 2003.

Aschan, G., Pfanz, H., Vodnik, D., Batič, F.: Photosynthetic performance of vegetative and reproductive structures of green hellebore (*Helleborus viridis* L. agg.). – Photosynthetica **43**: 55-64, 2005.

Aschan, G., Wittmann, C., Pfanz, H.: Age-dependent bark photosynthesis of aspen twigs. – Trees-Struct. Funct. **15**: 431-437, 2001.

Berveiller, D., Damesin, C.: Carbon assimilation by tree stems: potential involvement of phospho*enol*pyruvate carboxylase. – Trees-Struct. Funct. **22**: 149-157, 2008.

Berveiller, D., Fresneau, C., Damesin, C.: Effect of soil nitrogen supply on carbon assimilation by tree stems. – Ann. For. Sci. **67**: 609, 2010.

Berveiller, D., Kierzkowski, D., Damesin, C.: Interspecific variability of stem photosynthesis among tree species. – Tree Physiol. **27**: 53-61, 2007.

Björkman, O., Demmig, B.: Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77 K among vascular plants of diverse origins. – Planta **170**: 489-504, 1987.

Bloemen, J., McGuire, M.A., Aubrey, D.P., *et al.*: Assimilation of xylem-transported CO_2 is dependent on transpiration rate but is small relative to atmospheric fixation. – J. Exp. Bot. **64**: 2129-2138, 2013.

Bossard, C.C., Rejmanek, M.: Why have green stems? – Funct. Ecol. **6**: 197-205, 1992.

Bronson, D.R., English, N.B., Dettman, D.L., Williams, D.G.: Seasonal photosynthetic gas exchange and water-use efficiency in a constitutive CAM plant, the giant saguaro cactus (*Carnegiea gigantea*). – Oecologia **167**: 861-871, 2011.

Cerasoli, S., McGuire, M.A., Faria, J. *et al.*: CO_2 efflux, CO_2 concentration and photosynthetic refixation in stems of *Eucalyptus globulus* (Labill.). – J. Exp. Bot. **60**: 99-105, 2009.

Cernusak, L.A., Hutley, L.B.: Stable isotopes reveal the contribution of corticular photosynthesis to growth in branches of *Eucalyptus miniata.* – Plant Physiol. **155**: 515-523, 2011.

Cernusak, L.A., Hutley, L.B, Beringer, J., Tapper, N.J.: Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna. – Plant Cell Environ. **29**: 632-646, 2006.

Cernusak, L.A., Marshall, J.D.: Photosynthetic refixation in branches of Western White Pine. – Funct. Ecol. **14**: 300-311, 2000.

Cernusak, L.A., Marshall, J.D., Comstock, J.P., Balster, N.J.: Carbon isotope discrimination of photosynthetic bark. – Oecologia **128**: 24-35, 2001.

Cernusak, L.A., Tcherkez, G., Keitel, C. *et al.*: Why are non-

photosynthetic tissues generally ^{13}C enriched compared with leaves in C_3 plants? Review and synthesis of current hypotheses. – Funct. Plant Biol. **36**: 199-213, 2009.

Chaves, M.M., Pereira, J.S.: Water stress, CO_2 and climate change. – J. Exp. Bot. **43**: 1131-1139, 1992.

Comstock, J.P., Ehleringer, J.R.: Contrasting photosynthetic behavior of leaves and stems of *Hymenoclea salsola*, a green-twigged warm desert shrub. – Am. J. Bot. **75**: 1360-1370, 1988.

Comstock, J.P., Ehleringer, J.R.: Effect of variations in leaf size on morphology and photosynthetic rate of twigs. – Funct. Ecol. **4**: 209-221, 1990.

Damesin, C.: Respiration and photosynthesis characteristics of current-year stems of *Fagus sylvatica*: from the seasonal patterns to an annual balance. – New Phytol. **158**: 465-475, 2003.

Dima, E., Manetas, Y., Psaras, G.K.: Chlorophyll distribution pattern in inner stem tissues: evidence from epifluorescence microscopy and reflectance measurements in 20 woody species. – Trees-Struct. Funct. **20**: 515-521, 2006.

Ehleringer, J.R., Comstock, J.P, Cooper, T.A: Leaf-twig carbon isotope ratio differences photosynthetic-twig desert shrubs. – Oecologia **71**: 318-320, 1987.

Ehleringer, J.R., Cooper, T.A.: On the role of orientation in reducing photoinhibitory damage in photosynthetic-twig desert shrubs. – Plant Cell Environ. **15**: 301-306, 1992.

Evans, J.R.: Photosynthesis and nitrogen relationships in leaves of C_3 plants. – Oecologia **78**: 9-19, 1989.

Filippou, M., Fasseas, C., Karabourniotis, G.: Photosynthetic characteristics of olive tree (*Olea europaea*) bark. – Tree Physiol. **27**: 977-984, 2007.

Foote, K.C., Schaedle, M.: Diurnal and seasonal patterns of photosynthesis and respiration by stems of *Populus tremuloides* Michx. – Plant Physiol. **58**: 651-655, 1976.

Francino, D., Sant'Anna-Santos, B., Silva, K., Thadeo, M., Meira, R., Azevedo, A.: [Leaf and stem anatomy of *Chamaecrista trichopoda* (Caesalpinoideae) and histochemistry of extrafloral nectary.] – Planta Daninha **24**: 695-705, 2006. [In Portuguese]

Gibson, A.C.: Anatomy of photosynthetic old stems of nonsucculent dicotyledons from North American deserts. – Bot. Gaz. **144**: 347-362, 1983.

Gibson, A.C.: Photosynthetic organs of desert plants. – Bioscience **48**: 911-920, 1998.

Hibberd, J.M., Quick, W.P.: Characteristics of C_4 photosynthesis in stems and petioles of flowering plants. – Nature **415**: 451-454, 2002.

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

Kyriakis, G., Fasseas, C.: A novel type of tube network within the stem bark of *Olea europaea* L. – Flora **205**: 90-93, 2010.

Langenfeld-Heyser, R.: CO_2 fixation in stem slices of *Picea abies* (L.) Karst: microautoradiographic studies. – Trees-Struct. Funct. **3**: 24-32, 1989.

Levizou, E., Petropoulou, Y., Manetas, Y.: Carotenoid composition of peridermal twigs does not fully conform to a shade acclimation hypothesis. – Photosynthetica **42**: 591-596, 2004.

Levizou, E., Manetas, Y.: Photosynthetic pigment contents in twigs of 24 woody species assessed by in vivo reflectance spectroscopy indicate low chlorophyll levels but high carotenoid/chlorophyll ratios. – Environ. Exp. Bot. **59**: 293-298, 2007.

Levizou, E., Manetas, Y.: Maximum and effective PSII yields in the cortex of the main stem of young *Prunus cerasus* trees: effects of seasons and exposure. – Trees-Struct. Funct. **22**: 159-164, 2008.

Lindorf, H., De Parisca, L., Rodríguez, P.: [Botany. Classification, structure and reproduction].. – Ediciones de la Biblioteca-UCV, Pp. 295-356. Caracas 2006. [In Spanish]

Manetas, Y.: Probing corticular photosynthesis through *in vivo* chlorophyll fluorescence measurements: evidence that high internal CO_2 levels suppress electron flow and increase the risk of photoinhibition. – Physiol. Plantarum **120**: 509-517, 2004.

Manetas, Y., Pfanz, H.: Spatial heterogeneity of light penetration through periderm and lenticels and concomitant patchy acclimation of corticular photosynthesis. – Trees-Struct. Funct. **19**: 409-414, 2005.

McGuire, M.A., Cerasoli, S., Teskey, R.O.: CO_2 fluxes and respiration of branch segments of sycamore (*Platanus occidentalis* L.) examined at different sap velocities, branch diameters, and temperatures. – J. Exp. Bot. **58**: 2159-2168, 2007.

McGuire, M.A., Marshall, J.D., Teskey, R.O.: Assimilation of xylem-transported ^{13}C-labelled CO_2 in leaves and branches of sycamore (*Platanus occidentalis* L.). – J. Exp Bot. **60**: 3809-3817, 2009.

McGuire, M.A., Teskey, R.O.: Estimating stem respiration in trees by a mass balance approach that accounts for internal and external fluxes of CO_2. – Tree Physiol. **24**: 571-578, 2004.

Mooney, H.A., Strain, B.R.: Bark photosynthesis in ocotillo. – Madroño **17**: 230-233, 1964.

Nilsen, E.T.: Partitioning growth and photosynthesis between leaves and stems during nitrogen limitation in *Spartium junceum*. – Am. J. Bot. **79**: 1217-1223, 1992.

Nilsen, E.T.: Stem photosynthesis: extent, patterns, and role in plant carbon economy. – In: Gartner, B. (ed.): Plant Stems: Physiology and Functional Morphology. Pp. 223-240. Acad. Press, San Diego 1995.

Nilsen, E.T., Bao, Y.: The influence of water stress on stem and leaf photosynthesis in *Glycine max* and *Sparteum junceum* (Leguminosae). – Am. J. Bot. **77**: 1007-1015, 1990.

Nilsen, E.T., Karpa, D., Mooney, H.A., Field, C.: Patterns of stem photosynthesis in two invasive legumes (*Spartium junceum*, *Cytisus scoparius*) of the California coastal region. – Am. J. Bot. **80**: 1126-1136, 1993.

Nilsen, E.T., Meinzer, F.C., Rundel, P.W.: Stem photosynthesis in *Psorothamnus spinosus* (smoke tree) in the Sonoran desert of California. – Oecologia **79**: 193-197, 1989.

Nilsen, E.T., Sharifi, M.R.: Seasonal acclimation of stem photosynthesis in woody legume species from the Mojave and Sonoran Deserts of California. – Plant Physiol. **105**: 1385-1391, 1994.

Nilsen, E.T., Sharifi, M.R.: Carbon isotopic composition of legumes with photosynthetic stems from Mediterranean and desert habitats. – Am. J. Bot. **84**: 1707-1713, 1997.

Osmond, C.B., Smith, S.D., Gui-Ying, B., Sharkey, T.D.: Stem photosynthesis in a desert ephemeral, *Eriogonum inflatum*. Characterization of leaf and stem CO_2 fixation and H_2O vapor exchange under controlled conditions. – Oecologia **72**: 542-549, 1987.

Pfanz, H., Aschan, G., Langenfeld-Heyser, R., Wittmann, C.,

Loose, M.: Ecology and ecophysiology of tree stems: corticular and wood photosynthesis. – Naturwissenschaften **89**: 147-162, 2002.

Rentzou, A., Psaras, G.K.: Green plastids, maximal PSII photochemical efficiency and starch content of inner stem tissues of three Mediterranean woody species during the year. – Flora **203**: 350-357, 2008.

Saveyn, A., Steppe, K., McGuire, M.A., Lemeur, R., Teskey, R.O.: Stem respiration and carbon dioxide efflux of young *Populus deltoides* trees in relation to temperature and xylem carbon dioxide concentration. – Oecologia **154**: 637-649, 2008.

Saveyn, A., Steppe, K., Ubierna, N., Dawson, T.E.: Woody tissue photosynthesis and its contribution to trunk growth and bud development in young plants. – Plant Cell Environ. **33**: 1949-1958, 2010.

Schulze, E.-D., Robichaux, R.H., Grace, J.: Plant water balance. – BioScience **37**: 32-36, 1987.

Smith, S.D., Nobel, P.S.: Deserts. – In: Baker, N.R., Long, S.P. (ed.): Photosynthesis in Contrasting Environments. Pp. 13-62. Elsevier Sci. Publ. B.V., Amsterdam 1986.

Smith, S.D., Osmond, C.B.: Stem photosynthesis in a desert ephemeral, *Eriogonum inflatum*. Morphology, stomatal conductance and water-use efficiency in field populations. – Oecologia **72**: 533-541, 1987.

Teskey, R.O., McGuire, M.A.: Carbon dioxide transport in xylem causes errors in estimation of rates of respiration in stems and branches of trees. – Plant Cell Environ. **25**: 1571-1577, 2002.

Teskey, R.O., McGuire, M.A.: Measurement of stem respiration of sycamore (*Platanus occidentalis* L.) trees involves internal and external fluxes of CO_2 and possible transport of CO_2 from roots. – Plant Cell Environ. **30**: 570-579, 2007.

Teskey, R.O., Saveyn, A., Steppe, K., McGuire, M.A.: Origin, fate and significance of CO_2 in tree stems. – New Phytol. **177**: 17-32, 2008.

Tinoco-Ojanguren, C.: Diurnal and seasonal patterns of gas exchange and carbon gain contribution of leaves and stems of *Justicia californica* in the Sonoran Desert. – J. Arid Environ. **72**: 127-140, 2008.

Vick, J.K., Young, D.R.: Corticular photosynthesis: A mechanism to enhance shrub expansion in coastal environments. – Photosynthetica **47**: 26-32, 2009.

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

Wittmann, C., Pfanz, H.: General trait relationships in stems: a study on the performance and interrelationships of several functional and structural parameters involved in corticular photosynthesis. – Physiol. Plant. **134**: 636-648, 2008.

Yiotis, C., Manetas, Y., Psaras, G.K.: Leaf and green stem anatomy of the drought deciduous Mediterranean shrub *Calicotome villosa* (Poiret) Link. (Leguminosae). – Flora **201**: 102-107, 2006.

Yiotis, C., Psaras, G.K., Manetas, Y.: Seasonal photosynthetic changes in the green-stemmed Mediterranean shrub *Calicotome villosa*: a comparison with leaves. – Photosynthetica **46**: 262-267, 2008.