



## XV WORLD FORESTRY CONGRESS

Building a Green, Healthy and Resilient Future with Forests

2–6 May 2022 | Coex, Seoul, Republic of Korea

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

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## Abstract

*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. In this study we aimed to assess growth and physiological acclimation to shade in young of *A. bijuga* plants. 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, and 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) and live crown percentage ( $L_{crown}$ ) compared to the control treatment at full sun. However, light-saturated photosynthetic rate ( $A_{max}$ ), dark respiration rate ( $R_d$ ), and light compensation point ( $G_i$ ) were higher in TRT60 than in the other treatments. No differences were found among treatments for the apparent quantum yield ( $\alpha$ ). 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: Shade tolerance, photosynthesis, light acclimation, forest restoration.

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## Introduction, scope and main objectives

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, which is spatially restricted to 4 ha in the Maule Region of Central Chile (Gómez et al. 2014). Despite that the species has been listed as 'Critically Endangered' by the International Union for Conservation of Nature (IUCN) (Hahn and Gómez 2008; Gómez et al. 2012), it is not currently protected by the Chilean Government. Currently, the habitat of *A. bijuga* is fragmented and immersed in large extensions of *Pinus radiata* D. Don plantations.

Because of its floristic and biogeographical importance, as well as its conservation status, there is an interest in the ecological restoration of *A. bijuga*, but there is still little knowledge about to what extent *P. radiata* plantations might modify the environment and sanitary conditions of *A. bijuga*. The species seems to have a better recruitment performance in open sites, but little is known about its responses to shade when it grows beneath plantation canopies. To our knowledge, there are no studies on *A. bijuga* assessing 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 and 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. We aimed to assess 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.

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## Methodology/approach

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, 150 m. asl). Cuttings were planted in 140 mL pots containing composted bark of *P. radiata* and grown for two growing seasons. After that, 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<sup>MR</sup>, Santiago, Chile).

The study was a completely random design with two shading treatments and a control treatment at full sun. Two 1 m<sup>3</sup> domes differing in light interception were built for each shading treatment using black polyethylene mesh (Raschel<sup>MR</sup>, Santiago, Chile). 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 (c.a., 2,100  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), 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 represented closed-canopy on mature *P. radiata* stands. Light treatments were imposed on November 27, 2018, and maintained until March 7, 2019.

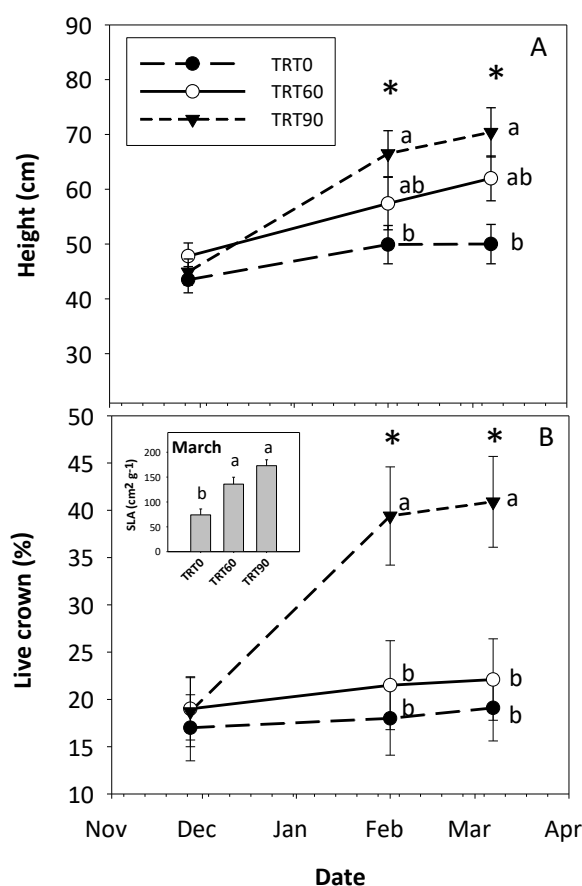
Growth and photosynthetic-light response curves were measured on three dates: Date 1 = a baseline measurement (November 27, 2018), Date 2 = mid-summer (February 1, 2019), and Date 3 = at the end of summer (March 7, 2019). Plant height (H) of the dominant shoot was measured using a metric tape, and increments 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<sub>2</sub> concentration of 400 ppm, a relative humidity of 50%, and PAR of 1,800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . These parameters were kept steady during the measurements and controlled by the LI6800. The light-response curve was obtained in a ten-step reduction process (1,800, 900, 600, 300, 200, 150, 100, 50, 10, 0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). 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 as: Leaf area in the chamber =  $(\pi \times l \times w) / 4 \times n$ , where  $l$  = lamina length,  $w$  = lamina width and  $n$  = number of leaves within the chamber. Similarly, the mean area of the lamina was calculated as  $LA_{\text{lamina}} = (\pi \times l \times w) / 4$ . With the dry weight of foliage, we estimated the Specific Leaf Area (SLA). The maximum photosynthetic rate ( $A_{\text{max}}$ ), dark respiration rate ( $R_d$ ), light compensation point ( $G_i$ ), and apparent quantum yield ( $\alpha$ ) were estimated fitting the non-rectangular hyperbola (Hanson et al. 1987).

All the analyses were made in 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 with the Tukey's adjustment test. Treatment effects were considered significant at an alpha level of 0.05.

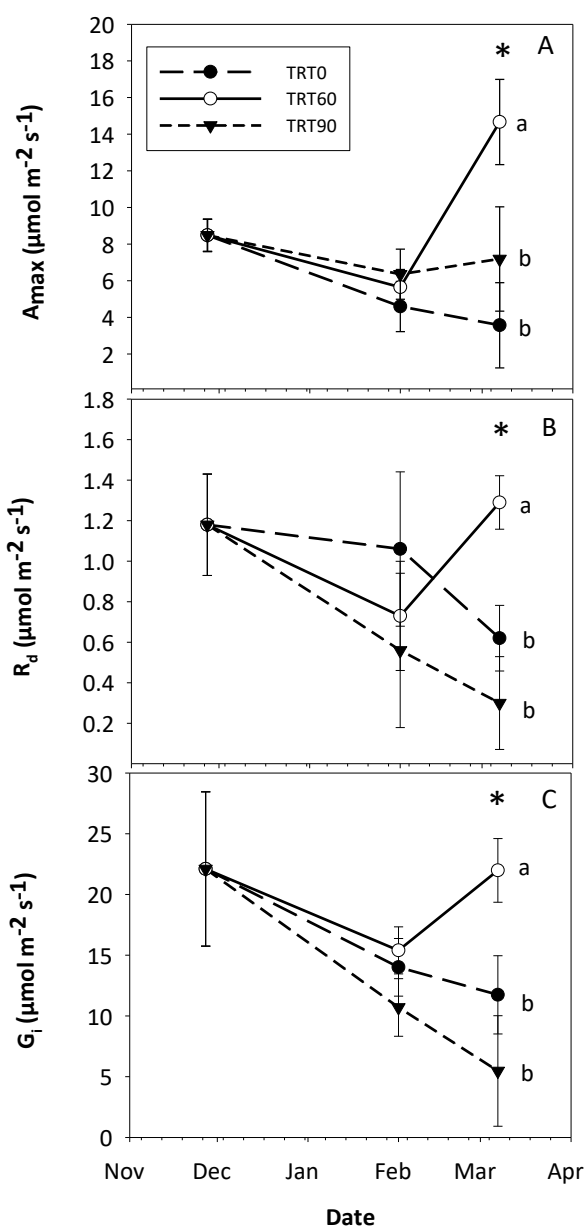
## Results

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. 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 ( $p=0.0016$ ). Differences among treatments for both traits were found since Date 2 (Fig. 1A). 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. 1A). At Date 3, plants at TRT90 had 97% higher  $L_{\text{crown}}$  than plants in the other treatments (Fig. 1B).



**Fig. 1.** Mean ( $\pm$  standard error) values per treatment (TRT0, TRT60, TRT90) and date for H and  $L_{\text{crown}}$  percentage in young *A. bijuga* plants. \* Denotes significant differences among treatments. Different lowercase letters denote 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.

With the exception of  $\alpha$ , 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. The differences among treatments were found only at the end of the experiment, i.e., Date 3 ( $p < 0.05$ ) (Fig. 2).  $A_{max}$ ,  $R_d$ , and  $G_i$  did not differ between TRT0 and TRT90, but these values were significantly lower than those on TRT60. Overall, these photosynthetic parameters tended to decrease with time for TRT0 and TRT90 (Fig. 2) and tended to decline in TRT60 toward Date 2 and then increased toward Date 3. Mean  $\alpha$  for the first, second, and third measurement dates were 0.051, 0.070, and 0.058  $\mu\text{mol CO}_2 \mu\text{mol photon}^{-1}$ , respectively. Overall, stomatal conductance ( $g_s$ ) ranged from 0.007 to 0.28  $\text{mmol m}^{-2} \text{s}^{-1}$ , whereas vapor pressure deficit (VPD) ranged from 1.29 to 1.79 MPa.



**Fig. 2.** Mean ( $\pm$  standard error) values per treatment (TRT0, TRT60, TRT90) and date for maximum photosynthetic rate ( $A_{max}$ ) (A), dark respiration ( $R_d$ ) (B) and light compensation point ( $G_i$ ) (C) in young *A. bijuga* plants. \* Denotes significant differences among treatments. Different lowercase letters denote differences among treatments according to the Tukey's adjustment test.

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## Discussion

We examined growth and leaf-level physiological acclimation of young *A. bijuga* plants to different light treatments. 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). 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, and 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.

At the full sun, *A. bijuga* reduced growth and live crown percentage. The lower  $L_{\text{crown}}$  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  $L_{\text{crown}}$  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. Thus, although the water was kept over 26%, there was likely thermal stress on those plants.

*A. bijuga* plants exhibited high photosynthetic rates up to 15  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the intermediate light level (i.e., TRT60) and 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 ( $A_{\text{max}}$ ), dark respiration ( $R_d$ ), and light compensation point ( $G_i$ ), but lower quantum efficiency relative to shade adapted leaves (Valladares and Niinemets 2008, Martinez and Fridley 2018). These findings partially agreed with our results as a greater physiological performance was obtained at TRT60, in which  $A_{\text{max}}$ ,  $R_d$  and  $G_i$  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 our study, the low values of the photosynthetic parameters obtained in TRT0 might be explained by damages to the plant's photosynthetic machinery. 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.

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## Conclusions/ wider implications of findings

*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.

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## Acknowledgements

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

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