iForest
Biogeosciences and Forestry

Research Article
doi: 10.3832/ifor3640-014
vol. 14, pp. 307-312

Growth and physiological acclimation to shade in young plants of *Adesmia bijuga* Phil., a critically endangered species in central Chile

Marco A Yáñez (1),
Persy Gómez (2),
John Gajardo (3),
Sergio Espinoza (4)

Adesmia bijuga Phil. is an endemic and endangered shrub species of central Chile. Its potential shade intolerance is one of the leading hypotheses for its vigor loss when the species grows beneath closed canopies. The objective of this study was to assess the growth and physiological acclimation to the shade of young plants of _A. bijuga_. A nursery experiment was established with three light levels based on the interception of photosynthetic active radiation (PAR) (TRT0: control at full sun; TRT60: 60% shaded; TRT90: 90% shaded), and maintained for 71 days during the summer season. Growth and leaf morpho-physiological responses were evaluated at the beginning, at the middle, and at the end of the experiment. The shading treatment increased plant height (H), live crown percentage (L_{crown}), and specific leaf area (SLA) compared to the control treatment at full sun. However, light-saturated photosynthetic rate (A_{max}), dark respiration rate (R_d), and light compensation point (Γ_i) were higher in TRT60 than in the other treatments, while no differences were found among treatments for the apparent quantum yield (a). At this stage of plant development, our results suggest high acclimation plasticity of _A. bijuga_ to light levels; however, a semi-shade environment (_i.e._, TRT60) favored a better performance of the species.

Keywords: _Adesmia bijuga_, Shade Tolerance, Photosynthesis, Light Acclimation, Forest Restoration

Introduction

Central Chile (30°-38° S) contains more than 60% of the country's total flora and endemic species, and is listed among the 25 global biodiversity hot spots due to its high endemism and loss of habitat (Myers et al. 2000, Gómez et al. 2012). Currently, while this area has a highly fragmented landscape, due to the extent of *Pinus radiata* D. Don plantations, it still contains some important natural biocoenoses such as the Maulino forest, the sclerophyllous forest, and species of the ecologically important South American genus *Adesmia*, whose populations are characterized by small size and low genetic diversity (Gómez et al. 2012, Guerra et al. 2018).

The genus *Adesmia* (Fabaceae) comprises 230 species distributed in South America (Burkart 1967). In Chile, there are 130 species, of which 85 are endemic (Moreira-Muñoz 2011) with social and agricultural importance (Gerding et al. 2017). *Adesmia bijuga* Phil. is one of the most endangered species of the genus, as it is spatially restricted over an area of 4 ha in the Maule Region of Central Chile (Gómez et al. 2014). Despite the species has been listed as "Critically Endangered" by the International Union for Conservation of Nature (IUCN – Hahn & Gómez 2008, Gómez et al. 2012), it is not currently protected by the Chilean Government. The species has small compound leaves with leaflets of 28-mm length and 7-mm wide. It has a shrubby habit and can reach up to 2 m height with long and straight branches (Hahn & Gómez 2008).

Currently, the habitat of *A. bijuga* is very fragmented and largely immersed in *P. radiata* plantations. Because of its floristic and biogeographical importance, as well as its conservation status, there is an interest in the ecological restoration of the species, but there is still little knowledge about to what extent *P. radiata* plantations might modify the environmental and ecological conditions of *A. bijuga* habitat. It is known that some native species might positively benefit from growing beneath *P. radiata* canopies (Simonetti et al. 2012), especially shade-tolerant species (Guerrero & Bustamante 2009, Gómez et al. 2014). Brockerhoff et al. (2003) reported a decrease in light-demanding pioneer species and an increase in shade-tolerant species with canopy closure and stands age. In the case of *A. bijuga*, the species seems to have a better recruitment performance in open sites, but little is known about the specie's responses to shade when it grows beneath plantation canopies.

Light is the driving force for photosynthesis, and plants acclimate their leaf physiology and morphology to optimize carbon assimilation. Acclimation to irradiance is typically addressed by studying photosynthetic light response curves. Leaf acclimation from high to low irradiance involves a reduction in the light-saturated photosynthetic rate, respiration rate, light compensation point, photoprotective compounds, palisade tissue, mesophyll cells, stomata per unit of leaf area, and chlorophyll *a*/*b* ratio, but also implies an increase in the apparent quantum yield, and in the nitrogen allocated to light-harvesting organs (Givnish 1988, Kazda et al. 2000, Pallardy 2008, Niinemets et al. 2015). To our knowledge, there are no studies on *A. bijuga* assessing

---

✉ (1) Núcleo Científico Multidisciplinario. Universidad de Talca. 2 Norte 685, Talca. P.O. Box 747 (Chile); (2) Jardín Botánico, Universidad de Talca, Casilla 747, Talca (Chile); (3) Instituto de Bosques y Sociedad, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Campus Isla Teja, Valdivia (Chile); (4) Facultad de Ciencias Agrarias y Forestales, Universidad Católica del Maule, Avenida San Miguel, 3605 Talca (Chile)

@ Marco A Yáñez (marcoyanez@utalca.cl)

Received: Sep 01, 2020 - Accepted: Apr 19, 2021

Citation: Yáñez MA, Gómez P, Gajardo J, Espinoza S (2021). Growth and physiological acclimation to shade in young plants of *Adesmia bijuga* Phil., a critically endangered species in central Chile. iForest 14: 307-312. - doi: 10.3832/ifor3640-014 [online 2021-07-01]

Communicated by: Gianfranco Minotta

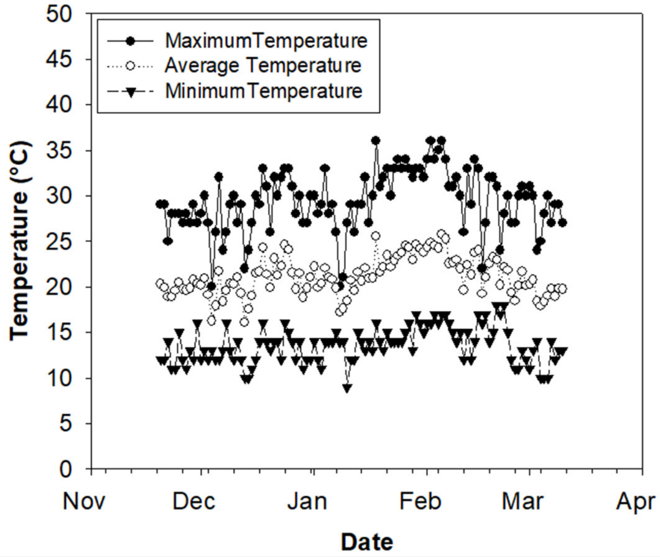


Fig. 1 - Daily maximum, minimum, and mean air temperature for the duration of the experiment.

the acclimation of the species to different light levels, but it has been observed that light is an important limiting factor for the development of understory vegetation in other conifer plantations (Hill & Jones 1978). In this study, a nursery experiment was established with young plants of *A. bijuga* grown under three different light levels and maintained under the warm conditions of the summer months in Central Chile. The objective of the study was to assess the growth and physiological acclimation of *A. bijuga* to shade at the early growing stage. The results of this study might provide information for the conservation and ecological restoration of the species.

Materials and methods

Plant material and study design

In winter 2016, *A. bijuga* cuttings were collected in the field from its natural population in the Coastal Range of the Maule Region in Central Chile (35° 27′ S, 72° 27′ W; elevation 150 m a.s.l.). Cuttings were obtained from healthy plants with no herbivore damage and were 33 cm long, with the presence of ax”illary buds. After collection, cuttings were planted in 140 mL pots containing composted bark of *P. radiata* and grown for two growing seasons in facilities of the Company "Forestal Mininco" S.A. Then, the plants were transferred to the nursery facilities at the Universidad de Talca, city of Talca, Chile (35° 24′ S, 71° 38′ W; elevation 112 m a.s.l.). Plants were transplanted to 1 L plastic bags filled with local topsoil and grown for six months in a nursery and covered with an 80% black polyethylene mesh (Raschel®, Santiago, Chile). The soil water content was maintained between 26% to 45% and monitored using a ThetaProve® soil moisture sensor (Delta-T Ltd, Cambridge, UK). No fertilizers were added to the growing substrate.

Fig. 2 - View of the *A. bijuga* plants under the different shading treatments (TRT0: full sun; TRT60: 60% shade; TRT90: 90% shade) during the second measurement.

The study was a completely random design with two shading treatments and a control treatment at full sun. Two 1 m^3 domes differing in light interception were built for each shading treatment using black polyethylene mesh (Raschel®, Santiago, Chile) and secured with 1.3 cm diameter polyvinyl chloride (PVC). Each treatment had two replicates that were randomly assigned within each dome and six plants were randomly assigned to each replication. Shading treatments were defined as the percentage of photosynthetic active radiation (PAR) intercepted by the domes relative to the maximum PAR recorded at midday during the summer months (about 2100 µmol m^{-2} s^{-1}), which was determined by using a quantum sensor LI-190® (LICOR Inc., Lincoln, NE, USA). Thus, the sun-exposed treatment was named TRT0, while the shading treatments were named TRT60 and TRT90 (60% and 90% of PAR interception, respectively). Light level at TRT90 represents closed-canopy on mature *P. radiata* stands. Light treatments were imposed on November 27, 2018, and maintained until March 7, 2019. Fig. 1 shows the minimum, average, and maximum temperatures recorded during the study period. Because the material available comprised a pool of genotypes, and there was a high variation in plant height, plants for the experiment were selected based on their growth uniformity and visual healthy condition.

Growth and physiological measurements

Growth and photosynthetic-light response curves were measured on three dates: Date 1, a baseline measurement a day before assigning the plants to the treatments (November 27, 2018); Date 2, mid-summer (February 1, 2019); and Date 3, at the end of summer (March 7, 2019). Plant height (H) of the dominant shoot was measured using a metric tape, and increments of this variable were determined among measurement dates. Light-response curves were made using a portable gas exchange system LI 6800® (LICOR Inc., Lincoln, NE, USA). Initial chamber conditions were set up at ambient conditions, with a temperature of 20 °C, CO$_2$ concentra-

Tab. 1 - *P*-values based on the analysis of variance for differences among treatments (TRT) and dates (DATE) in plant height, live crown percentage (L_{crown}), specific leaf area (SLA), leaf area per lamina (LA_{lamina}), maximum photosynthetic rate (A_{max}), dark respiration (R_d), light compensation point (Γ_i), and apparent quantum yield (α).

Source of variation	Growth and leaf morphology				Photosynthetic capacity			
	Height	L_{crown}	SLA	LA_{lamina}	A_{max}	R_d	Γ_i	α
TRT	0.0210	0.0073	0.0011	0.7069	0.0414	0.1845	0.0879	0.3821
DATE	<0.0001	<0.0001	-	-	0.0272	0.0105	0.0124	0.3609
TRT × DATE	0.0037	0.0016	-	-	0.0493	0.0056	0.0451	0.3490

tion of 400 ppm, a relative humidity of 50%, and PAR of 1800 µmol m^{-2} s^{-1}. These parameters were kept steady during the measurements and controlled by the LI 6800. The light-response curve was obtained in a ten-step reduction process (1.800, 900, 600, 300, 200, 150, 100, 50, 10, 0 µmol m^{-2} s^{-1}). Five plants per treatment were randomly selected at each date. At each plant, two leaflets of a compound leaf from the upper third were carefully placed in the chamber to avoid self-shading and acclimated to the initial conditions for 2 minutes. Measurements were performed between 09:00 and 13:00 hours local time. Because of the small leaf size, additional measurements of leaf size (*i.e.*, lamina's length and wide) were used to calculate leaf area in the chamber (L) as (eqn. 1):

$$L=\frac{\pi\cdot l\cdot w}{4}\cdot n \tag{1}$$

where *l* is the lamina length, *w* is the lamina width and *n* the number of leaves within the chamber. Similarly, the mean area of the lamina was calculated as $LA_{lamina} = L/n$. The maximum photosynthetic rate (A_{max}), dark respiration rate (R_d), light compensation point (Γ_i), and apparent quantum yield (α) were estimated fitting the non-rectangular hyperbola (Hanson et al. 1987).

In the third measurement date, the foliage was collected from plants on each treatment and scanned for leaf area determination using a bed scanner and the software Image J (developed by the National Institute of Health). Then, the foliage was dried at 65 °C to a constant weight to determine the specific leaf area (SLA, leaf area to dry weight ratio). Similarly, on the second and third measurement dates, the live crown percentage was calculated as the portion of the shoot with foliage divided by the total plant height.

Statistical analysis

All the analyses were made in the software SAS® version 9.2 (SAS Institute Inc., Cary, NC). Light-response curves parameters were obtained using non-linear least squares in the PROC NLIN procedure. Traits that were measured only at the end of the study were subjected to a one-way analysis of variance, with the light treatment as the main factor, whereas in the other traits, the model was extended to a repeated measures analysis. We used the unstructured (UN) function to model the variance-covariance matrix of the error terms. All the variables were analyzed using the PROC MIXED procedure. Mean comparisons were made using the Tukey's adjustment test. Treatment effects were considered significant at an alpha level of 0.05.

Results

Growth performance and leaf traits

Before imposing the light treatments, average plant diameter and height for the dominant branch were 3.7 mm and 45.4 cm, with coefficients of variation (CV) of 16% and 18%, respectively (Fig. 2). Plant survival within the domes varied from 41% to 75%. The results of the analysis of variance showed a significant interaction between the light treatment and measurement date for H (*p*=0.0037) and live crown percentage (*p*=0.0016 – Tab. 1). Differences among treatments for both traits were found since Date 2 (Fig. 3A). At the end of the experiment (*i.e.*, Date 3), plant H was 41% higher in TRT90 than TRT0, whereas plants at TRT60 had an intermediate value (Fig. 3A). At Date 3, plants at TRT90 had 97% higher L_{crown} than plants in the other treatments (Fig. 3B).

There was no effect of the treatments on LA_{lamina} (*p*=0.7069), but increasing the shading level increased SLA (*p*=0.0011 – Tab. 1). SLA did not differ between TRT60 and TRT90, and on average, plants at these treatments had a SLA 108% higher than plants at TRT0 (Fig. 3B).

Photosynthetic light response curves parameters

With the exception of α, there was a significant effect of the interaction between the light treatment and measurement date for all the variables derived from the photosynthetic light response curves (Tab. 1). The differences among treatments were found only at the end of the experiment, *i.e.*, Date 3 (*p*<0.05 – Fig. 4). A_{max}, R_d, and Γ_i did not differ between TRT0 and TRT90, but these values were significantly lower

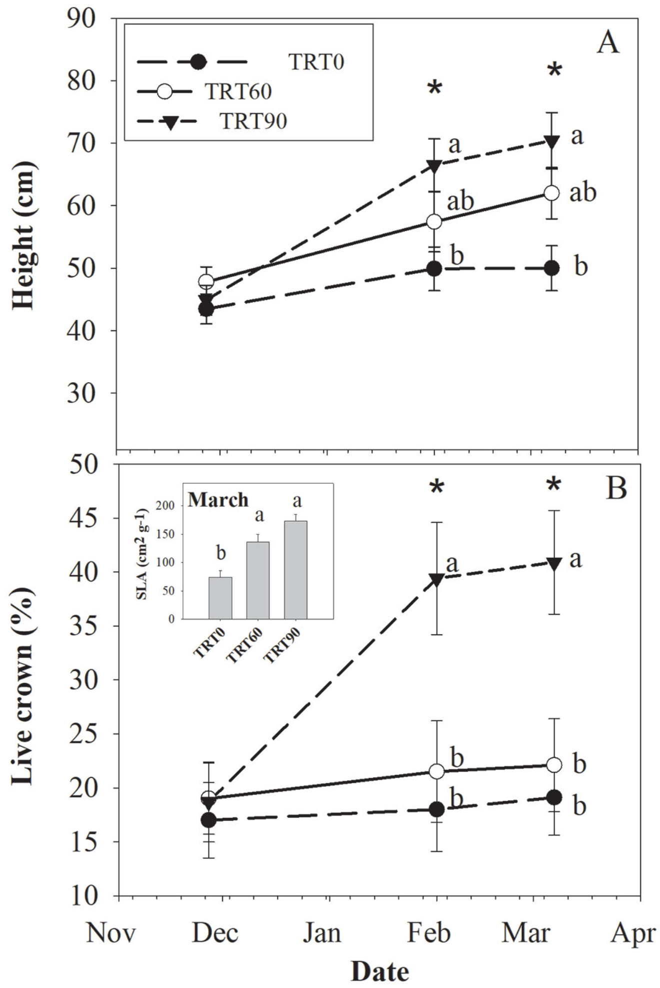
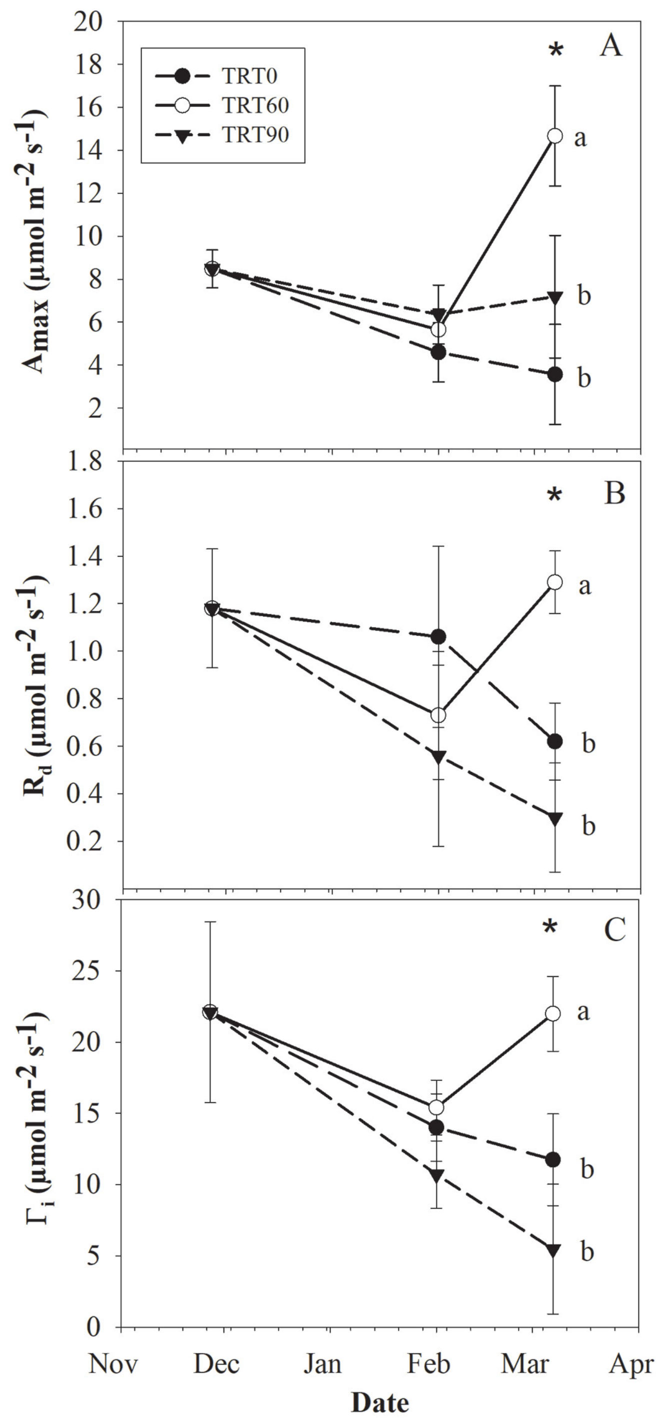


Fig. 3 - Mean (± standard error) values per treatment (TRT0, TRT60, TRT90) and date for (A) height and (B) live crown percentage in young *A. bijuga* plants. (*): denotes significant differences among treatments. Different lowercase letters denote significant differences among treatments, according to the Tukey's adjustment test. The inset graph shows the means for specific leaf area (SLA) per treatment at the end of the study period.

Fig. 4 - Mean (± standard error) values per treatment (TRT0, TRT60, TRT90) and (A) date for maximum photosynthetic rate (A_{max}), (B) dark respiration (R_d), and (C) light compensation point (Γ_i) in young *A. bijuga* plants. (*): denotes significant differences among treatments. Different lowercase letters denote significant differences among treatments according to the Tukey's adjustment test.



than those on TRT60. Overall, these photosynthetic parameters tended to decrease with time for TRT0 and TRT90 (Fig. 4) and tended to decline in TRT60 toward Date 2 and then increased toward Date 3. Mean α for the first, second, and third measurement dates were 0.051, 0.070, and 0.058 μmol CO_2 μmol photon^{-1}, respectively. Overall, stomatal conductance (g_s) ranged from 0.007 to 0.28 mmol m^{-2} s^{-1}, whereas vapor pressure deficit (VPD) ranged from 1.29 to 1.79 MPa.

Discussion

Several factors might be involved in the population decline of *A. bijuga*. There is thus a need to understand the ecological behavior of the species in order to develop strategies for its conservation. An important factor driving the population recruitment of the species is the ecological pressure that pine plantations might exert over the highly fragmented habitats where this species develops. Some studies have shown the negative effects of pine invasion on the richness of other native species (Franzese et al. 2017), which is related to the competition for light and soil resources. We started under the assumption that, in its natural growing environment, the observed loss of vigor and growth of *A. bijuga* in the understory might be related to its shade-intolerant behavior, a fact that is not well understood in this species. In this study, we examined the growth and leaf-level physiological acclimation of young *A. bijuga* plants to different light treatments. Overall, our results indicate that the species had high phenotypic plasticity to light intensity. However, its higher physiological performance was in the partial shade treatment (TRT60) and not in the full-sun exposed treatment (TRT0).

Small compound leaves, like those of *A. bijuga*, might be considered as an adaptive characteristic of species growing under high light or dry environments (Tozer et al. 2015). Small leaves are typically found in shade-intolerant species, while large leaves are found in shade-tolerant species (Rozendaal et al. 2006, Valladares & Niinemets 2008). Under high light, small leaves may improve the coupling with the atmosphere, reducing the boundary-layer resistance and consequently leaf temperature and water loss (Niinemets & Valladares 2004, Rozendaal et al. 2006). However, beyond their classification as shade-tolerant and intolerant species, each species may exhibit a different degree of acclimation to light (Liu & Su 2016). Some studies show that shade-intolerant species may have higher acclimation plasticity to different light levels than shade-intolerant species (Poorter et al. 2009), which may be the case of *A. bijuga*. The latter author also mentioned that the ability for acclimation of SLA and leaf mass per area (LMA, the inverse of SLA) to shade might be a good predictor of the relative growth and survival rate. This agreed with our results because SLA was highly plastic and exhibited an increase over 2-fold in the shaded treatments relative to the control full sun-exposed. A high SLA also implies a higher number of chloroplasts and enzymes on leaves and an improved photosynthesis capacity (Evans & Poorter 2001). The fact that treatments did not differ in LA_{lamina} suggests that differences in SLA (p=0.7069) are mainly due to the differences in dry mass, which implies a decreased leaf thickness, with lower investment in leaf construction and protective tissues (Poorter et al. 2009).

We are aware of the low replication of the study, which likely influenced the lack of significance of some traits such as LA_{lamina} (Tab. 1). Nevertheless, trends were clear for all the traits, and values for leaf morphological traits and height were lower at TRT0, which is consistent with the results found in other studies (Liu & Su 2016). However, Liu & Su (2016) mentioned that a lower investment in shoot development might favor leaf production and its competitiveness capability, which disagree with our study. At the full sun, *A. bijuga* reduced growth and live crown percentage (*i.e.*, leaf area). The lower L_{crown} at TRT0 might be associated to faster senescence due to transient plant water stress (Mazzanatti et al. 2016). Because plants in the nursery were acclimated to shade before treatment imposition, the lower L_{crown} at TRT0 was probably induced by the inability of older leaves to counteract photoinhibition (Mazzanatti et al. 2016). Otherwise, the new living foliage was developed and acclimated to the high light condition from the beginning. We argue that the high temperature and light conditions during the study period might have affected *A. bijuga* growth at TRT0. During the experimental period, maximum temperatures were over 30 °C most of the days (Fig. 1). Thus, although the water was kept over 26%, there likely was a thermal stress on those plants. The high thermal conductivity and the low volume of the plastic bags, likely affected the substrate heat dissipation and, consequently, the root functions and shoot growth.

The study of light response curves is used to assess the shade tolerance of the species (Feng et al. 2018) since shade tolerance is associated with several functional traits and is also influenced by other abiotic factors (Valladares & Niinemets 2008). In our study, *A. bijuga* plants exhibited high photosynthetic rates up to 15 $\mu mol\ m^{-2}\ s^{-1}$ at the intermediate light level (*i.e.*, TRT60 – Fig. 3). To our knowledge, little is known about the ecophysiology of *Adesmia* species. However, the photosynthetic rates found in this study were two-fold higher to the ones reported for other *Adesmia* species growing at high altitudes in the north-central Chilean Andes (Rada et al. 1999). Overall, sun acclimated leaves have high assimilation rates (A_{max}), dark respiration (R_d), and light compensation point (Γ_i), but lower quantum efficiency relative to shade adapted leaves (Pallardy 2008, Valladares & Niinemets 2008, Martinez & Fridley 2018). These findings partially agreed with our results as a greater physiological performance was obtained at TRT60, in which A_{max}, R_d and Γ_i were higher than in the other treatments, while there were no differences between the extreme light treatments TRT0 and TRT90. We argued that regarding the harsh environmental and experimental conditions (*i.e.*, light, temperature, rooting volume) described in this study, the low values of the photosynthetic parameters obtained in TRT0 might be explained by damages to the plants photosynthetic machinery. Although it was not measured, we observed a higher yellowing in plants exposed to TRT0 than the other treatments, suggesting a denaturation of leaf pigments. However, this photochemical damage was not expressed on differences among treatments in α, a parameter that is altered when the excess of light leads to photoinhibition. On the other hand, the low values of the physiological parameters in TRT90 compared with TRT60 suggests that the photosynthetic capacity of *A. bijuga* is considerably compromised at the low light level. Therefore, more research is needed in this respect, especially in field trials. We speculate that the species has high plasticity to light levels, but this might be a specific feature of young plants. Torres et al. (2018) mentioned that the acclimation capacity of a species to different light levels at early ontogenic stages is associated with its ability to prosper in the forest understory. Otherwise, as plants develop in the understory, they might also be limited for other resources than light, such as water acquisition and temperature. Pine species are good competitors for resources, and they decrease the composition and abundance of understory species as crown develops (Franzese et al. 2017). Thus, the low vigor of *A. bijuga* growing under pine canopies might be associated with complex interactions among light, temperature, and water availability (Torres et al. 2018), which needs further investigations. Overall, species of the genus *Adesmia* have great potential for forage and for medicinal purposes (Gerding et al. 2017), and are well adapted to the semi-arid condition in Mediterranean climates due to its high stomatal control (Rada et al. 1999). However, species such *A. bijuga* are under high anthropogenic pressure, thus basic information like the one provided by this study is needed for their restoration.

Conclusions

Our study showed that *A. bijuga* exhibited acclimation plasticity to different light levels. At the early stages of development, a semi-shade environment favored a better physiological performance of the species, but growth and leaf morphological traits were benefited in an environment with higher shading. Thus, the results of this study contradict our assumption that light availability is the main factor influencing the vigor loss of the species when this develops beneath *P. radiata* plantations. However, this contention needs further research to explore the potential interaction between light and other abiotic factors affecting the species development.

Conflict of interest

The authors declare that there is no conflict of interest.

Acknowledgments

We thank the Poplar Technology Center (PTC) of the University of Talca (Chile) for providing the LI-6800.

References

Brockerhoff E, Ecroyd GC, Leckie AC, Kimberley MO (2003). Diversity and succession of adventive and indigenous vascular understorey plants in *Pinus radiata* plantation forests in New Zealand. Forest Ecology and Management 185: 307-326. - doi: 10.1016/S0378-1127(03)00227-5

Burkart C (1967). Contribución al estudio del género *Adesmia* DC. VII Sinopsis del género Sudamericano de leguminosas *Adesmia* DC [Contribution to the study of the genus *Adesmia*. VII Synopsis of the genus in South America]. Darwiniana 14: 463-568. [in Spanish]

Evans J, Poorter H (2001). Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell and Environment 24: 755-767. - doi: 10.1046/j.1365-3040.2001.00724.x

Franzese J, Urrutia J, García R, Taylor K, Pauchard A (2017). Pine invasion impacts on plant diversity in Patagonia: invader size and invaded habitat matter. Biological Invasions 19: 1015-1027. - doi: 10.1007/s10530-016-1344-6

Feng J, Zhao K, He D, Fang S, Lee T, Chu C, He F (2018). Comparing shade tolerance measures of woody forest species. PeerJ 6 (3): e5736. - doi: 10.7717/peerj.5736

Gerding M, Oyarzúa P, García L, Fischer S, Noranbuena C, Barahona V, Del Pozo A, Ovalle C (2017). Diversity and symbiotic effectiveness of *Adesmia* spp. root nodule bacteria in central and southern Chile. Symbiosis 72: 61-72. - doi: 10.1007/s13199-016-0440-9

Givnish TJ (1988). Adaptation to sun and shade: a whole-plant perspective. Australian Journal of Plant Physiology 15: 63-92. - doi: 10.1071/PP9880063

Gómez P, Bustamante R, San Martín J (2012). Estructura poblacional de *Teline monspessulana* (L.) K. Koch en fragmentos de bosque maulino en Chile central [Population structure of *Teline monspessulana* (L.) K. Koch in the maulino forest in Central Chile]. Gayana Botanica 69: 197-200. [in Spanish] - doi: 10.4067/S0717-66432012000100022

Gómez P, Hahn S, San Martín J (2014). Estructura y fenología reproductiva de una población remanente de *Adesmia bijuga* Phil., Fabaceae, en un hábitat costero mediterráneo perturbado de Chile central [Structure and phenology of a population of *Adesmia bijuga* Phil., Fabaceae in a coastal habitat in Central Chile]. Gayana Botanica 71: 163-166. [in Spanish] - doi: 10.4067/S0717-66432014000100016

Guerra F, Gómez P, Gutiérrez A, Hahn S (2018). Genetic diversity of *Adesmia bijuga* Phil., an endangered Fabaceae species from Central Chile. Brazilian Journal of Botany 41: 247-251. - doi: 10.1007/s40415-018-0440-5

Guerrero P, Bustamante R (2009). Abiotic alterations caused by forest fragmentation affect tree regeneration: a shade and drought tolerance gradient in the remnants of Coastal Maulino Forest. Revista Chilena de Historia Natural 82: 413-424. - doi: 10.4067/S0716-078X2009000300008

Hahn S, Gómez P (2008). Hallazgo de *Adesmia bijuga* Phil. (Fabaceae) en la zona costera, Región del Maule, Chile central [Rediscovery of *Adesmia bijuga* Phil. (Fabaceae) in the coastal zone of the Maule Region, in central Chile]. Gayana Botanica 65: 119-121. [in Spanish] - doi: 10.4067/S0717-66432008000100013

Hanson P, McRoberts RE, Isebrands JG, Dixon RK (1987). An optimal sampling strategy for determining CO_2 exchange rate as a function of photosynthetic photon flux density. Photosynthetica 21: 98-101.

Hill M, Jones EW (1978). Vegetation changes resulting from afforestation of Rough Grazings in Caeo Forest, South Wales. Journal of Ecology 66: 433-456. - doi: 10.2307/2259145

Kazda M, Salzer J, Reiter I (2000). Photosynthetic capacity in relation to nitrogen in the canopy of a *Quercus robur*, *Fraxinus angustifolia* and *Tilia cordata* flood plain forest. Tree Physiology 20: 1029-1037. - doi: 10.1093/treephys/20.15.1029

Liu W, Su J (2016). Effects of light acclimation on shoot morphology, structure, and biomass allocation of two *Taxus* species in southwestern China. Scientific Reports 6 (1): 959. - doi: 10.1038/srep35384

Martinez KA, Fridley JD (2018). Acclimation of leaf traits in seasonal light environments: Are non-native species more plastic? Journal of Ecology 106: 2019-2030. - doi: 10.1111/1365-2745.12952

Mazzanatti T, Calzavara AK, Pimenta JA, Oliveira HC, Stolf-Moreira R, Bianchini E (2016). Light acclimation in nursery: morphoanatomy and ecophysiology of seedlings of three light-demanding neotropical tree species. Brazilian Journal of Botany 39: 19-28. - doi: 10.1007/s40415-015-0203-5

Moreira-Muñoz A (2011). Plant geography of Chile. Springer, New York, USA, pp. 346. [online] URL: http://books.google.com/books?id=hmH11ybGdQEC

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000). Biodiversity hotspots for conservation priorities. Nature 403: 853-858. - doi: 10.1038/35002501

Niinemets U, Keenan TF, Hallik L (2015). A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. New Phytologist 205: 973-993. - doi: 10.1111/nph.13096

Niinemets U, Valladares F (2004). Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. Plant Biology 6: 254-268. - doi: 10.1055/s-2004-817881

Pallardy S (2008). Physiology of woody plants. Academic Press, Oxford, UK, pp. 464.

Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytologist 182: 565-588. - doi: 10.1111/j.1469-8137.2009.02830.x

Rada F, Squeo F, Azocar A, Cabrera H (1999). Water and carbon relations in the genus *Adesmia* (Papilionaceace) at different altitudes in the high north-central Chilean Andes. Revista Chilena de Historia Natural 72: 201-211.

Rozendaal D, Hurtado MA, Poorter L (2006). Plasticity in leaf traits of 38 tropical tree species in response to light, relationships with light demand and adult stature. Functional Ecology 20: 207-216. - doi: 10.1111/j.1365-2435.2006.01105.x

Simonetti J, Grez A, Estades C (2012). Biodiversity conservation in agroforestry landscapes: challenges and opportunities. Editorial Universitaria, Santiago, Chile, pp. 162.

Torres CD, Magnin A, Varela SA, Stecconi S, Grosfeld JE, Puntieri JG (2018). Morpho-physiological responses of *Nothofagus obliqua* to light intensity and water status, with focus on primary growth dynamics. Trees - Structure and Function 32: 1301-1314. - doi: 10.1007/s00468-018-1712-1

Tozer W, Rice B, Westoby M (2015). Evolutionary divergence of leaf width and its correlates. American Journal of Botany 102: 367-378. - doi: 10.3732/ajb.1400379

Valladares F, Niinemets U (2008). Shade tolerance, a key plant feature of complex nature and consequences. Annual Review of Ecology, Evolution, and Systematics 39: 237-257. - doi: 10.1146/annurev.ecolsys.39.110707.173506