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Acclimation to sun and shade of three accessions of the Chilean native berry-crop murta

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Abstract Murta (*Ugni molinae* Turcz.) is an evergreen shrub of the native forest understorey of southern Chile that produces berries which are consumed in the local markets. Because of the natural adaptation of murta to growing under the shade of trees, we propose that an adequate way of domesticating this species would be its cultivation in agroforestry systems. In order to assess the suitability of three murta accessions from different regions in southern Chile for their cultivation in such systems, we established a trial in which these accessions were submitted to six light transmittance levels (20%–100% of full solar irradiance) from planting in spring to the following autumn. Optimum growth, as assessed through dry mass accumulation and emission of branches and metamers, was achieved at moderate light transmittance levels (50%–65%). These growth traits showed stable positive responses to the relative amount of light intercepted by the plants (as estimated from plant structural traits) up to these optimum light transmittance levels and diverged to lower values thereafter. These stable relationships suggest that the differences in plant growth at low and moderate light transmittance levels can be attributed to restrictions of photosynthesis by light availability. The reduction in growth for higher light transmittance levels may be partly attributed to photoinhibition as suggested by reduced chlorophyll content and relatively low increments in carotenoid content in leaves at high light transmittance levels.

Keywords Carotenoids · Chlorophyll · Vegetative growth · Light transmittance · Light interception · Southern Chile · *Ugni molinae*

Introduction

Murta (*Ugni molinae* Turkz.) is an evergreen perennial shrub of the *Myrtacea* family that grows spontaneously in the cold rain forests of southern Chile (Muñoz et al. 1986), from where it is native. This plant has progressively gained economic interest due to its intensely aromatic reddish to white rounded berries, used for the production of cakes, jams and marmalades which are increasingly demanded by the local market. The berries are mainly picked from wild growing plants in the forest but murta is also cultivated in association with fruit trees in family orchards. The species has been introduced to Tasmania were its commercial production has recently started under the registered trade name "Tazziberry$^{\mathrm{TM}}$" (Forbes-Smith 2006).

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In its natural habitat murta grows in poorly illuminated sites of the native forest understorey (Rodríguez 1986). Because of this intrinsic adaptation to shade, murta shows an interesting potential for its cultivation in agroforestry systems. Actually, for another shade plant as coffee (*Coffea arabica* L.), it has been shown that cultivation in agroforestry systems enhances plant growth and bean quality (Vaast et al. 2005) indicating that shade plants are particularly adapted to being cultivated in such systems (Franck 2005). Actually, under the sunnier climatic conditions of central Chile, Pastenes et al. (2003) showed that murta is severely affected by photoinhibition when grown in full sun, as compared to 50% shading, and concluded that the domestication of this species must consider light intensity. Actually, photoinhibition, the slow reversible decline of photosynthetic efficiency that occurs when absorbed light is in excess of that required for carbon assimilation (Powles 1984), has been shown to reduce whole plant growth in other species (Jordan and Ögren 1984; Winter and König 1991; Liang et al. 1995; Werner et al. 2001) and might hence reduce the agronomic performance of murta in full sun.

When plants are cultivated in environmental conditions which contrast with their native habitat, especially concerning light and temperature, their ability to grow and develop will mainly depend on their capacity of acclimating in order to efficiently photosynthesize (Pearcy 1977; Björkman 1981). In the specific case of light, plants possess a variety of strategies to acclimate both to low (Boardman 1977; Larcher 2003) and high light (Krause 1988; Demming-Adams and Adams 1992). Concerning acclimation to low light, increments in individual leaf area (LA_l), chlorophyll (Chl) content in leaves, internode length and the proportion of biomass allocated to leaves are typical plant adaptations which allow a better interception and absorption of light in shady environments (Boardman 1977; Larcher 2003). On the other hand, the strategies of acclimation to high light consist of either (i) reducing light absorption—among others by reducing Chl content in leaves (Krause 1988; Baker 1991; Demming-Adams and Adams 1992) and the amount of light harvesting antennae associated to photosystem II (Leong and Anderson 1984; Johnson et al. 1993)—or (ii) protecting the photosynthetic apparatus from excessive light—-mainly by increasing the content of protective pigments like carotenois (Car) in leaves (Demming-Adams and Adams 1992, 1996). Shade plants, as murta, have a good capacity of acclimating to low light but are very prone to develop photoinhibition under full sun irradiance (Rhizopoulou and Nunes 1981; Kitao et al. 2000). Moreover, leaf temperature linearly increases with increasing intercepted solar irradiance (Margolis and Ryan 1997) and high leaf temperatures have previously been observed for murta plants cultivated in full sun (Pastenes et al. 2003). These high leaf temperatures may negatively affect carbon assimilation either by increasing stomatal resistance to CO_2 transfer (Ball et al. 1987; Collatz et al. 1991; Leuning 1995) or by directly affecting the structure (Pastenes and Horton 1996a, b) and functioning (Pastenes and Horton 1999) of the photosynthetic apparatus and its enzymes (Bernacchi et al. 2001; Leuning 2002). Within a same species, genetic differences may confer better capacity to acclimate to either high or low light conditions (Corlett et al. 1994; Fahl et al. 1994; Pastenes and Horton 1996a; Yu et al. 2002; Sepehri and Modarres Sanavy 2003).

The objective of this study was to analyse the acclimation of three murta accessions to different light transmittances in its natural environment of southern Chile and to quantify the effect of light transmittance on plant growth. Three different accessions were submitted to six different light transmittance treatments (20%, 35%, 50%, 65%, 82% and 100% of full sun irradiance) and plant growth and development traits were periodically followed from planting in spring to the following autumn. At the end of the trial, pigment content in leaves, leaf area and plant dry mass were measured. Periodical and final measurements were used to (i) analyse acclimation to shade and high light at the leaf and whole plant level (ii) estimate light interception by plants throughout the trials duration and (iii) relate vegetative growth traits to these estimations of light intercepted by plants. The acclimation of these three murta accessions to different light transmittance levels and the effect of these light transmittance levels on plant growth are discussed from the perspective of the suitability of each accession for its future cultivation in agroforestry systems.

Materials and methods

Experimental site and plant material

The trial was carried out in the Puntiagudo valley of southern Chile (41°02′ 28 S, 72°15′ 00, 240 m.a.s.l.) on a deep volcanic sandy soil under a temperate rainy climate. Plants of murta (*Ugni molinae* Turcz.) were obtained from cuttings that had previously been harvested from spontaneously growing murta comunities in three different locations of southern Chile: Temuco (*Tirol* accession), Río Blanco (*Sajonia* accession) and the *Cayutúe* bay of the ‘‘Todos los Santos’’ lake (*Cayutúe* accession). These accessions were selected during the period of fruit maturity (March–April) of 1999 based on the following criteria: (i) fruit size (equatorial diameter >1 cm), (ii) skin color (homogenous bright red) and (iii) yielding potential (within each population, plants from the higher 30% range concerning fruit load). Cuttings from the three selected accessions consisted of herbaceous terminal shoots which were rooted in the experimental site during the winter of 1999 using a peat-vermiculite substrate. Rooted murta plants were planted in the field on October 18,1999, spaced 0.6 m within North–South oriented rows which were 3 m apart. Plants were regularly sprinkler irrigated so as to keep the soil water status at field capacity and weeds were manually eliminated when needed.

Light transmittance treatments

Six different light transmittance treatments (100% [LT_{100}]; 82% [LT_{82}]; 65% [LT_{65}]; 50% [LT_{50}]; 35 % [LT_{35}]; and 20% [LT_{20}] of full solar irradiance) were achieved by using black shade screens with the corresponding light transmittance coefficients. These shade screens were placed 10 days after plantating at a height of 0.8 m above the soil and forming 1.0 × 5.5 m continuous flat shade roofs oriented along the plantation rows. Each shade screen encompassed eight plants. Light transmittance of all shade screens had been previously checked by placing a photosynthetic photon flux density (PFD) sensors (PAR-CBE sensors, SOLEMS, Palaiseau, France) under each shade screen during a whole day and comparing measurements with those obtained with a PFD sensor placed in full sun.

Mesaurements

Measurements were performed at a two-week interval from the date of planting until May 10, 2000. At each measurement date, plant height (H_{PL}), number of primary (N_{A2}) and secondary shoots (N_{A3}; with N_{A2+3} = total number of primary and secondary shoots), total shoot length ($L_{A1\text{-}3}$) and the length of each internode (L_{IN}) on the central axis (A_1) were recorded on the six plants in the centre of the rows of each treatment. At the end of the trial (May 10, 2000) total plant leaf area (LA_{Pl}) (LI-3050A, LI-COR Bioscience, Lincoln, NE, USA) and total dry mass of leaves (DM_l), twigs (DM_t) and roots (DM_r; with DM_{Pl} = whole plant dry mass) of the six replicates was measured. At the same date, chlorophyll *a* (Chl_a), chlorophyll *b* (Chl_b; total Chl: $Chl_{a+b} = Chl_a + Chl_b$; Chl_a to Chl_b ratio: $Chl_{a/b} = Chl_a/Chl_b$) and carotenoid (Car) content in leaves was measured on compound samples of ten representative mature leaves of the same six plants of each treatment by means of a spectrophotometer (UV-1601, SHIMADZU, Kyoto, Japan) following Lichtenthaler and Wellburn (1983). Leaf dry mass to area ratio (LMA) was calculated by dividing total leaf dry mass by total leaf area and individual leaf area (LA_l) was calculated by dividing LA_{Pl} by the total number of leaves of the corresponding plant.

Daily rainfall (pp) and daily minimum (T_a^{min}) and maximum (T_a^{max}) air temperature were registered throughout the trials duration. Mean air temperature (T_a^{mean}) was calculated as the average between T_a^{min} and T_a^{max}.

Estimation of intercepted light

The fraction of incident light intercepted by the plants of each treatment was estimated from plant size and leaf area density (LAD). LAD corresponds to the $\mathrm{LA_{Pl}}$ divided by the crown volume (Röhrig et al. 1999). The crown volume was estimated by assuming a spherical crown envelope in which leaves were assumed to be homogeneously distributed:

$$\mathrm{LAD} = \frac{\mathrm{LA_{Pl}}}{4/3\pi r_{\mathrm{Pl}}^{2}} \tag{1}$$

where r_{Pl} is the radius of the sphere representing the crown envelope and was taken as the half of H_{Pl} ($H_{\mathrm{Pl}}/2$). This spherical crown representation was used because it approximates the geometry of the crown of the densely ramified murta plants (Rodríguez 1986). Because $\mathrm{LA_{Pl}}$ was only measured at the end of the trial, a multiple regression analysis was performed in order to find an allometric function allowing estimating $\mathrm{LA_{Pl}}$ from different plant structure traits which were periodically measured. The fraction of incident light intercepted by the plants (I_{c}), was estimated with the equation developed by Monsi and Saeki (1953):

$$I_{\mathrm{c}} = 1 - \exp^{-k\mathrm{LAI}} \tag{2}$$

where k is termed the extinction coefficient and reflects the geometric influence associated with the angle between leaves and the sun and LAI is the leaf area index. k was computed at a value of 0.5 representing a spherical leaf angle distribution and LAI was calculated from LAD (Röhring et al. 1999) as:

$$\mathrm{LAI} = H_{\mathrm{Pl}}^{\bar{x}}\mathrm{LAD} \tag{3}$$

where $H_{\mathrm{Pl}}^{\bar{x}}$ corresponds to the average length of the path of beams traversing a sphere from any given angle and was calculated as:

$$H_{\mathrm{Pl}}^{\bar{x}} = 4/3r_{\mathrm{Pl}} \tag{4}$$

The light intercepted by the foliage of each plant was termed I_{Pl} and estimated by multiplying I_{c} by the maximum cross sectional area of the crown envelope:

$$I_{\mathrm{Pl}} = I_{\mathrm{c}}\pi r_{\mathrm{Pl}}^{2} \tag{5}$$

It was considered that shading between plants was insignificant due to (i) the small size the plants achieved (plants did not overlap on the row), (ii) the large spacing between rows as compared to plant height (3 m v/s ~0.5 m) and (iii) the north–south orientation of rows. Logistic growth equations (Thornley and Johnson 2000) were then adjusted to relate the values of $\mathrm{LA_{Pl}}$ and I_{Pl} (estimated from periodical measurements) of each plant to the time elapsed from planting:

$$\mathrm{Var^{i}} = \frac{\mathrm{Var^{f}}}{1 + \exp\left(\mathrm{GR_{m}}\frac{\mathrm{TD_{m}} - \mathrm{TD}}{\mathrm{Var^{f}}}\right)} \tag{6}$$

where $\mathrm{Var^{i}}$ is the instantaneous value of the variable (Var: either $\mathrm{LA_{Pl}}$ or I_{Pl}) and TD the day after planting. The parameters in this function are the final value of Var ($\mathrm{Var^{f}}$); the maximum expansion rate of Var ($\mathrm{GR_{m}}$); and the day after planting at which $\mathrm{GR_{m}}$ was reached ($\mathrm{TD_{m}}$). The logistic equation adjusted to the $\mathrm{LA_{Pl}}$ values was used to analyse the dynamics of leaf area expansion (i.e., the transition between increasing and decreasing whole plant expansion rate). The logistic equation adjusted for estimating I_{Pl} was used to calculate daily I_{Pl} values which were summed in order to estimated the I_{Pl} cumulated along the whole trials duration ($I_{\mathrm{Pl}}^{\mathrm{C}}$). Because incident light was not measured, these $I_{\mathrm{Pl}}^{\mathrm{C}}$ values were multiplied by light transmittance in order to obtain a proportional estimation of the amount of light intercepted by the plants throughout the trials duration ($Q_{\mathrm{Pl}}^{\mathrm{C}}$) under the shade screens (i.e., taking light transmittance [LT] into account):

$$Q_{\mathrm{Pl}}^{\mathrm{C}} = I_{\mathrm{Pl}}^{\mathrm{C}}(\mathrm{LT}/100) \tag{7}$$

Statistical analysis

Analysis of variance, regression analysis and correlation analysis were carried out with the Analyse-it software (Analyse-it Software, Leeds, Yorkshire, UK) and logistic curves were fitted with the TableCurve2D software (Systat Software, Erkrath, Germany).

Results

Climate

Mean T_a^{min} and T_a^{max} showed a high seasonal fluctuation, were highest during the summer months (December to February), decreased thereafter and respectively averaged 7.3 ± 3.1 °C and 20.4 ± 5.6 °C during the whole period (Table 1). Rainfall was frequent, with an average of 8.7 ± 4.5 rainy days per month, accumulating a total of 1,062 mm during the whole period of the trial (Table 1).

Effect of treatments on plant morphology and pigment content in leaves

Leaf traits showed diverging responses to light transmittance: for all accessions LA_l was negatively correlated to light transmittance (Fig. 1a) whereas LMA was positively correlated to this variable (Fig. 1b). Concerning differences between the accessions, *Tirol* had the significantly (Tukey; $\alpha < 0.05$) largest LA_l and *Cayutúe* the significantly smallest LA_l which was 1.6 times lower than *Tirol* (Fig. 1a). *Sajonia* showed an intermediate LA_l, significantly different from the other two accessions, which was more responsive to light transmittance than in the former accessions, averaged 2.4 ± 0.6 cm^2 (all light transmittance treatments confounded) and was ~ two times higher in LT_{20} than in LT_{100} (Fig. 1a). The opposite ranking between accessions was observed for L_{IN}, which was negatively correlated to light transmittance for all accessions (Fig. 1c). The three accessions showed a similar responsiveness of this trait to light transmittance with an average increment of 1.3 from LT_{100} to LT_{20} (Fig. 1c). LMA (Fig. 1b) was significantly higher (Tukey; $\alpha < 0.05$) for *Sajonia* (152.3 ± 26.5 g m^{-2}) than for *Tirol* (128.5±10.2 g m^{-2}) with *Cayutúe* showing an intermediate LMA (142.4 ± 23.9 g m^{-2}), not significantly different to the LMA values of the other two accessions. LMA was increased by a factor of 1.62, 1.53 and 1.26 between LT_{20} and LT_{100} for *Sajonia*, *Cayutúe* and *Tirol*, respectively. Light transmittance treatments affected Chl_{a+b} and $Chl_{a/b}$ in all accessions (Fig. 2a, b): Chl_{a+b} showed a negative correlation to light transmittance and $Chl_{a/b}$ a positive correlation of to light transmittance. *Cayutúe* showed the significantly (Tukey; $\alpha < 0.05$) highest Chl_{a+b} contents and the significantly lowest $Chl_{a/b}$ and these pigment traits were similar (no significant difference) in the other two accessions (Fig. 2a, b). Taking the average values of the three accessions, Chl_{a+b} increased 44.6% between LT_{100} and LT_{20} whereas $Chl_{a/b}$ decreased by 33.7% between the same treatments. Car, on the other hand, was positively correlated to light transmittance for *Cayutúe* and *Sajonia* but no correlation of this pigment's content to light transmittance was observed for *Tirol* (Fig. 2c). The significantly highest Car content (Tukey; $\alpha < 0.05$) was observed for *Sajonia* whereas *Cayutúe* and *Tirol* had similar Car contents (Fig 2c). A similar negative linear correlation of Car to Chl_{a+b} was observed for all three accessions but Car content fell beneath this correlation line for light transmittance levels above 50% in the case of *Sajonia* and *Tirol* and above 82% for *Cayutúe* (Fig. 2d).

Table 1 Climatic conditions in the experimental plot: mean monthly minimum (T_a^{min}), maximum (T_a^{max}) and mean (T_a^{mean}) air temperature ± SD, monthly rainfall and number of rainy days per month

	Month						
	Nov	Dec	Jan	Feb	Mar	Aprl	May
Days	30	31	31	29	31	30	16
T_a^{min} (°C)	7.3 ± 2.2	7.5 ± 2.6	8.2 ± 2.7	9 ± 2.7	6.8 ± 3.5	7.1 ± 3.4	4.1 ± 2.5
T_a^{max} (°C)	20.8 ± 4.4	23.5 ± 5.0	22.7 ± 3.7	21.9 ± 5.3	19 ± 4.2	17.7 ± 4.7	16.2 ± 2.6
T_a^{mean} (°C)	14.1 ± 2.3	15.5 ± 2.8	15.5 ± 2.3	15.5 ± 3.1	12.9 ± 2.8	12.4 ± 2.9	10.1 ± 1.6
Rainfall (mm $month^{-1}$)	119	171	63	344	124	192	–
Rainy days	11	9	6	14	10	11	–

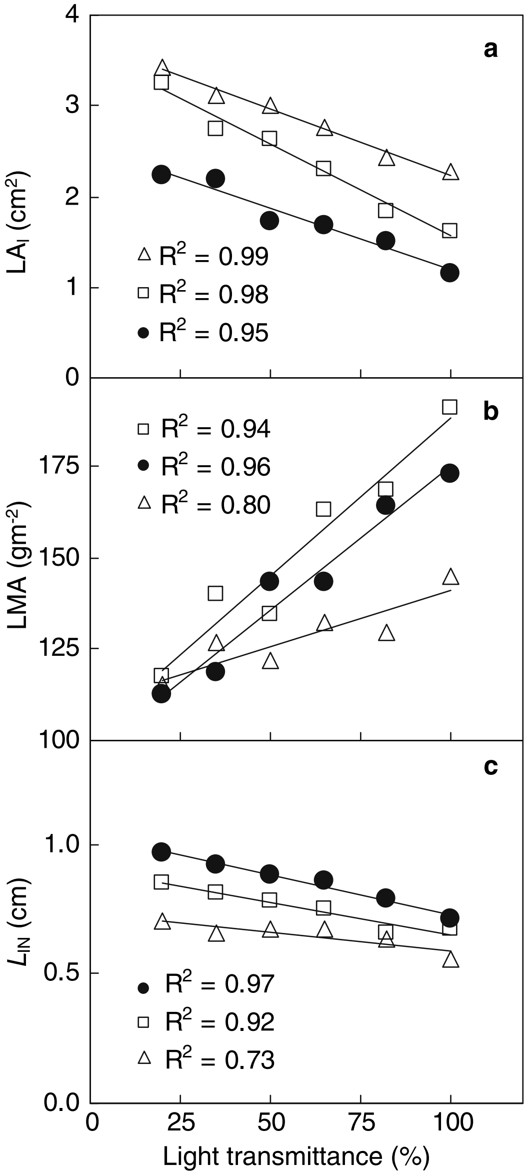

Fig. 1 Effect of light transmittance on (**a**) individual leaf area (LA_l); (**b**) leaf mass to area ratio (LMA); and (**c**) internode length (L_{IN}) of three murta accessions: *Cayutúe* (*closed circles*), *Sajonia* (*open squares*) and *Tirol* (*open triangles*)

Estimation of plant leaf area and light interception by plants

The regression analysis performed for estimating LA_{Pl} from different plant growth traits (Table 2) gave the best estimations when the final LA_{Pl} was related to the product of LA_l and the total amount of internodes on the plant ($N_{IN} = L_{A1-3}/L_{IN}$). In the case of *Sajonia*, this estimation was not strong enough but it significantly increased when including $N_{A1\text{-}3}$ as a second independent variable (Table 2). The evolution of LA_{Pl} along the trials duration and the adjusted logistic functions are shown in Fig. 3a, c, e. Light transmittance induced similar differences of ~300 cm^2 between the treatments exhibiting the lowest and highest final LA_{Pl} in all accessions (Fig. 3a, c, e) but the relative increment factor between these treatments was significantly higher in the case of *Cayutúe* (2.62) as compared to *Sajonia* (1.67) and *Tirol* (1.91). LT_{50} induced the highest final LA_{Pl} in all accessions, whereas the lowest LA_{Pl} were induced by the highest shade level in *Tirol* and by full exposure to sun light in the other two ectypes (Fig. 3a, c, e). *Sajonia* showed the highest maximum LA_{Pl} which was 1.28 times higher than the one of *Tirol* and 1.41 times higher than the one of *Cayutúe* (Fig. 3a, c, e). The estimated I_{Pl} values showed similar patterns of response to light transmittance as LA_{Pl} but the relative difference between treatments within each accession were smaller than for LA_{Pl} (Fig. 3b, d, f).

Effects of incident and intercepted light on plant growth

The proportions of biomass allocated to leaves, twigs and roots were not correlated to light transmittance levels (Table 3). The three accessions allocated the highest proportion of their biomass (>50%) to leaves and the lowest proportion (>20%) to roots (Table 3). These proportions of biomass in the different plant compartments were significantly different between accessions with *Cayutúe* exhibiting significantly higher proportion of dry mass in leaves and significantly lower proportion of dry mass in twigs as compared to the other two accessions (Table 3). Allocation of biomass to roots was significantly higher in *Tirol* than in *Cayutúe* with *Sajonia* not showing any significant difference with the other accessions for this variable (Table 3).

The estimations of the light intercepted by the plants during the trials duration (Q^{C}_{Pl}) showed a

Fig. 2 Effect of light transmittance on (**a**) leaf chlorophyll *a* and *b* content (Chl_{a+b}); (**b**) leaf chlorophyll *a* to *b* ratio ($\mathrm{Chl}_{a/b}$); (**c**) leaf carotenoid content (Car); and (**d**) relationship between Chl_{a+b} and Car of three murta accessions: *Cayutúe* (*closed circles*), *Sajonia* (*open squares*) and *Tirol* (*open triangles*)

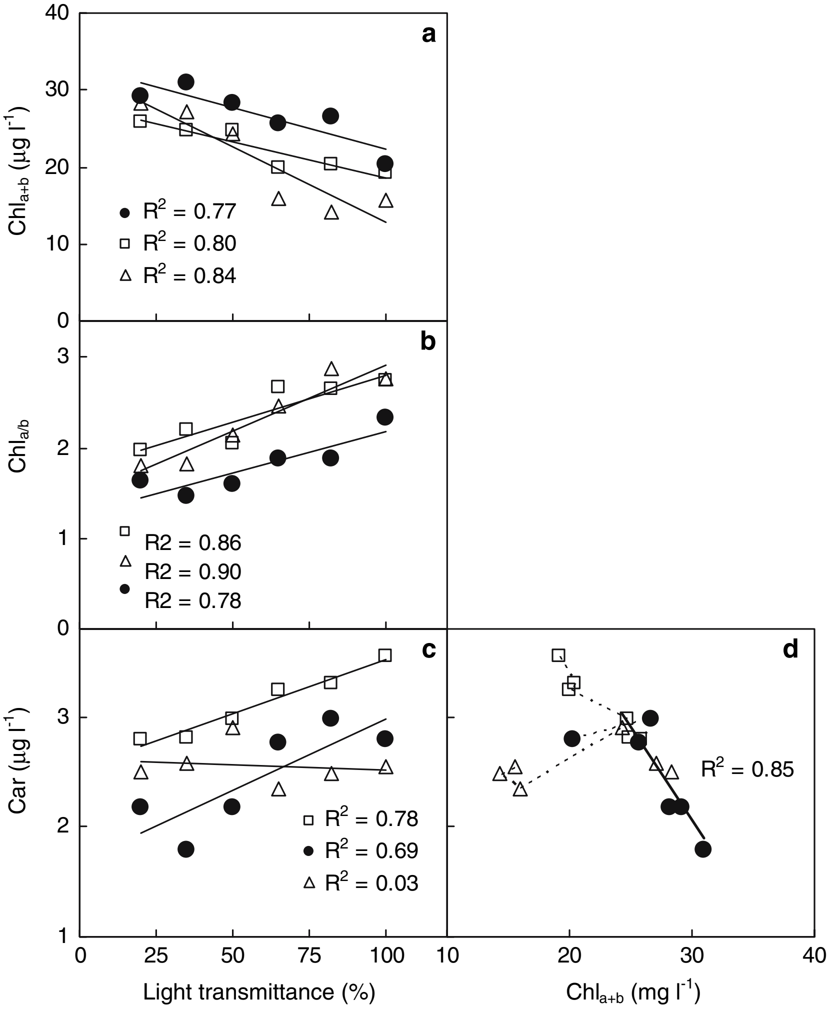

Table 2 Statistic parameters for the multiple regressions adjusted for murta plants of the accessions *Cayutúe*, *Sajonia* and *Tirol* to estimate total plant leaf area from the product of the total number of nodes of the plant and individual leaf area ($N_{\mathrm{IN}}\cdot\mathrm{LA}_{\mathrm{I}}$); and the total number of primary and secondary shoots on the plant ($N_{\mathrm{A2+3}}$)

Accession	Independent variables	Probabilities	R^2
Cayutúe	$N_{\mathrm{IN}}\cdot\mathrm{LA}_{\mathrm{I}}$	<0.001	0.98
Sajonia	$N_{\mathrm{IN}}\cdot\mathrm{LA}_{\mathrm{I}}$ and $N_{\mathrm{A2+3}}$	0.008 and 0.004	0.94
Tirol	$N_{\mathrm{IN}}\cdot\mathrm{LA}_{\mathrm{I}}$	<0.001	0.86

Probabilities for each selected independent variable and determination coefficient (R^2); n = 36

logarithmic response to light transmittance for all accessions with *Sajonia* showing the highest and *Tirol* the lowest $Q^{\mathrm{C}}_{\mathrm{Pl}}$ values (Fig. 4). The responses of three plant growth traits (N_{IN}, $N_{\mathrm{A2+3}}$ and $\mathrm{DM}_{\mathrm{Pl}}$) to light transmittance and $Q^{\mathrm{C}}_{\mathrm{Pl}}$ are shown in Fig. 5. The response of these three traits to light transmittance was generally bell-shaped with a maximum value at 50% for *Sajonia*, 65% for *Tirol* and, in the case of *Cayutúe* at 65% for $N_{\mathrm{A2+3}}$ and at 50% for $\mathrm{DM}_{\mathrm{Pl}}$ (Fig. 5a, c, e). The only exception to this bell-shaped response to light transmittance was N_{IN} of *Cayutúe* which nearly linearly increased with increasing light transmittance (Fig. 5a). The response of N_{IN} and

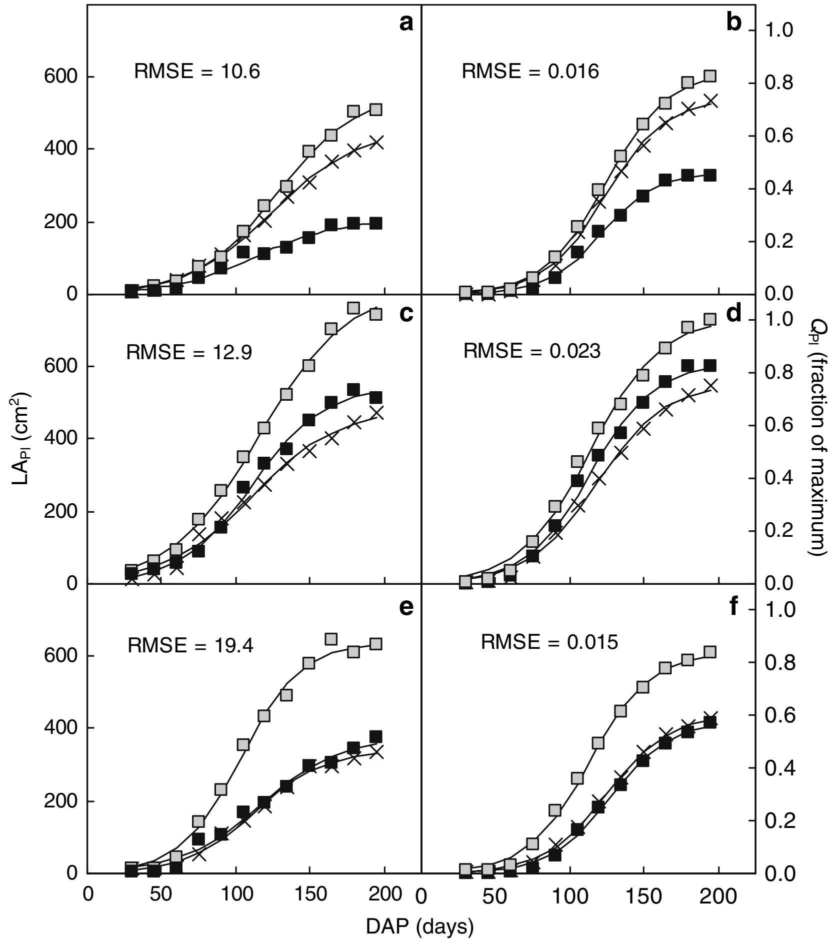

Fig. 3 Estimated whole plant leaf area (LA$_{Pl}$: **a**, **c** and **e**) and light intercepted by the whole plant (Q_{Pl}: **b**, **d** and **f**) as a function of time elapsed since planting (DAP) of three murta accessions: *Cayutúe* (**a** and **b**), *Sajonia* (**c** and **d**) and *Tirol* (**e** and **f**) for the highest (LT$_{100}$: *crosses*), optimum (LT$_{50}$: *grey squares*) and lowest (LT$_{20}$: *open squares*) treatments. Lines show adjusted logistic growth functions; root of the mean squared error (RMSE) was calculated for the totality of the light transmittance treatments, $n = 60$

Table 3 Proportion of dry mass in leaves, twigs and roots of murta plants of the accessions *Cayutúe*, *Sajonia* and *Tirol* and correlation of these proportions to light transmittance

Accession	Proportion of total dry mass			Correlation to light transmittance					
	Leaves %	Twigs %	Roots %	Leaves		Twigs		Roots	
				r	$P_{2tailed}$	r	$P_{2tailed}$	r	$P_{2tailed}$
Cayutúe	61.3 ± 0.5a	28 ± 1.2b	10.7 ± 1.1b	0.41	0.41	0.27	0.60	–0.49	0.32
Sajonia	56.4 ± 1.9b	28.9 ± 1.5a	14.6 ± 2.7ab	0.43	0.39	–0.39	0.44	–0.07	0.89
Tirol	54.5 ± 4.6b	29.4 ± 2.1a	16.2 ± 3.6a	0.27	0.60	–0.06	0.90	–0.38	0.46

Different letters in a same column indicate statistic significant differences (Tukey, $\alpha < 0.05$), r: Pearson's product moment correlation coefficient, $P_{2tailed}$: two tailed probability; $n = 36$

N_{A2+3} to Q^{C}_{Pl}, on the other hand, showed logarithmic responses up to a given light transmittance (according to accession and trait) after which the values of these traits were inferior to the predictions of these logarithmic functions (Fig. 5b, d). Regarding the response of N_{IN} to Q^{C}_{Pl}, for *Sajonia* and *Tirol* the values measured for this trait could be positioned on a same logarithmic equation for measurements at light transmittance levels ≤50% and ≤65%, respectively, thereafter N_{IN} decreased bellow the values predicted by the equation (Fig. 5b). For this same trait (N_{IN}), the values measured for *Cayutúe* could all be positioned on a single logarithmic

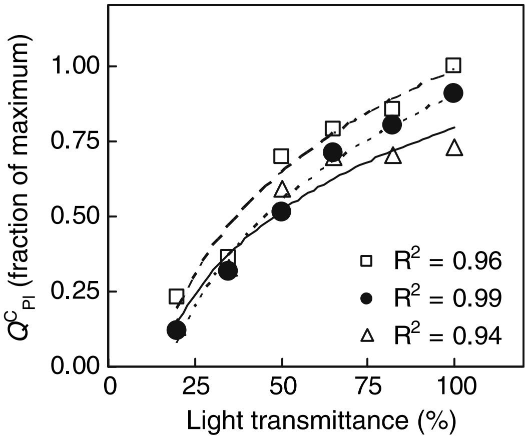

Fig. 4 Effect of light transmittance on the estimated relative amount of light intercepted by the whole plant (Q^{C}_{Pl}) of three murta accessions: *Cayutúe* (*closed circles*), *Sajonia* (*open squares*) and *Tirol* (*open triangles*)

function which was positioned at nearly half the values of the logarithmic function adjusted to *Sajonia* and *Tirol* (Fig. 5b). The response of branching to Q^{C}_{Pl} was different for each accession with *Sajonia* exhibiting the highest positioned logarithmic response up to LT_{50}, *Tirol* taking an intermediate position with a logarithmic response up to LT_{82} and *Cayutúe* exhibiting the lowest positioned logarithmic response up to LT_{65} (Fig. 5d). The response of DM_{Pl} to Q^{C}_{Pl} was linear up to a given light transmittance for all accessions, falling bellow the adjusted line thereafter (Fig. 5f). *Sajonia* exhibited a linear response for measurements at light transmittance levels ≤50% with a higher slope and positioned above the linear functions that encompassed measurements up to light transmittance = 65% for *Tirol* and light transmittance = 50% for *Cayutúe*. These linear functions of *Tirol* and *Cayutúe* showed similar slopes but the intercept was slightly higher in the case of *Tirol* (Fig. 5f). The divergence was slight in the case of *Cayutúe* and especially marked for *Tirol* (Fig. 5f).

Discussion

Acclimation to low light

The negative linear correlations of LA_l, L_{IN} and Chl_{a+b} to light transmittance (Figs. 1, 2) are typical features of shade acclimation of plants (Boardman 1977). Concerning leaf structural traits, the increment of LA_l with increasing shade (Fig. 1a), allows maximizing light interception under low light conditions whereas the increment in L_{IN} (Fig. 1c) allows increasing vertical growth towards less shaded environments in natural stands (Boardman 1977). Concerning pigment content in murta leaves, the increment in Chl_{a+b} as a response to lower light transmittance (Fig. 2a) allows leaves to increase the absorption of light and hence enhance photosynthesis in low light environments (Niinemets 1997). The average $Chl_{a/b}$ value (2.6±0.4; all treatments and accessions confounded) observed in this study (Fig. 2b) is relatively low (Johnson et al. 1993) which has been considered as a typical characteristic of shade plants (Marschall and Proctor 2004). Furthermore, the high investment of biomass in leaves observed for the three accessions (Table 3) is also considered to be a typical feature of shade plants (Boardman 1977).

Acclimation to high light

The observed increment in LMA with increasing light transmittance (Fig. 1b) has been related to an increased capacity of photosynthesis per unit leaf area under saturating light levels (Gutschick and Wiegel 1988; Niinemets and Tenhunen 1997). Concerning Chl pigments, because Chl_b prevails in the light harvesting antennae associated to photosystem (PS) II (Leong and Anderson 1984) the increment in $Chl_{a/b}$ in murta leaves in response to high light transmittance (Fig. 2b) reflects a decrease in the proportion of antennae associated to PSII which reduces the energy arriving to this photosystem (Leong and Anderson 1984), hence conferring some protection against photoinhibition (Horton and Ruban 1994). The present decrease in Chl_{a+b} in response to increasing light transmittance (Fig. 2a) can also be interpreted as a strategy for reducing excitation pressure on PSII (Giardi et al. 1996; Murchie and Horton 1997). On the other hand, photoinhibition causes damage to chlorophyll pigments (Krause 1988) so that the reduction of Chl_{a+b} with increasing light transmittance (Fig. 2a) could also be viewed as a

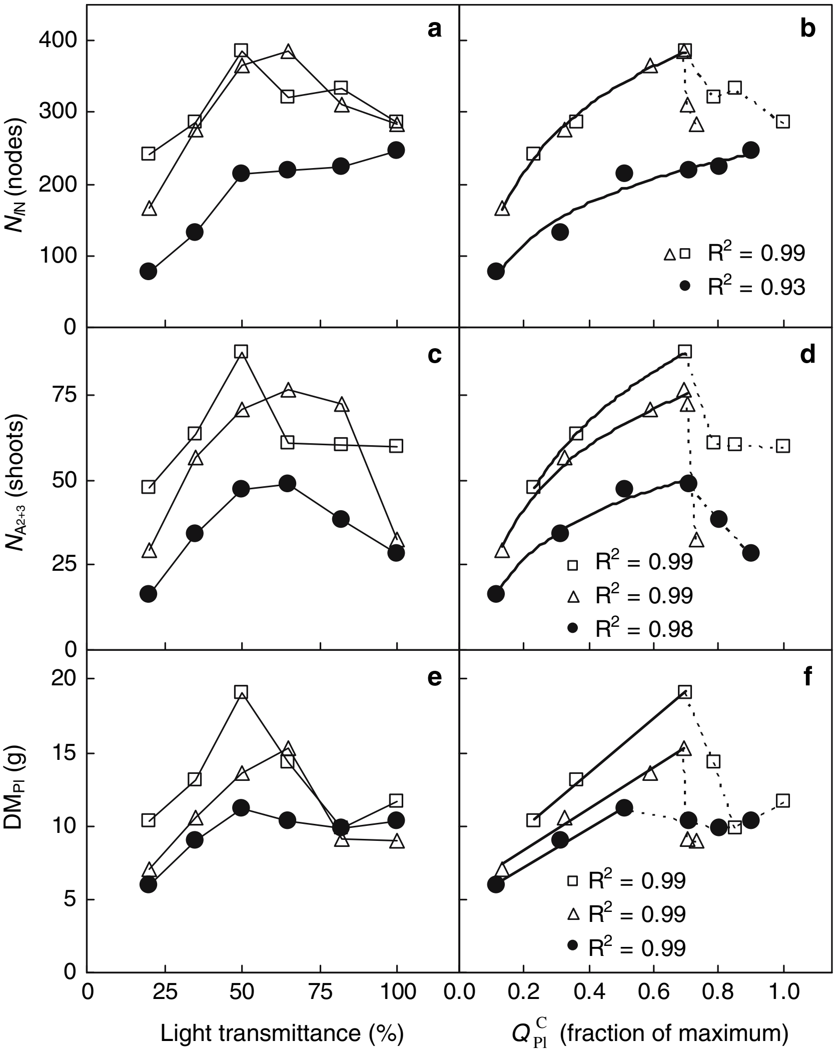

Fig. 5 Effect of light transmittance (**a**, **c** and **e**) and the estimated relative amount of light intercepted by the whole plant (Q^{C}_{Pl}: **b**, **d** and **f**) on the total amount of internodes of the plants (N_{IN}: **a** and **b**), the total amount of primary and secondary shoots of the plants (N_{A2+3}: **c** and **d**) and the total plant dry mass (DM_{Pl}: **e** and **f**) of three murta accessions: *Cayutúe* (*closed circles*), *Sajonia* (*open squares*) and *Tirol* (*open triangles*)

result of photodamage caused by excessive light, especially in the cases of *Sajonia* and *Tirol*, which showed abrupt decreases in this pigment content at light transmittance ≥65%. The increment in Car content in leaves with increasing light transmittance (Fig. 2c) also reflects an acclimation to high light conditions because these pigments have been shown to protect against photoinhibition (Demming-Adams and Adams 1996). Actually, Marschall and Proctor (2004) indicate that high carotenoid:chlorophyll ratios are associated to high levels of photoprotection. The tight relationship between Chl_{a+b} and Car, which encompassed all accessions for low light transmittance values (Fig. 2d), indicates a stable increment of Car content in leaves as Chl_{a+b} decreases with increasing light transmittance. The fact that this relationship no longer stood when light transmittance achieved higher levels (and hence Chl_{a+b} tended to lower levels; Fig. 2d) may indicate that, after a given light transmittance threshold, the Car content does not sufficiently increase in order to efficiently protect the photosynthetic apparatus of murta leaves from excessive light (Fig. 2d). Actually, photoinhibition of murta leaves exposed to full sun and even 50% light transmittance has been previously observed under the sunnier conditions of the central region of Chile (Pastenes et al. 2003).

Effects of low and high light on plant growth

Light transmittance treatments did not affect the proportion of biomass allocated to leaves, twigs and roots of murta (Table 3). This result contradicts the ''Functional Equilibrium'' theory (Brouwer 1983) which states that allocation of materials between shoots and roots is determined dynamically by the relative availability of resources in their respective parts of the environment. In this study, light, one of the most important resources in the aerial environment (Larcher 2003), was severely changed by treatments but no changes in the allocation pattern between aerial and subterraneous organs was found indicating an absence of a mechanism in murta that regulates resource allocation in response to changes in light availability.

The evolution of LA_{Pl} along the trials duration (Fig. 3a, c, e), as analysed from the parameters of the logistic growth equation (Thornley and Johnson 2000) indicate that the timing of the peak in whole plant leaf area expansion rate (i.e., TD_m parameter) was not affected by light transmittance (data not shown). The average value of TD_m for all light transmittance treatments and accessions was of ~120 days after planting (Fig. 3a, c, e) which situates the maximum growth rate of all accessions and light transmittance treatments around February 15. This date coincides with the higher T_a^{mean} period of the season (Table 1) which is consistent with the positive correlation between plant growth rate and air temperature (Johnson and Thornley 1985). This stable value of TD_m throughout light transmittance treatments and accessions may also indicate that the timing of the transition between phases of LA_{Pl} expansion is tightly conditioned by seasonal variations in environmental conditions. On the other hand, all other traits related to plant growth (LA_{Pl}, N_{IN}, N_{A2+3} and DM_{Pl}; at the exception of N_{IN} of *Cayutúe*) showed an optimum at moderate light transmittance levels (50% or 65%; Fig. 5a, c, e), indicating that insufficient light was intercepted at lower light transmittance levels and that, at higher light transmittance levels, excessive light was intercepted by the plant. Concerning intercepted light, the logarithmic increment of Q_{Pl}^{C} with increasing light transmittance (Fig. 4) indicate that progressive increments in incident light are accompanied by progressively lower increments in light intercepted by the plant owing to a decrease in crown volume and LAD when light transmittance overpasses optimal values (data not shown). The reduction in LAD when light transmittance increases may partly be explained by the observed negative effect of higher light transmittance values on LA_l (Fig. 1a) and branching (Fig. 5c). Regarding traits related to meristematic activity as branching (N_{A2+3}) and production of metamers (N_{IN}), these showed a logarithmic response to Q_{Pl}^{C} (Fig. 5b, d), the same kind of response leaf photosynthesis shows to intercepted light (Larcher 2003). This kind of logarithmic response of meristematic activity to light absorbed by whole plants had previously been observed for *Arabidopsis thaliana* by Chenu et al. (2005) who interpreted this as a response to assimilate availability in the meristems. Consistently, it has been shown that the amount of photosynthetic products in meristems directly relates to meristematic activity (Smeekens 2000; Pien et al. 2001; Freixes et al. 2002). The linear increment of DM_{Pl}, with increasing Q_{Pl}^{C} observed for moderate light transmittance treatments (Fig. 5f) is in conformity with the theoretical response of dry mass accumulation to intercepted light (Evans 1973). Strikingly, for higher light transmittance treatments, DM_{Pl} dropped bellow the predictions of the linear functions, and N_{IN}, N_{A2+3} bellow the prediction of the logarithmic functions that were adjusted to moderate light transmittance treatments (Fig. 5b, d, f) indicating that the increments in photosynthesis with increasing amount of intercepted light no longer persists for high light transmittance levels. As previously discussed, photoinhibition may partly explain these results through its effect of depressing photosynthesis (Powles 1984) and hence plant growth (Ögren and Sjöström 1990; Winter and König 1991; Liang et al. 1995; Werner et al. 2001) and assimilate availability in meristems (Chenu et al. 2005). Another part of this effect of high light may be related to changes in leaf temperature induced by light transmittance. Leaf temperature has been shown to have a direct linear response to incident light level (Margolis and

Ryan 1997) and, when leaf temperature overpasses optimum values, stomatal restriction to photosynthesis usually increases as a response to an increment in the air to leaf vapour pressure deficit (Ball et al. 1987; Collatz et al. 1991; Leuning 1995). Moreover, high leaf temperature may directly reduce net carbon fixation by (i) increasing leaf respiration (Thornley and Cannell 2000) (ii) a negative effect on the activity of enzymes involved in photosynthesis (Bernacchi et al. 2001; Leuning 2002) and (iii) alterations in the structure of the photosynthetic apparatus (Pastenes and Horton 1996a, b) and in electron transfer (Pastenes and Horton 1999). Actually, for another shade plants as *Coffea arabica*, restrictions to plant growth in full sun have been mainly explained by a negative effect of high leaf temperature (Nunes et al. 1968; Gutierrez et al. 1994; Da Matta 2004; Franck 2005). Moreover, for *Coffea arabica*, similar effects of high light transmittance which decreased branching, metamer emission and dry mass accumulation, as presently observed for murta (Fig. 5), were attributed to insufficient carbon assimilation due to direct limitations to photosynthesis by stomatal conductance and high leaf temperature, whereas the negative effect of photoinhibition on the whole plant carbon assimilation was marginal (Franck 2005). In studies with other species, the effect of photoinhibition on whole plant carbon assimilation has been found to be significantly less important than the effect of photoinhibition on carbon assimilation at the leaf level (Ögren and Sjöström 1990; Werner et al. 2001; Franck 2005).

Differences in acclimation to low and high light between accessions

The response of plant structure and leaf pigment content to light transmittance was different between accessions (Figs. 1, 2). *Tirol* showed the most abrupt reduction in the Car:Chl$_{a+b}$ ratio, which is consistent with the fact that this accession showed no response of Car to light transmittance (Fig. 2c), and exhibited the most steep reduction in Chl$_{a+b}$ in response to increasing light transmittance levels (Fig. 2a). These results indicate that *Tirol* would be more susceptible to photoinhibition because of (i) an inability to increase its Car content in leaves in order to protect the photosynthetic apparatus from excessive light (Demming-Adams and Adams 1996) and (ii) a consequent increased damage of Chl$_{a+b}$ pigments by the same excessive light levels (Krause 1988). Moreover, *Tirol* showed the lowest increment rate of LMA in response to increasing light transmittance (Fig. 1b) which may indicate a low plasticity of the leaf mesophyll in response to increasing light transmittance resulting in an insufficient increase in mesophyll thickness in order to maximize photosynthesis under high light (Gutschick and Wiegel 1988; Niinemets and Tenhunen 1997). Furthermore, the growth traits (N_{IN}, N_{A2+3} and DM$_{Pl}$) of *Tirol* were severely affected by light transmittance levels above 65 % (Fig. 5) indicating the lowest ability to acclimate to high light among the three accessions. *Sajonia*, on the other hand, would possess the best protection system against photoinhibition as shown by the very slight deviation of its Car:Chl$_{a+b}$ ratio when light transmittance exceeded 50% and its higher Car content in leaves (Fig. 2c, d). Concerning light interception, *Sajonia* showed the highest interception at any given light transmittance level (Fig. 4) which indicates a good acclimation to shade but a lower capacity of reducing light interception as a strategy of acclimation to high light (Demming-Adams and Adams 1992). This accession also showed the highest efficiency in using intercepted light to fix dry mass but DM$_{Pl}$ rapidly dropped for light transmittance levels above 50% (Fig. 5f), indicating a strong effect of photoinhibition and/or negative effect of temperature when light transmittance exceeds 50%, even if this accession exhibited features of good protection against photoinhibition at the leaf level (Fig. 2). This contradictory result might indicate that this accession could be less effective in other processes that alleviate the effect of photoinhibition such as chloroplast movements (Pastenes et al. 2003). Alternatively, the negative effect of high leaf temperature might be more marked in *Sajonia* than in the other accessions. In the case of *Cayutúe*, although the deviation from the indirect linear relationship between Car and Chl$_{a+b}$ is more marked than for *Sajonia* (Fig. 2d), it could be only observed in full sunlight, indicating that this accession may be better adapted to high incident light levels. Moreover, *Cayutúe* was the only accession showing the highest N_{IN} value at LT_{100} and a final DM_{Pl} with a lower relative decrease at higher light transmittance as compared to the other two accessions (Fig. 5b, f) indicating the best acclimation to high light.

Concerning indicators of shade acclimation at the organ level, some contradictions arise when comparing the accessions: higher LA_l and lower increment of L_{IN} in response to low light transmittance (Fig. 1a, c) level may indicate that *Tirol* is the best shade adapted accession whereas higher Chl_{a+b} contents (Fig. 2a) and proportion of biomass allocated to leaves (Table 3) would point out *Cayutúe* as the best shade adapted accession. Alternatively, if the efficiency for fixating biomass at low light transmittance levels would be considered as the indicator of better acclimation to shade, *Sajonia* could be considered as the most shade adapted accession (Fig. 5f).

Conclusions

The method for estimating light interception by plants used in this study relies on major simplifications and the use of data obtained from allometric functions. Nevertheless, this procedure seems to give adequate proportional estimations of intercepted light as indicated by the stable logarithmic or linear relationships between plant growth traits and light intercepted by the plant at low and optimum light transmittance levels. These stable functions indicate that, up to optimum light transmittance levels, the differences in plant growth can be attributed to the light availability for photosynthesis whereas, beyond optimum light transmittance levels, photosynthesis and plant growth no longer show the expected increments with increasing light interception. These results indicate that murta is susceptible to high light which induces a loss of the capacity of transforming intercepted light into dry mass which may partly be explained by an effect of photoinhibition as indicated by the effect on leaf pigment contents. Concerning genetic variability in the response of murta plants to light, *Cayutúe* and *Sajonia* presented a better protection against photoinhibition at the leaf level than *Tirol*. On the other hand, under low and moderate light transmittance levels, *Sajonia* was more efficient in intercepting incident light and showed a better efficiency in using this intercepted light for fixating biomass and producing metamers than the other two accessions. If in the case of murta fruit yield is positively related to dry mass accumulation and availability of metamers (potential fruiting sites) as is the case in many other fruit trees (Causton 1985), *Sajonia* can be considered as the most promising accession for production of murta in denser agroforestry systems. For production in less shady agroforestry systems, *Tirol* would be more adapted as it shows the highest optimum light transmittance level (65%) but has the most marked negative effect of photoinhibition thereafter. *Cayutúe* shows the lowest efficiency in using intercepted light for fixating dry mass but has a less marked decrease in dry mass fixing under high light, even in full sun. This accession might therefore be interesting for full sun cultivation if planted on a higher density than the other accessions. Independent of accession, it is concluded that murta is a plant that requires of shading for realising its photosynthetic potential and is hence an interesting crop to be included in agroforestry systems under the climatic conditions of southern Chile.

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