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Photosynthetic characteristics of olive tree (*Olea europaea*) bark

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Summary Functional and structural characteristics of corticular photosynthesis of sun-exposed bark of olive tree (*Olea europaea* L.) were examined. Stomata are only sporadically present during stem primary growth. Light transmission through the phellem was age dependent, decreasing rapidly in stems older than five years of age. Light transmission was also low in pubescent 1-year-old stems. Light transmission was about 50% higher in wet phellem than in dry phellem. Photosynthetic capacity on a unit area basis (measured with an oxygen disc electrode at 27 °C and about 5% CO_2 on chlorophyllous tissue discs isolated from the stem) was higher in 1-, 20- and 30-year-old stems compared with 2–10-year-old stems. Low chlorophyll a/b ratio and light compensation points were recorded in olive stems with low phellem light transmission, in accordance with the shade acclimation hypothesis. The intrinsic photochemical efficiency of photosystem II of all stems, especially young stems, was less than that of the leaves. Our results show that olive tree bark possesses an efficient photosynthetic mechanism that may significantly contribute not only to the reduction in concentrations of CO_2 in the inner bark, but also to whole-tree carbon balance.

Keywords: bark age, bark photosynthesis, corticular photosynthesis, intrinsic fluorescence, photosynthetic pigments.

Introduction

Olive (*Olea europaea* L.) is an evergreen sclerophyllous tree cultivated in the Mediterranean region since ancient times. Olive orchards have been reliable producers of food and oil for thousands of years, supporting successive civilizations in the Mediterranean area. Olive trees can reach a height of 15 to 20 m, are extremely long-lived (up to 1000 years), are tolerant to drought and salinity and have low nutritional requirements. A young olive tree has smooth gray bark, but with age, the bark becomes gnarled and gradually disintegrates into rectangular pieces.

In addition to that in green leaves, photosynthetic carbon dioxide assimilation has been measured in petioles, green flowers and fruits, stems, calyces and even roots. Among alternative photosynthetic organs, stems most frequently make a significant contribution to whole-plant carbon gain. Two main categories of photosynthesis within plant stems can be distinguished: stem photosynthesis (mainly herbaceous stems) and corticular or bark photosynthesis (mainly woody stems without stomata) (Nilsen 1995, Aschan and Pfanz 2003).

Green stems lacking a well-developed periderm and, bearing abundant and functional stomata, demonstrate clear photosynthetic characteristics (Nilsen 1995). Stem photosynthesis resembles leaf photosynthesis in many characteristics, such as the C_3 pathway (although enzymes typical of the C_4 pathway may participate in carbon metabolism of some herbaceous stems, see Hibberd and Quick 2002), gas exchange and CO_2 assimilation through stomata and similar responses to light and other environmental factors. Such stems are capable of considerable carbon gain, especially during leafless periods (Nilsen 1995, Gibson 1996, Aschan and Pfanz 2003).

Corticular or bark photosynthesis occurs in stems of woody plants, in chlorenchyma layers located under a well-developed stomata-free periderm. In this case, the outer peridermal, or rhytidomal, layers are characterized by high resistance to gas diffusion and low light transmittance (Pfanz and Aschan 2001). Carbon dioxide diffuses to chlorenchyma cells either from the atmosphere (through surface cracks or lenticels), or from the stem interior. It is believed that corticular photosynthesis plays a vital role in recapturing respiratory CO_2 and, thus, contributes to internal CO_2 recycling in stems and to overall annual carbon balance (Pfanz and Aschan 2001, Aschan and Pfanz 2003). Corticular photosynthesis may be common in temperate deciduous species because photosynthetic stems reduce respiratory carbon losses in winter (Nilsen 1995). For this reason, most studies have focused on species such as *Populus tremuloides* Michx., *P. tremula* L., *Fagus sylvatica* L., *Syringa vulgaris* L., *Betula pendula* Roth and *Tilia americana* L.

Rates of corticular photosynthesis are usually low (Pfanz and Aschan 2001), mainly due to the low light transmittance of the periderm (Schaedle 1975, Wittmann et al. 2001), despite high internal CO_2 concentrations (Pfanz and Aschan 2001, Manetas 2004*a*). These factors interact with others, such as

stem age, to modify the photosynthetic capacity of bark. For example, transmission of light by the periderm declines with increasing stem age (Pilarski 1989, Pfanz and Aschan 2001). Consequently, corticular chloroplasts show many features of shade-acclimated behavior (Pilarski 1999, Wittmann et al. 2001, Manetas 2004*a*). Chlorophyll concentration of stems also changes with age, although the available data are limited to comparisons of young stems with those about five years older (Pearson and Lawrence 1958, Pilarski 1984, Larcher et al. 1988, Kauppi 1991, Solhaug et al. 1995, Pfanz and Aschan 2001).

Chlorophyllous tissue is present in the bark of olive (*O. europaea*) stems up to several years old. Our study investigated the age dependency of photosynthesis in this tissue and compared bark and leaf photosynthetic variables in this species.

Materials and methods

Study site and plant material

Five 40–50-year-old olive (*O. europaea*) trees were selected from an olive grove at the Agricultural University of Athens, Greece (37°58′54″ N, 23°42′12″ E, 35 m a.s.l.). Trees were watered according to usual agricultural practice and were exposed to natural sunlight. To prevent intense shading of tree bark by the leaf canopy during the experiment, trees were pruned seven months before the start of experiments. Thus, most of the bark surfaces of the trees were exposed to full sunlight (2000 μmol m^{-2} s^{-1}).

Bark of *O. europaea* has a continuously active cork cambium as long as it remains smooth. Trunks of old trees (over 30 years old) are covered partly by smooth photosynthetically active bark and partly by rough bark that lacks photosynthetic tissues. The proportion of each type of bark seems independent of tree age, and smooth, photosynthetically active bark is widely distributed. Only smooth parts of south-facing bark of stems of different ages (1, 2, 3, 4, 5, 10, 20 and 30 years) were investigated. All measurements were made between August and early September. The approximate age of stems was estimated by counting annual rings in pruned branches of roughly the same diameter from the same or neighboring trees. Leaves of the current growth period (from the third node from the apex) were collected from sun-exposed, south-facing parts of the canopy. All samples were collected shortly after sunrise, placed within wet paper layers, wrapped in polyethylene bags and transferred immediately to the laboratory.

Scanning electron microscopy

For scanning electron microscopy (SEM), samples from the south-facing bark of stems of different ages were fixed in 3% glutaraldehyde in 0.1 M phosphate buffer, pH 7.3, washed in buffer, dehydrated in an acetone series, dried in a Polaron E3000 critical point drier and sputter coated with gold (Polaron Equipment). Some specimens were observed fresh at 2.5 kV without any preparation. Specimens were observed and photographed with either a Cambridge Stereoscan S-150 (Cambridge Instrument Comp.) or a Jeol 6360 SEM.

Light microscopy

Samples several mm deep were taken with a razor blade from the surface of the south-facing bark of stems and fixed in 3% glutaraldehyde in 0.1 M phosphate buffer, pH 7.3, at 4 °C for 24 h. The solution contained 1% caffeine to retain phenolic substances within the vacuoles (Müller and Greenwood 1978). Samples were post-fixed in 0.1% OsO_4 for 24 h, washed in buffer, dehydrated in an ethanol series followed by propylene oxide, embedded in Spurr epoxy resin and polymerized at 70 °C for 36 h. Semi- and ultra-thin sections were cut with a Reichert OMU-3 ultramicrotome with glass knives. Semi-thin sections (0.5 μm) were stained with 1% toluidine blue in 1% borax solution. Sections were observed with an Olympus BX40 microscope.

Chlorophyll measurements

Sample discs for chlorophyll and photosynthetic measurements were cut from branches, stems and leaves with a cork borer. Leaf and stem discs, with a total disc area of 2.355 cm^2 for all years (except current-year bark disks, which were 0.784 cm^2), were used for O_2 evolution and chlorophyll determination. All non-chlorophyllous woody tissues from stem discs were removed. Chlorophyll (total chlorophyll, chl a and chl b) concentrations were determined in 80% acetone extracts by the method of Graan and Ort (1984).

Chlorophyll a fluorescence

The intrinsic photochemical efficiency of photosystem II (PS II) was evaluated from the variable fluorescence to maximum fluorescence ratio (F_v/F_m), which was measured with a portable chlorophyll fluorescence instrument (FIM 1500, ADC Bioscientific Ltd.). Samples were taken to the laboratory as described above. The phellem remained intact and was dark adapted for 30 min in a standard leaf clip before measurement. Excitation light was adjusted to 1500 μmol m^{-2} s^{-1} for bark and 1150 μmol m^{-2} s^{-1} for leaves from red light emitting diodes. Fluorescence induction was recorded over a 5-s period.

Light penetration measurements

Light penetration through the cork layers (phellem) was measured with a Li-Cor Li 185B quantum sensor. Mechanically separated (peeled off) dead cork layers were used for the experiments. Samples were large enough to cover the entire surface of the quantum sensor, which was placed directly below the sample, and the optical fiber of the light source (Intralux 6000, Volpi) was mounted above it, and illumination was adjusted to yield a photosynthetic photon flux (PPF) of 1900 μmol m^{-2} s^{-1}. Measurements were taken of both dry and wet cork layers. Relative PPF transmission was calculated as a proportion (%) of incident PPF directly above the sample surface.

Photosynthetic O_2 evolution

Photosynthetic capacity and dark respiration were measured

as oxygen gas exchange with a leaf disk electrode (Model LD2, Hansatech Instruments) in a thermostatically controlled oxygen electrode at 27 °C and about 5% CO_2 concentration to overcome gas diffusion resistance through the cork layers (in bark) or through stomata (in leaves). For every sample, three leaf or stem disks (r = 0.5 cm), of 2.355 cm^2 total area, were placed in the cuvette, and O_2 evolution was measured with increasing photon fluence rates in the range of 0–1900 μmol m^{-2} s^{-1} from light emitting diodes (LH36U, Hansatech Instruments). Tissues were not pre-illuminated before each measurement. Six samples from bark and six from leaves were measured.

Stem/leaves surface area ratio

A 15-year-old branch was detached and transferred to the laboratory. The branch was cut into pieces, which were grouped into five categories according to age and diameter: current growth, 1, 2, 4 and about 15 years old. Stems were defoliated, and their surface area was estimated from their diameter and length, assuming them to be cylindrical. Leaf surface area was estimated by image analysis.

Statistical analysis

Student's *t*-test was used to identify significant differences between means. The effect of stem age was assessed by one-way analysis of variance (ANOVA). Differences between means were determined by Tukey's post-hoc test or Tamhane's post-hoc test depending on homogeneity of variance.

Results

Age-dependent changes in the morphology of olive bark

Young stems were covered by a dense indumentum of multicellular peltate hairs similar to those that cover the abaxial surface of mature leaves (Figures 1A and 1B). The morphology of the epidermis and trichome bases were observed in dehaired samples (Figure 1B). Stomata were observed only sporadically during the primary growth of the stems (Figures 1B and 1C). In transverse sections, substomatal chambers were filled with an electron lucent material of unknown composition (Figure 1D). At the onset of secondary growth (established by the formation of secondary protective tissues, data not shown), trichomes appeared to be sparse because of organ expansion. At the same time, a gradual appearance of longitudinal cracks and lenticels was observed (Figures 1E and 1F). The long axis of lenticels was parallel to that of the stem. Stomata were not apparent. In older stems, the epidermis, together with trichomes, had been replaced by a cork layer interrupted by numerous large lenticels that had formed by the unification of neighboring lenticels (Figures 1G and 1H). Cork cells of the lenticel possessed the characteristic appearance of such tissues, being flattened and stacked in columns, leaving large intercellular spaces (Figure 1H).

Light penetration through the cork layers

There were notable differences among stems of different ages in the penetration of visible light through the dry peridermal cork layers. One-, 20- and 30-year-old stems transmitted only 10% of incident light—only about 200 μmol m^{-2} s^{-1} reached the first layers of chlorenchyma tissue of these stems. In 5- and 10-year-old stems, light transmission reached up to 28%. Light penetration of wet stems was almost 50% greater than that of dry stems of all ages (Table 1).

Pigment concentration and chlorophyll a/b ratio

Total chlorophyll concentration of olive tree bark on a unit surface area increased up to the age of four years, reaching 30.65 μg ml^{-1} cm^{-2} and remained constant in older stems. This value corresponds to 50% of the total chlorophyll concentration of the leaves (Figure 2A). Total chlorophyll concentration was twofold higher in stems older than four years old compared with 1- and 2-year-old stems. Age had no significant effect on bark chlorophyll a/b ratio except in 1-year-old stems (Figure 2B) where chl a/b was 1.49, and the ratio rapidly increased in older stems where it ranged between 1.92 and 2.19. The chl a/b ratio was higher in leaves than in stems, reaching 2.57.

Photosynthetic capacity and dark respiration of the bark

Corticular photosynthesis of stems of all ages appeared not only to compensate for the corresponding dark respiration rates, but to yield a net carbon gain (Figure 3). Maximum photosynthetic capacity of *O. europaea* stems on a unit stem surface area basis increased with stem age in stems 1, 20 and 30 years of age and reached more than 80% of that of leaves (about 17 μmol m^{-2} s^{-1} versus 21.3 μmol m^{-2} s^{-1} for leaves) (Figure 3A). Leaves had a dark respiration rate of 7.3 μmol m^{-2} s^{-1} (Figure 3C). Dark respiration rates were between 4.08 and 8.12 μmol m^{-2} s^{-1} in all stems except for the 1-year-old stems where dark respiration rates reached 12 μmol m^{-2} s^{-1} (Figure 3C). No relationship was found between stem photosynthetic capacity and dark respiration rate. Photosynthetic capacity expressed on a unit chlorophyll basis in young stems and in branches older than 20 years was up to threefold higher than that of leaves (Figure 3B).

The response of photosynthetic capacity to irradiance differed among leaves and stems of different ages (Table 2). Leaves showed light saturation at 1680 μmol m^{-2} s^{-1}, 1- and 20-year-old stems at 982 μmol m^{-2} s^{-1}, whereas 5-year-old stems showed light saturation at 1850 μmol m^{-2} s^{-1}. Light compensation points were measured at 58, 253, 62 and 48 μmol m^{-2} s^{-1} for 1-, 5- and 20-year-old stems and mature leaves, respectively (Table 2). If incident light was corrected, according to Table 1, for the percentage of transmitted light through the dry phellem (assuming that leaf epidermis transmits nearly 100% of the incident light), the above-mentioned values changed. The corrected light compensation points were measured at 7, 59 and 7 μmol m^{-2} s^{-1} for 1-, 5- and 20-year-old stems, respectively. Corrected values for light saturation were 115, 431 and 111 μmol m^{-2} s^{-1} for 1-, 5-, and 20-year-old stems, respectively (Table 2).

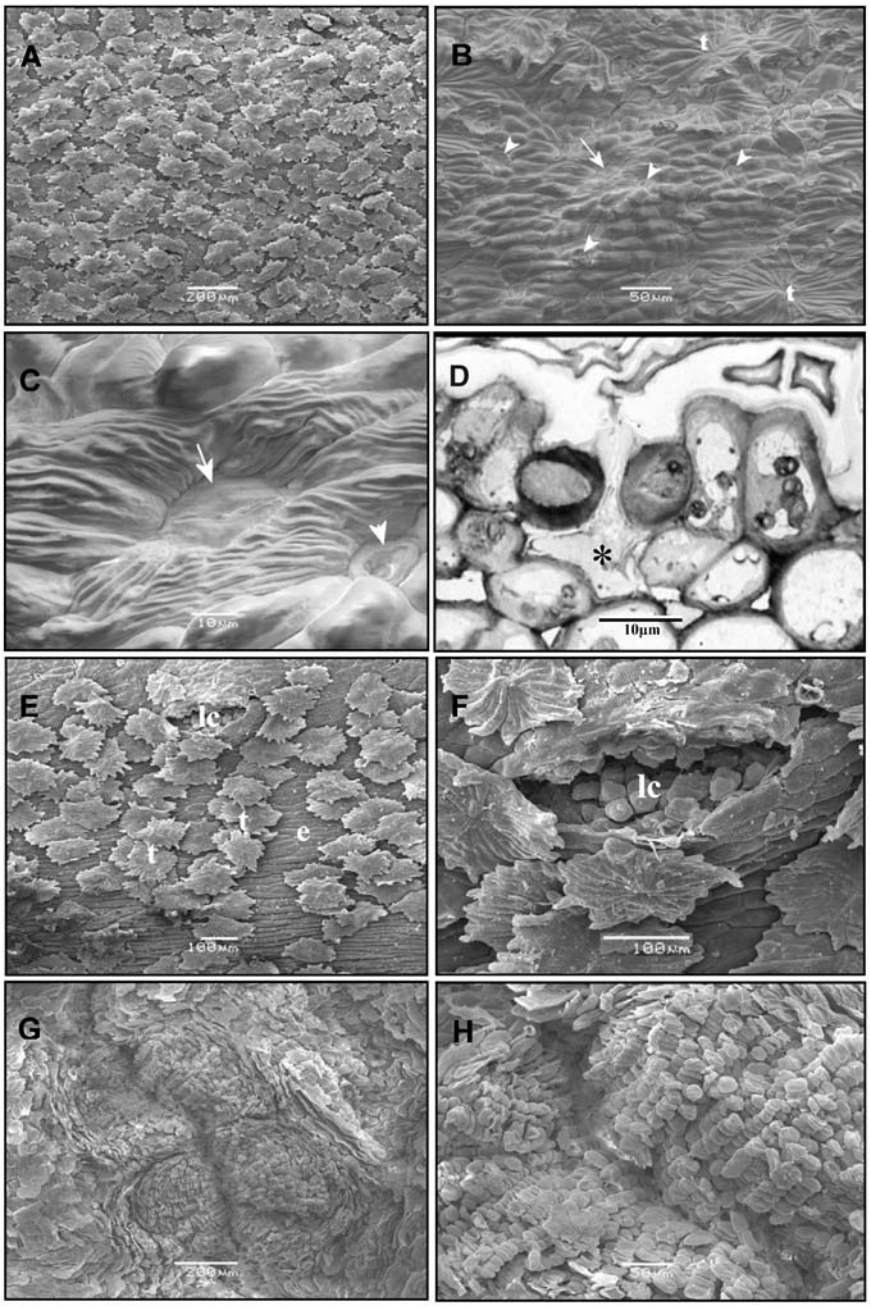

Figure 1. Scanning electron microphotographs of young and old *Olea europaea* tree bark. (A) Surface of a young stem. Notice the dense trichomes that cover the epidermis. (B) The surface of the stem after removing trichomes. (C) Detail from B, showing a stoma. (D) Semi-thin transverse sections of young stem stoma. (E) Details on the surface of one-year-old stem. Notice that trichomes are more sparse than on the surface of a newly formed stem and that a lenticel is present. (F) Detail from E, showing a young lenticel. (G) An old stem. (H) Detail from G, showing mature lenticels. Notice the characteristic appearance of lenticel cork cells. Arrowheads denote trichome bases. Arrows denote a stoma on young stem surface. Asterisk denotes an amorphous gelatinous material that fills the substomatal chamber of the stoma. Abbreviations: e, epidermis; lc, lenticel; and t, trichome.

Age variation in F_v/F_m

In stems, the intrinsic photochemical efficiency of PS II, expressed as F_v/F_m, showed an age-dependent increase from 0.687 in 1-year old-stems to 0.809 in 10-year-old stems. The highest F_v/F_m ratio in leaves was 0.847 (Figure 2C).

Age-depended changes in leaf/stem surface area

The contribution of stems to the % total area (stems and bearing leaves) of a 15-year-old branch was age-dependent (Table 3). We observed a gradual increase in this parameter, as well as a gradual decrease in leaf/stem surface area, with age.

Discussion

Stomata were sporadically present only during the primary growth of the stem. Moreover, the observed stomata appeared to be non-functional because the substomatal chambers were filled with electron-lucent materials (Figure 1D). These characteristics suggest that corticular photosynthesis of olives is similar to that of other species.

Light transmission through the isolated cork layers varied with stem age, decreasing rapidly in stems older than 5 years (Table 1). This is partly explained by the gradual replacement of epidermis by protective cork tissues (Pilarski 1989, Kauppi 1991, Pfanz and Aschan 2001, Aschan et al. 2001). Light

Table 1. Light penetration through the cork layers (phellem) of *Olea europaea* stems of different ages. Data are means ± SE, $n = 5$. Asterisks denote significant differences: **, $P < 0.01$; *, $P < 0.05$; and ns, not significant.

Stem age (yrs)	Light transmission (%)		
	Dry phellem		Wet phellem
1	11.7 ± 0.6	**	16.8 ± 0.7
2	26.0 ± 1.7	**	37.7 ± 1.9
3	23.3 ± 1.7	**	38.5 ± 2.1
5	30.9 ± 3.3	*	37.5 ± 4.1
10	28.0 ± 5.5	**	39.3 ± 3.2
20	11.3 ± 1.1	**	18.8 ± 1.8
30	10.4 ± 1.4	ns	15.1 ± 1.9

transmission by phellem could be affected by openings in the cork layers and by the number of lenticels present (Pfanz et al. 2002). Recently, Manetas and Pfanz (2005) suggested that, contrary to previous hypotheses, lenticels represent bark areas with lower light transmittance than neighboring non-lenticel areas. Reduced light transmission in old stems (Table 1) could be caused both by thicker cork layers and by an abundance of lenticels. Unusually, low light transmission by 1-year-old stems (Table 1) compared with 2-, 3-, 5- and 10-year-old stems has been noted previously for *Populus tremula* (Pfanz and Aschan 2001). In the case of olive trees, reduced transmittance by 1-year-old stems may be related to pubescence (Figure 1A). Similarly to young olive leaves (Karabourniotis and Fasseas 1996, Karabourniotis et al. 1998, Karabourniotis and Bornman 1999, Karabourniotis et al. 1999), trichomes on

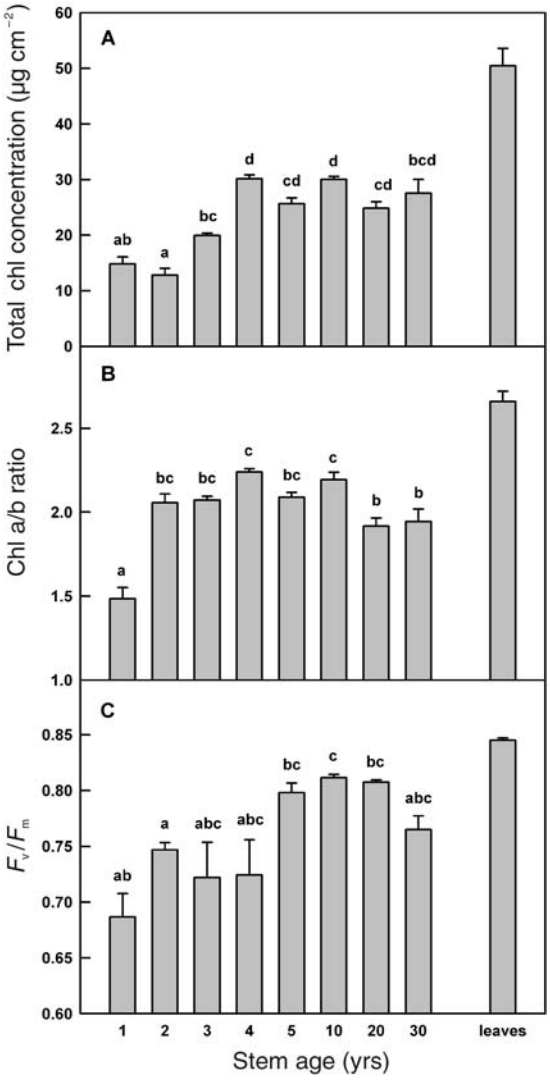

Figure 2. (A) Total chlorophyll concentration, (B) chl a/b ratio and (C) F_v/F_m of *Olea europaea* tree bark in relation to stem age. Corresponding values for leaves are shown for comparison. Data are means ± SE, $n = 6$. Significant differences at $P < 0.05$ are indicated by different letters.

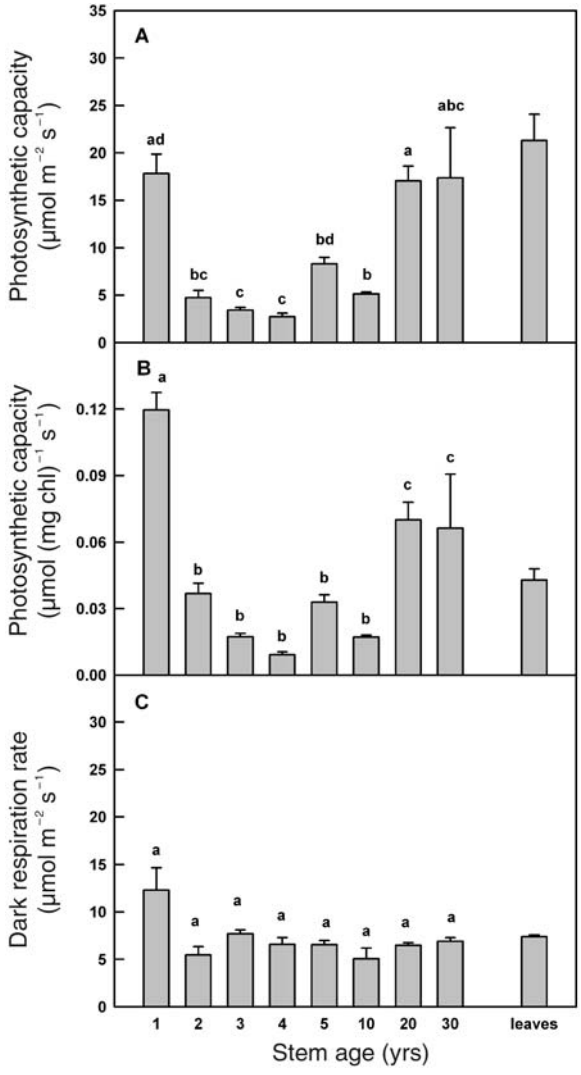

Figure 3. (A) Photosynthetic capacity on a tissue area basis and on (B) a chlorophyll content basis and (C) dark respiration rates of *Olea europaea* tree bark in relation to stem age. Corresponding values of leaves are shown for comparison. Data are means ± SE, $n = 6$. Significant differences at $P < 0.05$ are indicated by different letters .

Table 2. Light compensation point (LCP), light saturation irradiance (LSI) and quantum yield of *Olea europaea* stems of different ages. Values of mature leaves are shown for comparison. Values in parentheses represent LCPs and LSIs of the bark corrected according to the dry phellem transmission. Data are means ± SE, $n = 6$.

Stem age (yrs)	LCP ($\mu mol\ m^{-2}\ s^{-1}$)	LSI ($\mu mol\ m^{-2}\ s^{-1}$)	Quantum yield
1	58 ± 5 (7.0 ± 0.7)	982 ± 27 (115 ± 3)	0.097 ± 0.004
5	253 ± 21 (59 ± 5)	1850 ± 38 (431 ± 9)	0.061 ± 0.004
20	62 ± 6 (7.1 ± 0.7)	982 ± 56 (111 ± 6)	0.075 ± 0.008
Leaves	48 ± 3	1682 ± 65	0.105 ± 0.004

young olive stems may have a protective function, as in the case of the hair mat covering the photosynthetic stems of *Verbascum speciosum* (Schrader) (Manetas 2003).

Light transmission of wet phellem was about 50% greater than that of dry phellem (Table 1), as reported by Manetas (2004*b*) for olive and by Solhaug et al. (1995) for *P. tremula*. Manetas (2004*b*) suggested that rapid and reversible changes in peridermal optical properties upon wetting and drying are of dual adaptive significance, allowing corticular photosynthesis during rain (under low irradiances) and minimizing the risk of photoinhibition after sudden exposure to full sunlight.

The photosynthetic capacities of 1-, 20- and 30-year-old olive tree stems (Figures 3A and 3B) were high, considering that positive photosynthetic rates of intact twigs are the exception rather than the rule (see Phanz and Aschan 2001). The method we used to determine photosynthetic capacity, contrary to the methods using CO_2 gas exchange cuvettes, probably does not limit photosynthesis caused by gas diffusion resistance through the cork layers, first because of the high CO_2 concentration used, and second because CO_2 may diffuse to the photosynthetic active cells through the cut edges of the bark disks. Therefore the measured photosynthetic rates probably represent the in vitro maximum photosynthetic capacity and not the actual net photosynthesis of the whole bark. Moreover respiration rates obtained by this method are not representative of in vivo rates because a considerable part of respiring tissues (the non chlorophylous woody tissues) had been removed from the sample before measurements. Our measuring conditions may be responsible for the absence of a relationship between photosynthetic and dark respiration rates, contrary to previous studies (Foote and Shaedle 1976, Cernusak and Marshall 2000, Damesin 2003). However, our measurements offer an approach for determining the ability of corticular chlorenchyma to photosynthesize and making comparisons between leaves and stems.

Age dependency of corticular photosynthesis was previously reported by Aschan et al. (2001), but only for deciduous trees. Photosynthetic capacity was high in 1-year-old stems and, unexpectedly, in stems more than 20 years old, despite their low light transmission (Figures 3A and 3B, Table 1). It is common for young twigs and branches to have higher photosynthetic activities than older twigs and branches (Pfanz et al. 2002). Our values for bark photosynthetic capacity in stems up to 5 years old are similar to those reported in other studies (Pilarski 1995, Schmidt et al. 2000, Pfanz and Aschan 2001). In olive trees, however, much older stems also show a high and constant carbon gain that may be related to the high quantum yields attained by these tissues, which were comparable with those of leaves. There is no available information for old stems of other species.

The age-dependent changes in chlorophyll concentration of olive bark that we observed (Figure 2A) are in accordance with the results of other studies (Pearson and Lawrence 1958, Pilarski 1984, Kauppi 1991, Phanz and Aschan 2001, Pfanz et al. 2002). The comparison of the chlorophyll concentration between olive stem and leaves (Figure 2A) gave similar results to other studies suggesting that on a surface area basis, young twigs can contain up to 70% of the chlorophyll concentration of leaves (Pilarski 1984, Larcher et al. 1988, Kharouk et al. 1995, Phanz and Aschan 2001).

Chlorophyll a/b ratios of olive tree stems (Figure 2B) are similar to those reported by Larcher et al. (1988) for other species and resemble those of shade-adapted leaves. High concentrations of chlorophylls and low chl a/b ratios are indicative of acclimation to low irradiances (Anderson et al. 1988, Brugnoli et al. 1994). In the case of olive stems, the shade acclimation characteristics can be explained by low light penetration through cork layers (Table 1) and possibly by the canopy shading effect. Shade acclimation characteristics were further confirmed by the low light compensation points, as well as by the low irradiances causing photosynthetic saturation in these stems, which were lower than the corresponding values of

Table 3. Stem and leaf surface area, stem surface area as % of the total and leaf/stem surface area ratio of a 15-year-old branch of *Olea europaea*. The branch was cut into pieces, which were then grouped into five age categories.

Stem age range (yrs)	Stem surface area (cm^2)	Bearing leaves surface area (cm^2)	Stem surface area as % of the total	Leaf/stem surface area ratio
0	241	2.264	9.6	9.39
0–1	350	2.379	12.8	6.79
0–2	428	2.379	15.2	5.56
0–4	2.774	13.499	17.1	4.87
0–15	46.661	173.823	26.8	3.72

leaves (cf. Table 2).

An age-dependent increase in F_v/F_m of olive stems was observed (Figure 2C). The lowest value of this parameter was found in 1-year-old stems, probably because of the immaturity of the photosynthetic apparatus. Similar results were obtained for young leaves. The susceptibility of young leaves to photooxidative damage caused by light has been noted by several researchers (Krause et al. 1995, Bisba et al. 1997). The decreased values of PS II photochemical efficiency (F_v/F_m) of the bark tissues compared with the leaves suggest a higher risk of photoinhibition of bark tissues, a characteristic frequently displayed by shade-adapted chloroplasts (Anderson 1988, Björkman and Demmig-Adams 1994, Flexas et al. 2001, see also Levizou et al. 2004, Manetas and Pfanz 2005).

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