

Growth, Leaf Gas Exchange and Leaf Anatomy of three Ornamental Shrubs Grown under different Light Intensities

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Summary

The aim of this work was to determine the long-term response of growth, leaf morphology and gas exchange of three widely grown shrubs to the level of irradiance. To this purpose, one-year-old uniform rooted cuttings of *Camellia x williamsii* W.W.Sm. 'Debbie', *Photinia x fraseri* Dress 'Red Robin' and *Viburnum tinus* L. 'Eve Price' grown in containers were placed for 2 years under different woven polypropylene fabrics that reduced light intensity by 60 % and 30 % and, as a control, plants were also grown in full sun. Plant dry weight, LAI, LAR, NAR, RGR, mean leaf area, number, ultrastructure and gas exchange were measured during the experiment. The species reacted in different

ways to shading, indicating a strong genetic influence, even if some parameters as transpiration, leaf thickness, leaf size and stomatal frequency responded similarly to irradiance. *Camellia* showed a great adaptability to light conditions. Shading *photinia* greatly reduced root biomass but did not alter leaf gas exchange, thus is not a recommendable practice for this species. *Viburnum* increased leaves and stems biomass and increased net photosynthesis and water use efficiency under shaded conditions. In conclusion, effects of shading can positively affect plant growth and physiology, but response to shading is species-specific.

Key words. *Camellia x williamsii* – carbon assimilation – leaf internal structure – light reduction – *Photinia x fraseri* – *Viburnum tinus*

Introduction

Plant acclimation to different levels of light intensity depends on both environmental conditions and plant genotype (BOARDMAN 1977; ABRAMS et al. 1992), and thus is species-specific. Improper light levels may negatively affect plant growth and physiology: excessive radiation may lead to photoinhibition and damage the photosynthetic machinery (MEDINA et al. 2002) whereas excessive shading can reduce photosynthesis rates, decrease root growth and result in reduced capacity to survive to drought (KRAMER and DECKER 1944). Previous research (ANDERSEN et al. 1991a, b; CHARTZOULAKIS et al. 1993) has shown that different levels of shading greatly influence growth and leaf gas exchange. By shading we mean a reduction of light quantity without any change of light quality and photoperiod. Light quality, expressed as the ratio between R/FR wave length is probably of secondary importance for shade acclimation of the photosynthetic apparatus (TINOCO-OJANGUREN and PEARCY 1995). Plants can acclimate to changes in light quantity, at the whole-plant level, changing the biomass partitioning among leaves, stem, roots (EVANS and POORTER 2001). Leaves are the most exposed plant organ to aerial conditions and it is well documented that the variation in light intensity can induce morphological (NOBEL 1976; BOARD-

MAN 1977), physiological (BARDEN 1978; SYVERTSEN and LLOYD 1994) and ultrastructural (ARAUS et al. 1986; KLICH 2000) modifications in leaf tissues.

Shading reduces air temperature and, by consequence, increases relative humidity: it helps prevent heat stress and water deficits, limits transpiration (E) and can lead to improved productivity (SYVERTSEN and LLOYD 1994) and water-use efficiency (WUE) (CHARTZOULAKIS et al. 1993; JIFON and SYVERTSEN 2003). Therefore, shading, in a certain limit, can be an useful mean to improve sustainability and efficiency in plant nursery production by reducing water consumption, by fastening growth and decreasing time needed for getting plants ready for sale and by increasing plant quality. Anyway, since the different species respond in different ways to the reduction of light intensity, the choice and study of some plants with different behaviours in relation to light intensity among the 2000 genus of horticultural plants is interesting. In this study three shrub species were selected: *Camellia x williamsii* 'Debbie', *Photinia x fraseri* 'Red Robin' and *Viburnum tinus* 'Eve Price'. *Camellia* is a species which grown naturally in cool and wet temperate climates. It's considered a species which thrives in mild shade conditions. *Photinia* is a fast-growing species which tolerate very well drought, heat and pollution, widely use for landscaping in Europe and United States. *Viburnum* is a

typical Mediterranean species adapted to live both under high radiation as a part of the Mediterranean maquis and in the partially shaded environments of the understorey. These species were selected among widely-used plants for urban horticulture in Europe because of their different sensitivity to radiation level.

The aim of this work was to determine the relationship between level of irradiance, growth, leaf morphology and gas exchange in three widely grown ornamental shrubs grown in container.

Materials and Methods

Area description

The study was conducted in an experimental nursery (Fondazione Minoprio) located in Vertemate con Minoprio (Como, Italy; 45° 44' N, 9° 04' E; 250 m above sea level), a town 15 km far from the lake of Como, which influences the climate of the area. Mean annual precipitation, calculated on 20 years basis, is 1086 mm. May (134 mm) is the wettest month while July (65 mm) is the driest. Average temperature of the last 20 years was 12.9 °C; December and January (3.6 °C) are the coldest months, July (23.2 °C) is the warmest.

Plant material and experimental conditions

One-year-old uniform rooted cuttings of *Camellia x williamsii* W.W.Sm. 'Debbie' (120 plants), *Photinia x fraseri* Dress 'Red Robin' (120 plants) and *Viburnum tinus* L. 'Eve Price' (120 plants) were potted in April into 15 cm (2 L) diameter plastic containers. Potting substrate was sphagnum peat (pH=4.5) and pumice (4/1, w/w). Calcium carbonate (4 kg m⁻³) was added to the substrate for *Photinia* and *Viburnum* plants. 4 kg m⁻³ of Ficote® (Scott International B.V., Geldermasel, The Netherlands) (15-8-12/NO₃, K₂O, P₂O₅), was added to the growing medium. In May, plants from each species were moved from the greenhouse to three tunnels. Each of them was covered for one third of its length with black woven polypropylene fabric (Agriombra, Arrigoni Spa, Uggiate Trevano, CO) that acted as a neutral filter and reduced radiation by 30 % (mild shade, 70 % of full sun); for one third of its length was covered with a 60 % (heavy shade, 40 % of full sun) shade cloth and for the remaining third of its length was exposed to full, natural sunlight as a control. Radiation was measured every 10 minutes from May to September using a weather station (MS906C, Soender-soe, DK) (Fig. 1). The experimental design was a randomized block where each tunnel acted as a replicate. Each replicate was made of 15 plants per species per level of light intensity. Water requirement was provided by sprinkler irrigation with different timing and amount adjusted to the different shading treatment so that a 20 % leaching fraction was maintained. The following spring, all planted were transplanted to 18 cm (3 L) containers with the same substrate and the same slow-release fertilizer.

Biometric measurements

Height was measured on 6th December on *Camellia* and *Viburnum*, but not on *Photinia* because of the horizontal growth of this cultivar. Fresh and dry weight were meas-

ured at the beginning (26th May), at the middle (14th July) and at the end (6th December) of the second growing season on 2 randomly harvested plants per replicate, taxon and shade treatment. Harvested plants were replaced by substitution plants, so that environmental conditions were not affected by sampling. In order to determine biomass production, shoots and leaves were excised and weighted separately. Roots were cleaned from the potting medium with a flush of air. To determine dry weight, leaves, stems and roots were oven-dried at 70 °C till constant weight was reached, so the shoot to root ratio could be determined on dry weight basis at three dates during the growing season (26th May, 14th July, 6th December). Leaf area was determined by scanning all the leaves on a A3 scanner and image analysis was performed using Image Tool 1.3 (UTHSCSA). Leaf Area Index (LAI) was determined as leaf area over crown projected area on the ground at the beginning (26th May) and at the end (6th December) of the second growing season. Leaf Area Ratio (LAR, cm² g⁻¹), was calculated by dividing leaf area by plant dry weight. Relative Growth Rate (RGR, mg g⁻¹ day⁻¹), was calculated as:

$$RGR = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad (1)$$

where W_1 and W_2 are respectively the dry matter at the beginning and at the end of the experiment, t_1 and t_2 are the number of days of the sampling (TATTINI et al. 2006). Net Assimilation Rate (NAR, g day⁻¹ cm⁻²), defined as the increase in total plant dry weight per unit leaf area was calculated as the RGR to LAR ratio (POORTER and REMKENS 1990).

Leaf gas exchange measurements

Leaf gas exchange measurements were performed six times from May to September with a portable infrared gas analyzer (CIRAS-2, PP Systems, Hertfordshire, UK). Measured variables were current net photosynthetic rate (A ; $\mu\text{mol m}^{-2} \text{s}^{-1}$) and transpiration rate (E ; $\text{mmol m}^{-2} \text{s}^{-1}$). Water Use Efficiency (WUE; $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$) was calculated as A to E ratio (JIFON and SYVERTSEN 2003). Measurements were taken between 8.00 and 12.00 h. Six fully expanded leaves per species, shading treatment and replicate (in total 72 leaves per species) were checked for gas exchanges. Before starting the experiment, light curves were drawn per each species to evaluate the saturating light intensity. Measurements were taken under saturated and standardized light conditions ($\text{PAR} = 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and with CO_2 concentration = 360 ppm. Temperature (T ; °C) and Vapor Pressure Deficit (VPD; kPa) were maintained near ambient at the moment of the measure. Mean net photosynthetic rate (A_y ; $\mu\text{mol m}^{-2} \text{s}^{-1}$), transpiration (E_y ; $\text{mmol m}^{-2} \text{s}^{-1}$) and water use efficiency (WUE_y ; $\mu\text{mol CO}_2 \text{ mmol}^{-1} \text{ H}_2\text{O}$) were calculated as the average of all instant measurements obtained during the season.

Leaf morphology

The total leaf thickness and the thickness of adaxial and abaxial cuticle, adaxial and abaxial epidermis, palisade parenchyma and spongy mesophyll layers were measured

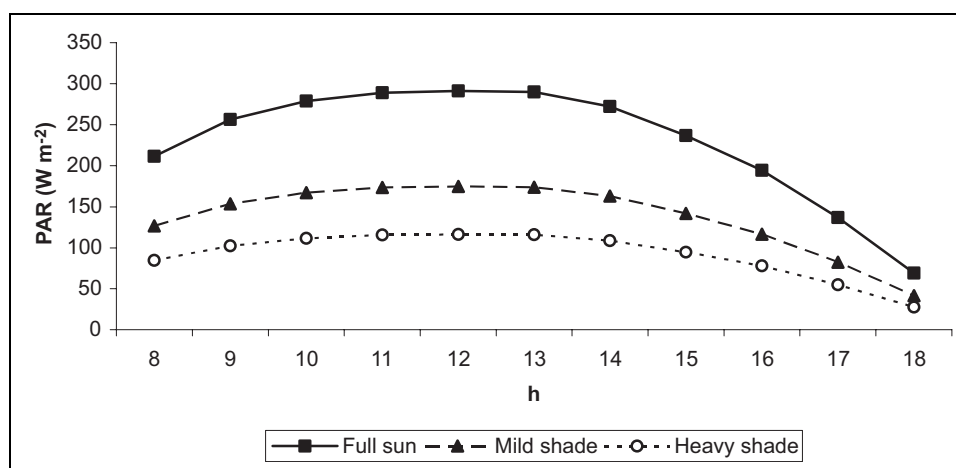


Fig. 1. Daily trend of radiation in the three light treatments. Data are the average of the measurements performed from May to September.

on transverse sections of thickness of 10 and 25 μm obtained from fully expanded leaves. Sections were cut on fresh leaf tissue, with a vibratory microtome (Vibratome 1000 Plus, Vibratome, St. Louis, MO, USA) at a point approximately one-third of the lamina length basal to the leaf tip. Observations were carried out in a microscope Reichter Zetopan 30W (Reichter, Vienna, Austria). The number of stomata per area was analysed on fresh material using a Fei Quanta 200 Environment Scanning Electron Microscope (ESEM, Fei Corporation, Eindhoven, The Netherlands) operating in low-vacuum mode (1 Torr chamber pressure). ESEM analysis was carried out on four fully expanded leaves per species, replicate and light treatment (108 leaves in total), at a point approximately one-third of the lamina length from the tip.

Data analysis

All data were analyzed using One- and Two-ways analysis of variance (ANOVA) with SPSS statistical package for Windows (SPSS Inc., Chicago, IL, USA). Duncan's multiple range test ($P \leq 0.05$) was used to separate means of the main effects. Parameters which showed significant interaction between factors were plotted separately in order to compare each level of factor A (light intensity) for each level of factor B (species) (CHEW 1976).

Results

Light intensity affected all investigated parameters except RGR (Table 1). Species were highly different for all investigated parameters except root dry weight, net assimilation rate (NAR) and palisade parenchyma thickness. Anyway, most of the parameters were subjected to species-light interaction (Table 1).

Growth and morphology

Root dry weight, shoot to root ratio and mean area per leaf were the only morphological parameters which responded to shading in a species-independent manner (Table 1). In all species, root dry weight was higher in full sun than in mild and heavy shade (Table 2). Contrary to this, shoot to root ratio and leaf size were lower in full sun than in mild and heavy shade.

In *Camellia*, 60 % shading increased plant height if compared to 30 % shading and full sunlight (Table 3). Leaves, stem and root dry weight, whole plant dry weight, Leaf Area Index (LAI), Leaf Area Ratio (LAR), Relative Growth Rate (RGR) and Net Assimilation Rate (NAR) were not affected by shading. In *Photinia*, shading

Table 1. Two-ways ANOVA of the investigated parameters. * and ** within the same row indicate significant effects of treatments and their interaction at $P \leq 0.05$ and $P \leq 0.01$ respectively.

| Parameter (unit) | Light intensity | Species | Light * Species |
|---|-----------------|---------|-----------------|
| Leaf dry weight (g) | ** | ** | ** |
| Stem dry weight (g) | * | ** | ** |
| Root dry weight (g) | ** | n.s. | n.s. |
| Total plant dry weight (g) | ** | ** | ** |
| shoot/root | ** | ** | n.s. |
| leaf number | ** | ** | ** |
| mean area per leaf (cm^2) | ** | ** | n.s. |
| LAI | * | ** | ** |
| LAR (final) ($\text{cm}^2 \text{g}^{-1}$) | ** | ** | ** |
| RGR ($\text{mg g}^{-1} \text{day}^{-1}$) | n.s. | ** | ** |
| NAR ($\text{g cm}^{-2} \text{day}^{-1}$) | ** | n.s. | ** |
| A_y ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | ** | ** | ** |
| E_y ($\text{mmol m}^{-2} \text{s}^{-1}$) | ** | ** | n.s. |
| WUE _y ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$) | ** | ** | n.s. |
| Total leaf thickness (μm) | ** | ** | ** |
| Upper cuticle thickness (μm) | ** | ** | ** |
| Lower cuticle thickness (μm) | ** | ** | ** |
| Upper epidermis thickness (μm) | ** | ** | * |
| Lower epidermis thickness (μm) | ** | ** | * |
| Mesophyll thickness (μm) | ** | ** | ** |
| Palisade thickness (μm) | ** | n.s. | ** |
| Spongy parenchyma thickness (μm) | ** | ** | ** |
| Palisade/Spongy ratio (μm) | ** | ** | ** |
| Number of palisade layers | ** | ** | ** |
| Stomata frequency (stomata cm^{-2}) | ** | ** | n.s. |

Table 2. Parameters which showed no significant species * light interaction. Data are presented as the average of the values obtained in the three species for a certain light intensity.

| Parameter (unit) | Full sun | Mild shade | Heavy shade |
|--|----------|------------|-------------|
| Root dry weight (g) | 26.8 a | 17.8 b | 14.1 b |
| Shoot/root (g/g) | 3.0 b | 4.3 a | 4.7 a |
| Mean area per leaf (cm ²) | 10.4 b | 13.9 a | 14.9 a |
| Stomata frequency (stomata cm ⁻²) | 21936 a | 18211 ab | 14249 c |
| E (mmol m ⁻² s ⁻¹) | 2.4 a | 2.5 a | 2.1 b |
| WUE (μmol CO ₂ mmol ⁻¹ H ₂ O) | 1.9 b | 2.3 a | 2.2 a |

determined a significant decrease in leaves, stem, roots and whole plant dry weight and leaf number (Table 3). LAI was not affected by shading. LAR was higher in 60 % shade than 30 % shade and full sun. RGR and NAR were higher in full sun than 60 % shade. In *Viburnum*, full sun determined a significant reduction of plant height and internode length, which resulted in a greater self-shading in full sun plants than 40 % and 60 % shaded ones (Table 3). These findings are consistent with what observed in other Mediterranean species grown under high light intensity (GUIDI et al. 2008). Plant dry weight and leaf number weren't affected by shading. Plants grown in 60 % shade had higher LAI than plants grown in 30 % shade which, in turn, had higher LAI than those grown in full sun. RGR was higher in 60 % and 30 % shade than in full sun. LAR and NAR were not affected by light intensity.

Carbon assimilation and gas exchange

Mean transpiration (E_y) and Water Use Efficiency (WUE_y) were affected by shading in a species-independent manner (Table 1). E_y was higher in full sun and 30 % shade than 60 % shade (Table 2). WUE_y was higher in 30 % and 60 % shade than in full sun. Shading had a species-specific effect on mean carbon assimilation (A_y) (Fig. 2). A_y was higher in full sun and mild shade camellias if compared to heavy shaded plants. A_y was unaffected by light intensity in photinia. In viburnum, A_y was higher in heavy- and mild-shade plants if compared to plants grown with no reduction of light intensity.

Leaf anatomy

Leaf anatomy was affected by light treatment but the different species changed in a different way the structure of their leaves (Table 4). In camellia and photinia, leaves were thicker under full sun and 30 % shade than under 60 % shade. In viburnum, plants grown in full sun had thicker leaves than those grown in mild shade which had thinner leaves than plants grown in 60 % shade. The thickness of the upper and lower epidermis and cuticle were higher in full sun and 30 % shade camellias and photinias than in 60 % shaded plants. In viburnum, thickness of the epidermis was similar in heavy and mild shaded plants and both these treatments had thinner epidermis than leaves grown in full sun. No difference was found in viburnum for cuticle thickness between full sun and 60 % shade plants. In camellia, mesophyll thickness decreased with light intensity. In photinia and viburnum, heavy shade growing conditions were necessary to induce a decrease of mesophyll. The development of palisade parenchyma was particularly sensitive to radiation. In camellia, both thickness and number of palisade layers increased with increasing radiation. Full sun grown

Table 3. Plant height, leaf, stem, root and whole plant dry weight, mean leaf number per plant, Leaf Area Index (LAI), Leaf Area Ratio (LAR), Relative Growth Rate (RGR) and Net Assimilation Rate (NAR) in the three species exposed to different light intensities. * and ** indicate significant differences at $P \leq 0.05$ and $P \leq 0.01$ respectively at One-Way ANOVA. Different letters within the same column and species indicate significant differences among light treatments.

| Species | Light intensity | Plant height (cm) | Dry weight (g) | | | | Mean leaf number plant ⁻¹ | LAI | LAR (cm ² g ⁻¹) | RGR (mg g ⁻¹ day ⁻¹) | NAR (cm ² g ⁻¹ day ⁻¹) | |
|------------------------------|-----------------|-------------------|----------------|-------|-------|-------------|--------------------------------------|------|--|---|--|------|
| | | | Leaves | Stem | Roots | Whole plant | | | | | | |
| <i>Camellia x williamsii</i> | Full sun | 89.0 b | 49.0 | 53.2 | 33.2 | 135.5 | 237 | 3.4 | 22.6 | 4.4 | 0.20 | |
| | Mild shade | 93.0 b | 41.5 | 45.3 | 18.6 | 105.4 | 177 | 2.7 | 23.3 | 3.1 | 0.13 | |
| | Heavy shade | 122.7 a | 47.7 | 53.0 | 18.7 | 119.3 | 228 | 2.7 | 20.6 | 3.8 | 0.18 | |
| | P | ** | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | n.s. | |
| <i>Photinia x fraseri</i> | Full sun | | 66.1 a | 49.8a | 29.0a | 144.9 a | 351 a | 4.7 | 29.4 b | 9.6 a | 0.30 a | |
| | Mild shade | | 58.8 a | 45.2a | 20.0b | 123.9 a | 276 b | 5.0 | 42.1 b | 6.8 ab | 0.20 ab | |
| | Heavy shade | | 35.0 b | 19.7b | 8.8 c | 63.6 b | 203 c | 4.7 | 70.6 a | 4.7 b | 0.07 b | |
| | P | | ** | ** | ** | ** | ** | n.s. | * | * | * | |
| <i>Viburnum tinus</i> | Full sun | | 32.3 b | 19.8 | 9.1 | 18.2 | 47.2 | 453 | 1.7 c | 83.7 | 6.6 b | 0.19 |
| | Mild shade | | 43.7 b | 26.3 | 14.4 | 17.9 | 58.6 | 483 | 3.0 b | 89.8 | 10.2 a | 0.22 |
| | Heavy shade | | 71.0 a | 23.7 | 12.6 | 14.8 | 51.0 | 388 | 4.8 a | 75.2 | 10.4 a | 0.12 |
| | P | | ** | n.s. | n.s. | n.s. | n.s. | n.s. | ** | n.s. | * | n.s. |

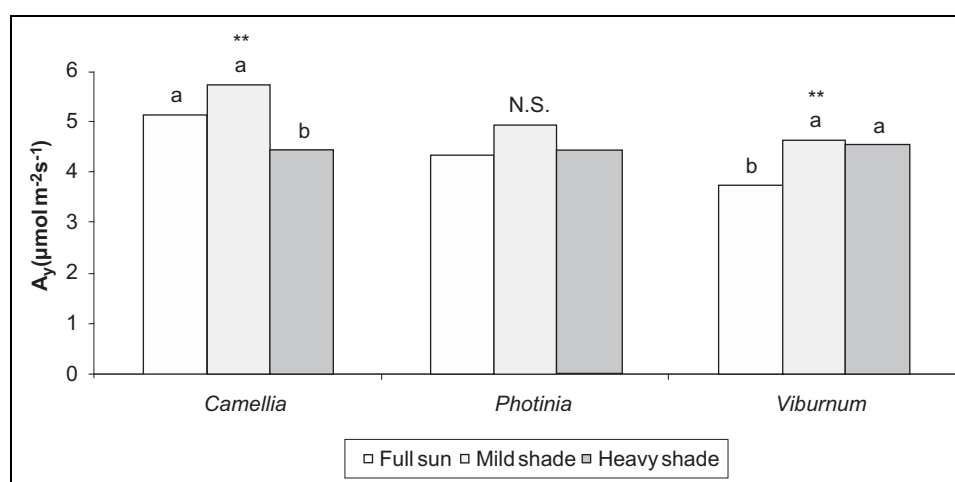


Fig. 2. Mean carbon assimilation (A_y) in the three species exposed to different light intensities. Data are the average of the six measurements performed during the experiment. * and ** indicate significant differences at $P \leq 0.05$ and $P \leq 0.01$ respectively at One-Way ANOVA. Different letters within the same species indicate significant differences among light treatments.

Table 4. leaf anatomical features in the three species exposed to different light intensities. Letters within the same row indicate significant differences among light treatments.

| Species | Parameter | Full sun | Mild shade | Heavy shade |
|------------------------------|---|------------|-------------|-------------|
| <i>Camellia x williamsii</i> | total leaf thickness (μm) | 195.16 a | 182.37 a | 156.08 b |
| | upper cuticle thickness (μm) | 2.86 a | 2.28 b | 2.19 b |
| | lower cuticle thickness (μm) | 2.31 a | 1.35 b | 0.99 c |
| | upper epidermis thickness (μm) | 11.80 a | 11.74 a | 8.63 b |
| | lower epidermis thickness (μm) | 7.90 a | 8.08 a | 5.22 b |
| | mesophyll thickness (μm) | 175.50 a | 162.67 b | 142.40 c |
| | palisade thickness (μm) | 61.50 a | 43.09 b | 40.32 b |
| | spongy thickness (μm) | 113.88 a | 119.34 a | 102.09 b |
| | n. palisade layers | 2.70 a | 1.90 b | 1.70 b |
| | n. stomata cm^{-2} | 18259.10 a | 17199.50 ab | 12149.50 b |
| <i>Photinia x fraseri</i> | total leaf thickness | 182.21 a | 194.41 a | 173.99 b |
| | upper cuticle thickness (μm) | 2.96 a | 2.65 b | 2.36 c |
| | lower cuticle thickness (μm) | 2.88 a | 1.82 b | 1.76 c |
| | upper epidermis thickness (μm) | 15.53 a | 14.28 a | 12.60 b |
| | lower epidermis thickness (μm) | 10.47 a | 9.74 a | 7.64 b |
| | mesophyll thickness (μm) | 163.10 a | 170.45 a | 153.70 b |
| | palisade thickness (μm) | 60.22 a | 49.65 b | 45.03 b |
| | spongy thickness (μm) | 102.86 b | 121.31 a | 108.88 b |
| | n. palisade layers | 3.15 a | 2.55 b | 2.00 c |
| | n. stomata cm^{-2} | 36597.00 a | 26340.00 ab | 21688.00 b |
| <i>Viburnum tinus</i> | total leaf thickness (μm) | 163.40 a | 152.52 b | 140.86 c |
| | upper cuticle thickness (μm) | 2.21 | - | 1.94 |
| | lower cuticle thickness (μm) | 1.15 | - | 1.14 |
| | upper epidermis thickness (μm) | 11.46 a | 9.48 b | 9.29 b |
| | lower epidermis thickness (μm) | 9.73 a | 8.09 b | 7.77 b |
| | mesophyll thickness (μm) | 142.25 a | 134.93 a | 123.49 b |
| | palisade thickness (μm) | 52.58 a | 53.13 a | 42.61 b |
| | spongy thickness (μm) | 89.67 a | 81.79 b | 80.97 b |
| | n. palisade layers | 1.00 | 1.00 | 1.00 |
| | n. stomata cm^{-2} | 10952.00 | 9396.00 | 8340.00 |

camellias often presented a three layered and 61.5 μm thick palisade parenchyma, while plants grown under 30 % and 60 % shade showed a two layered parenchyma that was significantly thinner, respectively 43 and 40 μm . Photinias grown in full sun produced a thicker palisade parenchyma, made of 3 well developed layers of cells. 30 % shaded photinias presented, alternately, two or three layers of palisade cells; 60 % shaded leaves had only two layers. In viburnum, despite of variation of thickness, no difference was found concerning number of palisade layers: only one layer was found both in full sun and shaded leaves. Mean number of stomata per cm^2 was significantly higher in full sun camellias and photinias than in 60 % shaded leaves, while 30 % shaded leaves showed no difference compared to the other two treatments (Table 4). In viburnum, no difference in stomata number per unit area was found among the different treatments.

Discussion

The present research aimed to identify how three different container-grown shrubs react to shading and the way where plants modify their morphological, physiological and anatomical characteristics. We found that some parameters (i.e. root biomass, shoot to root ratio, transpiration, leaf size) were similarly affected by shading in all the species investigated. Higher allocation to roots in response to full sunlight and the consequent decline of shoot to root ratio has already been observed by several authors and its considered a morphological adaptation to increase, at the whole plant level, the ability to supply water in environments characterized by high evapo-transpirational demand by the atmosphere (ANDERSEN et al. 1991b; POORTER and NAGEL 2000; RUTER 2002). Root growth in *Photinia* was particularly reduced by shading. Similar results were found on cherrybark oak (*Quercus pagoda*) (LOCKHART et al. 2008). The authors found that oak roots acted as a preferential sink of assimilated ^{14}C in full sunlight, while shoots were the main sink for ^{14}C under reduced light availability. We can hypothesize that a higher production of auxines in response to high light environment, stimulates roots growth, as previously reported by KNOX and HAMILTON (1983).

Smaller leaves were observed in full sun-grown plants of all species. Small leaves have thin boundary layer and this helps the leaf to prevent over-heating through increased heat dissipation by convection than bigger leaves with thicker boundary layer (NOBEL 2005). The decline of E in response to shade provide further evidence that shading can be a sustainable way to reduce water use by plants and thus, to save irrigation water in nurseries and urban plantings. In all species, shading modified leaf morphological and anatomical characteristics. As also reported in previous works, leaves appeared thinner but more expanded in shade than in full sun to improve light interception (BOARDMAN 1977; ARAUS et al. 1986; ANDERSEN et al. 1991b). In *Camellia*, carbon assimilation was higher in plants grown in full sun and mild shade than in those grown in heavy shade. An increase in mesophyll and spongy parenchyma thickness in response to high radiation results in a greater cell surface area for CO_2 diffusion and decreases liquid-phase resistance (MEDIÁVILLA et al. 2001), explaining the higher A in full sun and mild

shade than heavy shade. In *Photinia*, changes in leaf ultrastructure didn't produce any leaf gas exchange difference among treatments. In *Viburnum*, the analysis of leaf internal structure explained why full sun plants were not able to use the high radiation to increase saturated carbon assimilation. Although mesophyll is thicker in full sun, there was no increase in number of palisade parenchyma layers and in light-harvesting. Then, full sun plants had to use more resources to increase epidermis and cuticle thickness while shaded could benefit from a lower evapotranspirative demand (BAKER 1974; KOCH et al. 2006). Biomass production was not related to carbon assimilation. A possible explanation is that, in this experiment, gas exchange measurements were performed at only one standardized light intensity. This provided information on the maximum carbon assimilation of sun and shade leaves, but didn't reflect the real assimilation of leaves because chlorophyll wasn't probably saturated under shade. Despite of higher gas exchange, *Camellia* showed similar biomass and growth rate in all light treatments, even if plants grown in full sun allocated more resources in root production relative to shoot production. In *Photinia*, growth rate was reduced by shading. According to what reported by JEFFERSON and PENNACCHIO (2005), we hypothesized that the lower leaves and stems dry weight of plants grown under 60 % shade is caused by a smaller root absorbing surface and low nutrient absorption from soil.

Viburnum tinus 'Eve Price' showed a different pattern compared to the other two species. Although no significant difference was found in total plant dry weight and leaf number, LAI and LAR, carbon assimilation and Water Use Efficiency were higher in shaded plants. The down-regulation of photosynthesis has also been observed on other Mediterranean species in response to unfavorable conditions and was considered a trait of adaptive value (TATTINI et al. 2006), but can be detrimental during the production phase of ornamental plants where high aesthetic quality and high carbon storage are required. Larger photosynthetic area and higher net photosynthesis per area resulted in a greater RGR by shaded plants than full sun ones. In conclusion, *Camellia x williamsii* 'Debbie', generally classified as a facultative shade species, performed better in full sun and mild shade than in heavy shade; *Photinia x fraseri* 'Red Robin' demonstrated to be a sun-requiring species, particularly because of insufficient root growth in shade; *Viburnum tinus* 'Eve Price', a typical Mediterranean shrub, performed better in shade. Maybe *Viburnum* developed an elevated shade tolerance in the early stages of its life to compete better with other species and survive in the understorey, as also observed on pedunculate oak (*Quercus robur* L.) by WELANDER and OTTOSSON (1998) and by VAN HEES and CLERKX (2003). Anyway, if viburnum is exposed to full sunlight, it has the ability to adapt to high light growing conditions through morphological (i.e. internodes shortening, compact growth, increased self-shading), physiological (i.e. downregulation of photosynthesis) and anatomical (i.e. changes in leaf thickness and size) adaptations.

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