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**Evaluación de los efectos de la fertilización en el desarrollo de rasgos
funcionales que mejoran la tolerancia a la sequía de las plantas
nativas producidas para los programas de restauración**

Tesis para optar al grado de Magíster en Ciencias Forestales

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EVALUACIÓN DE LOS EFECTOS DE LA FERTILIZACIÓN EN EL DESARROLLO DE RASGOS FUNCIONALES QUE MEJORAN LA TOLERANCIA A LA SEQUÍA DE LAS PLANTAS NATIVAS PRODUCIDAS PARA LOS PROGRAMAS DE RESTAURACIÓN.

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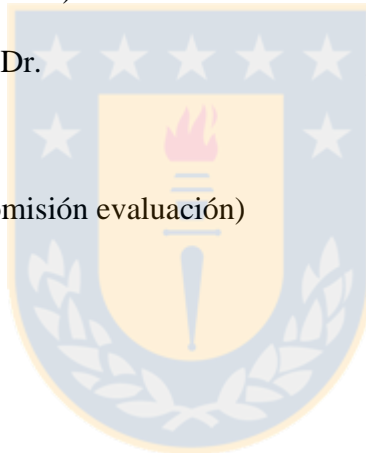
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I. INTRODUCCION GENERAL

Los ecosistemas de tipo mediterráneo albergan una alta proporción de la biodiversidad del planeta, sin embargo, desde tiempos históricos han estado sometidos a constantes amenazas debido a las actividades humanas (Cowling *et al.* 1996, Rundel *et al.* 1998). Particularmente, el ecosistema mediterráneo chileno, es reconocido como un hotspot de biodiversidad (Arroyo *et al.* 1999, Myers *et al.* 2000) debido a la alta diversidad de especies de plantas y animales, donde una fracción importante corresponde a especies endémicas. Los esfuerzos de conservación que se realizan en estas áreas son insuficientes (CONAMA 2007), por lo tanto es necesario llevar a cabo actividades de restauración ecológica para revertir la degradación y recuperar la biodiversidad.

La disponibilidad de agua es un factor que limitante para las plantas en zonas con clima Mediterráneo, especialmente en la fase de establecimiento de sucesos de restauración ecológica efectuados en estas zonas (Rey-Benayas *et al.* 2002; Padilla & Pugnaire 2009; Becerra *et al.* 2011), en donde las tasas de sobrevivencia posterior al primer trasplante en campo suelen ser bajas producto del estrés hídrico al cual son sometidas las plantas (Vilagrosa *et al.* 1997, Maestre *et al.* 2003, Cortina *et al.* 2004, Matías *et al.* 2011). Además, de acuerdo a las proyecciones de cambio climático propuestas para el centro-sur de Chile, en donde se pronostican aumentos en la temperatura e intensificación de los períodos de sequía, se espera que el estrés hídrico al que están sometidas las plantas se intensifique en el futuro (Klausmeyer & Shaw 2009). Por tanto, generar técnicas para la producción de plantas en vivero que tengan como objetivo incrementar la sobrevivencia, aumentando el desempeño de las plantas bajo condiciones de estrés hídrico es crucial para la restauración ecológica de zonas con clima Mediterráneo.

En condiciones naturales, las especies vegetales han desarrollado diversas estrategias para enfrentar condiciones de estrés hídrico (Chaves *et al.* 2002), mediante ajustes en su morfología y fisiología (Wood 2005), aumentando sus posibilidades de sobrevivencia en el campo. Rasgos morfológicos relacionados con la parte aérea (tallos y hojas) y radicular de la planta, parecen ser los responsables de los diferentes niveles de tolerancia al estrés hídrico. Las especies vegetales de ambientes semi-áridos que tienen una estación seca prolongada poseen raíces más largas (Markestijn y Poorter 2009), pues la disponibilidad de agua es mayor en las napas más profundas

del suelo en tiempos de sequía. La habilidad de asignar más biomasa a raíces que a tallos se ha relacionado positivamente a la sobrevivencia de las plantas bajo sequía de verano en zonas con climas Mediterráneos (Lloret *et al.* 1999). Por lo que tener una mayor longitud específica de raíz (SLR), puede ser una ventaja bajo condiciones de baja disponibilidad de agua (Wright & Westoby 1999), ya que maximizar el SRL significará un aumento en la interface de raíz-suelo por unidad de inversión de carbono, y por lo tanto un mayor potencial de absorción de agua por la raíz (Eissenstat 1992), ya que esto mejora la capacidad de la planta para explorar el suelo y adquirir agua. A su vez, plantas que presentan una menor área foliar sobreviven mejor bajo condiciones de sequía, al disminuir la superficie de transpiración de la planta (Leiva y Fernández-Aléz 1998).

Para fomentar rasgos morfo-fisiológicos relacionados con la tolerancia a la sequía podemos utilizar prácticas culturales de vivero como la fertilización (Landis 1985, Vilagrosa *et al.* 2003a, Luis *et al.* 2004, Vilagrosa 2006, Chirino *et al.* 2008), mediante la modificación en las concentraciones de macro y micronutrientes. Se ha documentado que el estado nutricional de la planta afecta directamente sus procesos fisiológicos, tales como la regulación del crecimiento y la síntesis de moléculas orgánicas, lo cual puede mitigar ciertas restricciones impuestas por los recursos más limitantes del suelo para la planta (Chapin *et al.* 1987). Por ejemplo, una modificación en la asignación de biomasa desde el tallo a las raíces es una respuesta bien documentada bajo condiciones de limitación de nutrientes (Poorter & Nagel 2000), generando y/o potenciando rasgos de tolerancia a la sequía de plantas que coexisten bajo estrés hídrico en zonas con clima Mediterráneo aumentando la capacidad de la planta para acceder a los recursos del suelo y mejorar el suministro de agua (Hernández *et al.* 2009).

Dado que aún no existe consenso sobre el conjunto de rasgos funcionales de plantas de zonas con clima Mediterráneo que pudiesen determinar un establecimiento exitoso en ecosistemas cuya limitante es el agua, ni en los protocolos de cultivo de plantas en vivero necesarias para lograr estos rasgos de tolerancia a la sequía (Oliet *et al.* 2013, Cortina *et al.* 2013), resulta de suma importancia para aumentar la sobrevivencia en campo en la fase de establecimiento de sucesos de restauración ecológica, el estudio de los rasgos morfo-funcionales relacionados con la pérdida de agua por las hojas y la maximización de la adquisición de agua por la planta en períodos de estrés hídrico por parte de las raíces (Burghardt & Riederer 2003, Bacelar *et al.* 2007). Plantas de zonas con clima

Mediterráneo cultivadas en vivero con alta disponibilidad de nutrientes han demostrado una mayor sobrevivencia al ser trasplantadas a condiciones de campo (Villar-Salvador *et al.* 2004, Oliet *et al.* 2009), pudiendo mantener su crecimiento, fotosíntesis y conductancia estomática, ya que afecta al crecimiento del tallo y raíz, mejorando la capacidad de enraizamiento post-trasplante, pudiendo aumentar la resistencia al estrés hídrico, estrés por bajas temperaturas y a las enfermedades. Otros estudios muestran resultados opuestos (Hechler *et al.* 1991, Cortina *et al.* 2006), en donde plantas crecidas con baja disponibilidad de nutrientes podrían estar mejor preparadas para resistir el estrés post-trasplante (Burdett 1990, Trubat *et al.* 2008), debido a su pequeño tamaño al final del tratamiento de cultivo en vivero, su reducida área foliar y una elevada asignación de biomasa al sistema radicular, aumentando así la eficiencia del uso del agua por la planta en campo (Forde & Lorenzo 2001). En cuanto a la mayor capacidad de generar raíces producto de la baja disponibilidad de nutrientes durante su crecimiento, ésta aumentaría la posibilidad de colonizar la tierra bajo condiciones de estrés hídrico siendo crucial para garantizar el éxito del trasplante en campo y así asegurar la sobrevivencia de las plantas (Lloret *et al.* 1999, Vilagrosa *et al.* 2003). Es importante considerar que la respuesta de las plantas a la disponibilidad de nutrientes es variable y puede ser especie-específica cuando estas son llevadas a terreno (Rubio *et al.* 2003, Cuesta *et al.* 2010), por lo que debe ser analizada caso a caso.

En Chile, aún existe limitada información acerca de los rasgos funcionales que le permitan a las plantas sobrevivir en zonas mediterráneas durante la fase de establecimiento en campo, además de delimitar hasta qué punto dependen de los rasgos funcionales para tolerar a la sequía y como los protocolos de producción de vivero podrían ser mejorados basándose en el manejo adaptativo de las especies para que sean implementados en programas de restauración de la zona Mediterránea. En consecuencia, resulta necesario comprender el potencial de cada especie y su manipulación para optimizar su establecimiento bajo condiciones de estrés hídrico. En este trabajo estudiaremos como la fertilización de suelo durante la producción en vivero genera cambios intraespecíficos en los rasgos aéreos y radicales de las plantas relacionados con la eficiencia del uso del agua. Nuestra hipótesis apuesta que plantas cultivadas con bajas concentraciones de nutrientes ajustan su morfología, reduciendo el tamaño de las plantas, aumentando la asignación de biomasa hacia las raíces y por lo tanto aumentando la eficiencia del uso del agua.

II. Evaluating the effects of fertilization on the development of functional traits that enhance drought tolerance of seedlings produced for restoration programs

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Resumen

El estrés hídrico es una de las principales causales de fracaso en la restauración ecológica en los ecosistemas mediterráneos. Por lo tanto, promover los rasgos relacionados con la eficiencia del uso del agua de las plantas durante el cultivo en vivero puede contribuir a mejorar el éxito de la restauración. Los rasgos funcionales se pueden modificar mediante la fertilización. Las plantas bien fertilizadas pueden desempeñarse mejor que las plantas limitadas en nutrientes bajo condiciones de sequía. Sin embargo, el efecto de la fertilización depende de la intensidad de la sequía durante la etapa de establecimiento en terreno. Exploramos cómo la fertilización durante la producción en vivero promueve cambios intraespecíficos en los rasgos aéreos y radiculares relacionados con la eficiencia del uso del agua en las plantas. Nuestra hipótesis apunta a que plantas cultivadas con baja fertilización de suelo ajustan su morfología mediante la reducción de la altura de las plantas, el aumento de la asignación de biomasa hacia la raíz y por tanto un aumento de la eficiencia del uso del agua. Se pone a prueba a prueba esta hipótesis midiendo un conjunto de rasgos aéreos y radiculares de las plantas relacionados con la alta eficiencia del uso del agua en cinco especies mediterráneas chilenas cultivadas a lo largo de un gradiente experimental desde fertilización baja a alta del suelo. En segundo lugar, hipotetizamos que los rasgos generados bajo un régimen de baja fertilización mejoran la eficiencia del uso del agua de las plantas en condiciones de sequía moderada. Corroboramos esta hipótesis mediante el seguimiento de las respuestas morfológicas y fisiológicas de las plantas de *Cryptocarya alba* cultivadas bajo regímenes de fertilización baja y alta, sometidas a su vez a una sequía moderada experimental. En las cinco especies nativas

estudiadas, los tratamientos con baja fertilización de suelo durante la fase de cultivo en vivero produjeron cambios intraespecíficos en los rasgos aéreos y radiculares, promoviendo aquellos que aumentan la eficiencia del uso de agua de la planta: reducción biomasa foliar, reducción área foliar, baja S: R y alto SRL. Adicionalmente, en el experimento de sequía, los rasgos generados en las plantas de *Cryptocarya alba* sometidas al tratamiento con fertilización baja en nitrógeno mejoraron la eficiencia del uso del agua bajo condiciones de sequía moderada.

Palabras claves: Ecosistema mediterráneo, nitrógeno, fertilización en vivero, nutrientes, fósforo, calidad de plántula, estrés hídrico.

Abstract

Water stress is a major cause of failure in forest restoration in Mediterranean ecosystems. Thus, promoting traits related to plant water use efficiency during nursery cultivation may contribute to enhance restoration success. Functional traits can be modified by fertilization. Well- fertilized seedlings may perform better than nutrient-limited seedling under drought conditions. However, the effect of fertilization is dependent on the drought intensity during the establishment stage. We explored how soil fertilization drives intra-specific changes in above and belowground traits related to plant water use efficiency. We hypothesize that seedlings grown at low soil fertilization adjust plant morphology by reducing seedling size, increasing below-ground biomass allocation and hence water use efficiency. We tested this hypothesis by measuring a set of above- and below-ground plant traits indicative of high water use efficiency on five Chilean Mediterranean species cultivated along an experimental gradient of low to high soil fertility. Secondly, we hypothesize that traits generated under low fertilization regime improve seedling water use efficiency under moderate drought. We examined this hypothesis by monitoring morphological and physiological responses of *Cryptocarya alba* seedlings grown in low and high fertilization regimes and subjected to moderate experimental drought. In, Low soil fertilization during nursery cultivation of the five native species studied drove intra-specific changes in above and below-ground traits promoting those that enhance plant water use efficiency: low leaf biomass, low leaf area, low S:R and high SRL. Additionally, in the drought experiment, traits generated in *Cryptocarya alba* seedlings in low nitrogen fertilization enhanced water use efficiency under moderate.

Keywords: Mediterranean ecosystem, Nitrogen, nursery fertilization, nutrients, Phosphorous, seedling quality, water stress.

1. Introduction

Plant establishment in Mediterranean ecosystems is severely limited by drought (Lloret, Casanovas, & Peñuelas 1999, Valladares & Sánchez-Gómez, 2006). Climatic predictions suggest that this will become even more problematic in the future (IPCC 2014). Consequently, plant production in nurseries for restoration projects will need to be adapted to increased soil water limitations (Vallejo *et al.*, 2012). Plant traits related to water uptake are of paramount importance for explaining plant persistence in Mediterranean-type ecosystems (Valladares & Sánchez-Gómez, 2006), thus promoting traits related to plant water use efficiency during nursery cultivation can contribute to enhancing species' success in restoration projects (Vallejo *et al.*, 2012).

Plants have developed several drought strategies to cope with drought conditions (Joffre, Rambal, & Damesin 1999). Coexisting species may differ considerably in their tolerance and response to water limitations and ecophysiological traits (Ogaya & Peñuelas, 2003). Several root, stem and leaf traits seem to be responsible for the levels of tolerance to drought. For example, the ability to produce more roots than shoots has been positively related to seedling drought survival (Lloret, Casanovas, & Peñuelas 1999) as it may enhance water uptake. Similarly, seedlings with a high root to shoot ratio (R:S) and a small leaf area performed better under drought (Lopez-Iglesias, Villar, & Poorter 2014). Root depth is also important, as water availability is higher in deeper soil layers. Woody species from drier environments with a longer dry season have deeper roots (Sack, Grubb, & Marañón 2003), and higher maximum root depth per leaf area (Paz, 2003). Besides, a high specific root length (SRL) may be an advantage in water-limiting conditions (Wright & Westoby, 1999), as maximizing SRL means an increased root-soil interface for the same carbon investment, and hence, a higher root absorption potential (Eissenstat, 1992). Considering aboveground traits, a high specific leaf area (SLA) implies a high surface to volume ratio of leaves, and hence high water loss. Similarly, high photosynthetic rates involve high transpiration rates, and consequently, lower drought tolerance (Valladares & Sánchez-Gómez, 2006).

Morpho-physiological functional traits are in part genetically controlled (Van Andel, 1998) but can be modified by cultural practices such as fertilization (Vilagrosa, Cortina, & Gil-Pelegrín 2003). The availability of nutrients triggers changes in functional traits that determine the ability of plants to acquire resources, either above- or below-ground. Plants can adjust biomass allocation to roots or shoots according to whether the most limiting resource is above- or below-ground (Poorter *et al.*, 2012). They make changes, according to the availability of nutrients, to increase uptake of the most limiting resource modifying the morphology and efficiency of their tissues (Hill, Simpson, & Moore 2006). For example, a change in biomass allocation to roots is a well- documented response resulted from nutrient limitation (Poorter & Nagel, 2000), and can enhance the ability of the plant to access soil resources and improve water supply (Hernández *et al.*, 2009). Plants also respond to nutrient limitation by modifying branching patterns and root system architecture, driving intra-specific increases in specific root length (SRL) (Hill, Simpson, & Moore 2006; Ostonen *et al.*, 2007; Trubat, Cortina, & Vilagrosa 2012). Nitrogen and Phosphorous deficiency reduce hydraulic conductance of entire plants (Radin & Matthews, 1989). N is positively related with transpiration because of increase in leaf area, shoot to root ratio, and stomatal conductance. Plants fertilized with high amounts of N would, therefore, increase water consumption in absolute terms (Cortina, Green, & Baddeley 2008). Several studies suggest that well-fertilized seedlings may perform better than nutrient-limited seedlings under drought conditions (Oliet, Puértolas, & Planelles 2013). The effect of the fertilization, however, is dependent on the drought intensity during the establishment stage (Cortina, Vilagrosa, & Trubat 2013).

A proper study of the particular variations in drought resistance traits and the factors involved in their development is of particular interest to forecast the success of restoration programs in Mediterranean areas (Vallejo *et al.*, 2012; Oliet, Puértolas, & Planelles 2013). For example, traits advantageous under high water availability conditions, such as high seedling growth rates, may be disadvantageous under low-water conditions (Lopez-Iglesias, Villar, & Poorter 2014). Such dependencies are predicted based on trait-environment relationships and may have potentially important consequences for restoration success, but have received little testing in a restoration context (Sandel, Corbin, & Krupa 2011; Clark *et al.*, 2012). In Chile, exists scarce information on which are the drought strategies of many Mediterranean species at the seedling stage, to what extent

depend on these strategies for their establishment, how we can strengthen them efficiently through nursery and field techniques, and how these manipulations during nursery production can alter seedling performance under drought (but see Ovalle *et al.*, 2016; Espinoza, Santelices, & Cabrera 2017). These issues are of paramount importance under the actual climate change scenario, where Central Chile since 2010 has suffered an uninterrupted sequence of dry years (so-called mega-drought), with annual rainfall deficits ranging from 25 to 45% (Garreaud *et al.*, 2017). In this study, we explore how soil fertilization during nursery production drives intra-specific changes in above and below-ground traits related to water use efficiency. We hypothesize that seedlings grown at low soil fertilization adjust plant morphology by reducing seedling size, increasing biomass allocation below-ground and hence water use efficiency. We tested this hypothesis by measuring a set of above- and below-ground plant traits indicative of high water use efficiency on five Chilean Mediterranean species cultivated along an experimental gradient of low to high soil fertility. Secondly, we hypothesize that traits generated under low fertilization regime improve seedling water use efficiency under moderate drought. We examined this hypothesis monitoring the morphological and physiological responses of *Cryptocarya alba* seedlings grown in low and high fertilization regimes and subjected to moderate experimental drought.

2. Materials and methods

2.1. Studied species, seedling cultivation, and nursery fertilization

Seedlings of five species were selected for this study (Table 1). These are all common species in the Mediterranean forests and two of them, *Cryptocarya alba* (Mol.) Looser and *Quillaja saponaria* Mol., are widely used in reforestation projects in central Chile (Agurto 2017). The selected species have different functional strategies: *Azara integrifolia* R et. P., *C. alba*, *Luma apiculata* (D.C.) Burret and *Rhaphithamnus spinosus* (Juss.) Moldenke are shade-tolerant and slow growing species characteristic of late successional stages. By contrast, *Q. saponaria* is fast growing shade-intolerant, pioneer species (Donoso, 2013).

Table 1. Characteristics of the five species used in the experimental studies of fertilization (F) and drought (D). Life form: T = tree, S = shrub.

Species	Family	Life form	Seed dispersal	Strategy	Study
<i>Azara integrifolia</i>	Salicaceae	T	Abiotic	Late-sucessional	F
<i>Cryptocarya alba</i>	Lauraceae	T	Biotic	Late-sucessional	F, D
<i>Luma apiculata</i>	Myrtaceae	T	Biotic	Late-sucessional	F
<i>Quillaja saponaria</i>	Rosaceae	T	Abiotic	Pioneer	F
<i>Rhaphithamnus spinosus</i>	Verbenaceae	S	Biotic	Late-sucessional	F

Seeds of the five species were collected from local provenance in the Bío-Bío region (36° 49' S and 72° 43' W) and sown in 140 cc forestry containers in August of 2013 in a nursery located in Constitución (35° 18' S and 72° 23' W). The substrate used was natural pine forest soil. Seedlings were grown in the nursery from August 2013 to June 2014. In January of 2014, seedlings were subjected to four experimental fertilization treatments where nutrient concentrations were varied. A group of plants received a Control solution (hereafter C) corresponding to a modified Hoagland's solution containing 150 mg N L⁻¹ (as CO(NH₂)₂, NaNO₃ and (NH₄)₂SO₄), 80 mg P L⁻¹ (as KH₂PO₄), 100 mg K L⁻¹ (as K₂CO₃ and KH₂PO₄), 80 mg Ca L⁻¹ (as CaCO₃), 40 mg Mg L⁻¹ (as MgSO₄) and 60 mg S L⁻¹ (as (NH₄)₂SO₄ and MgSO₄). Low fertilization treatments were prepared using the same solution for the Control treatment, but without addition of N, P, or NP (low-nitrogen treatment (LN), low-phosphorus treatment (LP), or low-nitrogen-phosphorus treatment, (LNP), respectively). Fertilization was applied every two weeks from January to June of 2014 by saturating the growing media. The fertilizer dose applied to Control seedlings is recommended for forest species and is widely used in forest nurseries (Landis, 1985).

2.2. Effects of fertilization on morphological traits and nitrogen content of the seedlings

At the end of the fertilization phase (June of 2014), the following morphological measures were assessed: biomass accumulation, stem height, main root length, and leaf area. The measurements were performed in 15 randomly selected seedlings per fertilization treatment per species (300 seedlings in total).

Seedlings were separated into leaves, stems, and roots, and dry weight of each of these fractions was determined after drying the samples in an oven (65 °C for 48 hours). Biomass allocation was estimated by calculating the shoot to root ratio (S:R). Root length (R_L , cm) was measured after washing out the substrate from the roots. The projected leaf area of seedlings (LA , cm^2) was obtained with a scanner (EPSON Expression 1680 110 Pro scanner). The images were processed using the software ImageJ. Specific leaf area (SLA , $\text{cm}^2 \text{g}^{-1}$) was calculated by dividing total LA and dry leaf weight, specific root length (SRL , m g^{-1}) by dividing R_L and root dry weight, and root depth per leaf area ($RDLA$, cm cm^{-2}) by dividing R_L and LA .

Due to the small size of the seedlings, it was not possible to make analyses of all the nutrients. Only nitrogen tissue concentration was assessed. N concentration was determined in samples of 0.3 g of dry mass by Kjeldahl analysis in the same seedlings used for the morphological characterization. Analyses were done at the Soil Laboratory of the Faculty of Agronomy of the University of Concepción.

2.3. Effects of fertilization on physiological traits

Gas exchange measurements were carried out at the end of the fertilization phase (June of 2014) in five plants per fertilization treatment per species. Before performing the gas exchange measurements, seedlings were maintained in a growth chamber during five weeks for acclimation. Average maximum and minimum temperatures for the period of measurement were 20 and 11 °C, day and night, respectively. The mean relative humidity was 30 %, the photoperiod of 12 h, and an average daily PPFD of $157 \text{ mol m}^2 \text{ d}^{-1}$. After the acclimation period, gas exchange measurements were performed with a portable gas exchange system (Li-6400; Li-Cor Inc., USA) equipped with a leaf chamber fluorometer (Li-6400-40, Li-Cor INC.). Seedlings were irrigated to field capacity the night before the measurements. Measurements were carried out in fully expanded leaves between 10:00-13:00 h. The net photosynthesis rate (A_N) was measured under light-saturating photosynthetic photon flux density (PPFD) of $1800 \mu\text{mol m}^2 \text{ s}^{-1}$. The CO_2 concentration in the leaf chamber was set to $400 \mu\text{mol CO}_2 \text{ mol}^{-1}$, and air and leaf temperature to 18°C. The parameters estimated in these measurements were: net photosynthetic CO_2 assimilation (A_N), stomatal conductance (g_s) and instantaneous water use efficiency (WUE_i) (as a ratio between A_N and

transpiration). It was not possible to make gas exchange measurements in the seedlings of *C. alba* belonged to the LNP fertilization treatment due to the small size of the seedlings, and stomatal conductances values close to 0 ($\mu\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$).

2.4. Effects of fertilization on physiological traits

We selected one of the species most employed in reforestation projects in central Chile (*C. alba*) and conducted an experimental greenhouse trial to evaluate the effect of fertilization treatments and moderate drought on seedling performance. *C. alba* seedlings were transplanted to 6,30 cm³ PVC pots filled with a natural substrate product of leaf composting. A group of 50 seedlings of *C. alba* per fertilization treatment (C, LN, LP, and LNP) was selected to conduct a drought experiment. Half of the plants were irrigated to field capacity (well-watered treatment), and the other half were irrigated between 20-30% of field capacity (moderate drought treatment) corresponding to -2.5 MPa of soil. The experimental unit and sampling unit were an individual plant. The drought experiment was maintained for four months, from December to March. At the end of the experiment, we measured morphological (N = 15 seedlings per fertilization and drought treatments) and physiological (N = 5 seedlings per fertilization and drought treatments) traits as explained in the previous section.

2.5. Statistical analyses

To assess the effects of fertilization and drought on the morpho-physiological responses of each species we used ANOVA (INFOSTAT software, 2015) for normally distributed variables, and PERMANOVA (PRIMER+ software, Anderson (2001)) for variables did not match the normality assumptions. Separate tests were conducted for each species.

3. Results

3.1. Nitrogen content of the seedlings

Fertilization had a significant effect on seedling nutritional status in three of the five species analyzed (Table 2). *C. alba* showed a reduced seedling N concentration in LN and LNP treatments, with reductions close to 30% in relation to control treatment, and *R. spinosus* seedlings presented a 56% of reduction in the percentage of nitrogen in LN treatments. In contrast, *L. apiculata* showed an increase in seedling N concentration in LP treatment in comparison with control seedlings.

Table 2. Seedling Nitrogen concentration (%N) of five Mediterranean woody species growing in nursery under four fertilization treatments. Data were recorded at the end of the nursery phase in June 2014. Data are means \pm S.E. (N = 5 plants). LP = Low Phosphorus treatment, LN = Low Nitrogen treatment, and LNP = Low Nitrogen and Phosphorus treatment. Results of a posteriori tests of means (following significant main effects) are coded by lower-case letters.

Species	Fertilization treatment			
	Contrl	LP	LN	LNP
<i>Azara integrifolia</i>	0.77 \pm 0.17a	0.83 \pm 0.13a	0.93 \pm 0.07a	---
<i>Cryptocarya alba</i>	0.85 \pm 0.02a	0.79 \pm 0.02a	0.60 \pm 0.02b	0.64 \pm 0.01b
<i>Luma apiculata</i>	0.72 \pm 0.04a	0.92 \pm 0.07b	0.72 \pm 0.06a	0.60 \pm 0.04a
<i>Quillaja saponaria</i>	1.04 \pm 0.05a	1.01 \pm 0.05a	0.74 \pm 0.09a	1.14 \pm 0.35a
<i>Rhaphithamnus spinosus</i>	1.61 \pm 0.10a	1.58 \pm 0.18ab	0.70 \pm 0.00b	---

Fertilization had a significant effect on all morphological variables measured (Table 3). Leaf biomass showed a significant decrease in the five species studied mainly due to reductions in LN and LNP treatments. Reductions in leaf biomass ranged from 59% to 81%, in *R. spinosus* and *L. apiculata*, respectively. Stem biomass showed a similar trend, with significant decreases in four of the five species. These reductions in stem biomass ranged from 76 to 86% in *C. alba* and *L. apiculata*, respectively. Root biomass was significantly reduced in four of the five species. Reductions in this trait ranged from 32 to 82% in *C. alba* and *L. apiculata*, respectively. Total biomass showed a significant decrease in four of the five species studied. Decreases in total biomass ranged from 63 to 76% in *C. alba* and *Q. saponaria*, respectively. Shoot to root ratio was significantly increased in one of the species and decreased in four of the species studied. *L.*

apiculata increased the S:R ratio between 104% and 154% in LP and LN treatments, respectively. While decreases in S:R ranged from 45 to 68% in *A. integrifolia* and *Q. saponaria*, respectively. SLA had a significant decrease in four of the five species in the treatments of LP, LN and LNP. Reductions in SLA ranged from 22 to 59% in *C. alba* and *L. apiculata*, respectively. While one of the species (*A. integrifolia*), presented an increase in SLA in low fertilization treatments ranging from 27 and 106% in LNP and LP treatments, respectively. SRL increased significantly in three of the five species. Increments in SRL ranged from 180 to 389 % in *A. integrifolia* and *L. apiculata*, respectively. Root depth per leaf area showed a significant increase in the five species. All the species incremented RDLA in LP, LN and LNP treatments. Increases in RDLA ranged from 260 to 533% in *C. alba* and *Q. saponaria*, respectively.



Table 3. Morphological traits of seedlings of five Mediterranean woody species growing in a nursery under four fertilization doses. Data recorded at the end of the nursery phase in June 2014. Data are means \pm S.E. (N = 15 plants). Results of a posteriori tests of means (following significant main effects) are coded by lower-case letters. Codes for the fertilization treatments as indicated in Table 2. SRL = Specific Root Length, SLA = Specific Leaf Area, RDLA = Rooting Depth per Leaf Area.

	Leaf biomass (g)	Stem biomass (g)	Root biomass (g)	Total biomass (g)	Shoot to root (g g ⁻¹)	SLA (cm ² g ⁻¹)	SRL (m g ⁻¹)	RDLA (cm cm ⁻²)
<i>Azara integrifolia</i>								
C	0.39 \pm 0.04a	0.36 \pm 0.03a	0.71 \pm 0.05a	2.20 \pm 0.15a	1.07 \pm 0.08a	144.71 \pm 7.21a	18.95 \pm 1.58a	0.25 \pm 0.03a
LP	0.25 \pm 0.04b	0.22 \pm 0.03bc	0.51 \pm 0.07b	1.45 \pm 0.16a	1.02 \pm 0.08a	298.00 \pm 56.69b	34.39 \pm 6.65b	0.50 \pm 0.13b
LN	0.10 \pm 0.02bc	0.10 \pm 0.02b	0.34 \pm 0.06c	0.73 \pm 0.14b	0.61 \pm 0.06b	252.44 \pm 49.15b	53.02 \pm 13.53b	1.09 \pm 0.19c
LNP	0.09 \pm 0.01bc	0.07 \pm 0.01bc	0.30 \pm 0.05c	0.62 \pm 0.09b	0.59 \pm 0.07b	184.32 \pm 30.60ab	48.95 \pm 7.81b	1.33 \pm 0.16c
<i>Cryptocarya alba</i>								
C	0.81 \pm 0.10a	0.45 \pm 0.06a	0.79 \pm 0.09a	3.30 \pm 0.40a	1.57 \pm 0.09a	98.70 \pm 5.60a	18.05 \pm 1.92a	0.20 \pm 0.03a
LP	0.47 \pm 0.07b	0.21 \pm 0.03b	0.57 \pm 0.08ab	1.95 \pm 0.27b	1.22 \pm 0.03b	90.79 \pm 7.48ab	28.50 \pm 4.56a	0.45 \pm 0.10b
LN	0.29 \pm 0.03bc	0.14 \pm 0.02bc	0.61 \pm 0.06ab	1.46 \pm 0.15bc	0.71 \pm 0.04bc	77.38 \pm 2.74b	23.89 \pm 2.22a	0.67 \pm 0.07b
LNP	0.23 \pm 0.03c	0.11 \pm 0.02bc	0.54 \pm 0.07b	1.22 \pm 0.15c	0.66 \pm 0.05bc	82.81 \pm 4.44b	26.83 \pm 4.08a	0.72 \pm 0.09b
<i>Luma apiculata</i>								
C	0.74 \pm 0.14a	0.87 \pm 0.11a	0.91 \pm 0.13a	2.60 \pm 0.35a	1.57 \pm 0.25a	86.80 \pm 3.44a	13.52 \pm 3.91a	0.23 \pm 0.07a
LP	0.70 \pm 0.09a	0.36 \pm 0.07b	0.40 \pm 0.06b	1.36 \pm 0.16b	3.20 \pm 0.37b	63.73 \pm 3.97b	33.42 \pm 3.93b	0.29 \pm 0.03a
LN	0.43 \pm 0.05ab	0.12 \pm 0.02c	0.16 \pm 0.04bc	0.71 \pm 0.10c	3.98 \pm 1.00b	35.59 \pm 6.70c	66.15 \pm 10.24c	0.93 \pm 0.30b
LNP	0.14 \pm 0.04b	0.13 \pm 0.03c	0.41 \pm 0.07bd	0.68 \pm 0.13c	0.63 \pm 0.06bc	91.10 \pm 18.03a	38.32 \pm 9.20bc	1.03 \pm 0.17b
<i>Quillaja saponaria</i>								
C	0.84 \pm 0.04a	0.45 \pm 0.03a	0.59 \pm 0.04a	1.88 \pm 0.09a	0.59 \pm 0.04a	94.48 \pm 4.80a	24.45 \pm 1.52a	0.18 \pm 0.01a
LP	0.60 \pm 0.05b	0.33 \pm 0.02b	0.49 \pm 0.03b	1.41 \pm 0.09a	0.49 \pm 0.03b	88.54 \pm 4.70ab	31.79 \pm 2.36b	0.29 \pm 0.04b
LN	0.18 \pm 0.03bc	0.09 \pm 0.01bc	0.19 \pm 0.03bc	0.46 \pm 0.07b	0.19 \pm 0.03bc	77.04 \pm 5.0bc	86.65 \pm 15.98bc	1.40 \pm 0.27bc
LNP	0.20 \pm 0.03bd	0.09 \pm 0.01bd	0.21 \pm 0.03bd	0.51 \pm 0.07b	0.21 \pm 0.03bd	73.12 \pm 4.19c	76.02 \pm 10.03bd	1.14 \pm 0.14bd
<i>Rhaphithamnus spinosus</i>								
C	0.22 \pm 0.03a	0.18 \pm 0.02a	0.18 \pm 0.02a	0.57 \pm 0.06a	2.52 \pm 0.35a	241.57 \pm 13.88a	72.50 \pm 10.98a	0.28 \pm 0.05a
LP	0.14 \pm 0.02b	0.13 \pm 0.03a	0.15 \pm 0.03a	0.50 \pm 0.10a	2.02 \pm 0.17a	232.80 \pm 14.09a	112.54 \pm 20.84a	0.42 \pm 0.06b
LN	0.12 \pm 0.02b	0.13 \pm 0.02a	0.28 \pm 0.05a	0.53 \pm 0.08a	1.02 \pm 0.13b	123.69 \pm 5.23b	69.15 \pm 23.62a	0.76 \pm 0.10c
LNP	0.09 \pm 0.02b	0.09 \pm 0.02a	0.23 \pm 0.04a	0.40 \pm 0.07a	0.82 \pm 0.06b	143.94 \pm 17.67b	72.01 \pm 12.63a	1.23 \pm 0.15c

3.2. Physiological traits responses to fertilization treatments

Net photosynthetic CO₂ assimilation rate (A_N) was significantly reduced mainly in the low fertilization treatments in all the species studied (Table 4). Reductions of A_N ranged from 51% to 95% in *L. apiculata* and *C. alba*, respectively. Stomatal conductance was only decreased in *L. apiculata*, presenting a 40% of reduction in the LNP treatment. Finally, the five species studied had a significant decrease in WUE_i with reductions ranging from 60 up to 83% in *L. apiculata* and *R. spinosus*, respectively (Table 4).

Table 4. Physiological traits of seedlings of five Mediterranean woody species growing in nursery under different fertilization treatments. Data recorded at the end of the nursery phase in June 2014. Data are means ± S.E. (N = 5 plants). Results of a posteriori tests of means (following significant main effects) are coded by lower-case letters. Codes for the fertilization treatments as indicated in Table 2. A_N = Net photosynthetic CO₂ assimilation, g_s = Stomatal conductance, WUE_i = Instantaneous Water Use Efficiency (as a ratio between A_N and transpiration).

Physiological traits under different fertilization treatments			
	A _N (μmol CO ₂ m ⁻² s ⁻¹)	g _s (μmol H ₂ O m ⁻² s ⁻¹)	WUE _i
<i>Azara integrifolia</i>			
C	3.53±0.43a	0.09±0.01a	4.48±0.46a
LP	2.66±0.22b	0.10±0.02a	2.65±0.25b
LN	2.25±0.29b	0.09±0.01a	2.43±0.45b
LNP	1.30±0.05c	0.10±0.02a	1.19±0.05c
<i>Cryptocarya alba</i>			
C	5.12±0.16 a	0.09±0.00a	7.21±0.26a
LP	3.55±0.15b	0.09±0.00a	4.51±0.20b
LN	2.95±0.28b	0.09±0.01a	2.91±0.18c
LNP	-	-	-
<i>Luma apiculata</i>			
C	3.51±0.18a	0.10±0.01a	5.24±0.21a
LP	3.51±0.15a	0.09±0.01a	4.82±0.31a
LN	2.19±0.15b	0.09±0.01a	1.98±0.18b
LNP	1.73±0.04c	0.06±0.00b	1.48±0.10c
<i>Quillaja saponaria</i>			
C	7.22±0.18a	0.12±0.01a	8.52±0.31a
LP	6.12±0.16b	0.11±0.01a	6.22±0.29b
LN	3.06±0.15c	0.10±0.00a	2.40±0.17c
LNP	2.84±0.20c	0.11±0.01a	2.13±0.12c
<i>Rhaphithamnus spinosus</i>			

C	7.30±0.25a	0.12±0.01a	9.69±0.47a
LP	6.12±0.20ab	0.10±0.01a	7.13±0.45b
LN	4.00±0.12bc	0.09±0.00a	3.71±0.11c
LNP	3.07±0.14c	0.09±0.01a	1.67±0.08d

3.3. Morphological and physiological traits responses to fertilization and drought treatments in *C. alba* seedlings

There was a significant interaction between fertilization and drought treatments in one of the three morphological variables analyzed (Table 5). Leaf biomass showed reductions in drought in comparison with well-watered treatment ranging from 37% up to 46% in Control and LN treatments. On the other hand, SRL and root biomass did not show a significant interaction between factors. Seedlings under low fertilization treatments showed reductions in root biomass, whereas SRL was increased. Root biomass decreased and SRL increased under moderate drought (Table 5).

Table 5. Morphological traits of *Cryptocarya alba* seedlings grown under four fertilization treatments and two levels of water stress. Data are means ± S.E. (N = 15 plants). Results of a posteriori tests of means are coded by lower-case letters. Codes for the fertilization treatments as indicated in Table 2. SRL = Specific Root Length.

c	Fertilization treatment	Leaf biomass (g)	Root biomass (g)	SRL (cm ² g ⁻¹)
Well-watered	C	1.36±0.12a	2.55±0.20a	7.26±0.59a
	LP	1.04±0.17ab	2.35±0.35ac	8.80±1.25ab
	LN	0.70±0.09bd	1.25±0.12bde	15.72±2.65cd
	LNP	0.36±0.03c	0.92±0.07e	16.95±1.97cd
Moderate-drought	C	0.82±0.10b	1.73±0.15abc	9.07±0.85ab
	LP	0.62±0.09bcd	1.54±0.18bcd	14.39±2.20bc
	LN	0.38±0.04c	0.85±0.09e	22.28±2.23d
	LNP	0.46±0.08cd	1.05±0.15ed	18.66±3.49cd

Three of the four photosynthetic performance variables analyzed showed a significant interaction between drought stress and fertilization treatments (Fig. 1). A_N was 55 and 79% lower in drought than in well-watered plants only in C and LP fertilization treatments (Fig. 1a), while seedlings in LN treatment and under drought maintained its photosynthesis rates in comparison to well-watered and well-nurtured seedlings. On the other hand, g_s only showed an effect of drought in LN fertilization treatment, increasing in 312% in drought than in well-watered plants (Fig. 1b, c). In contrast to the increments observed in g_s

under drought, transpiration rate under drought was lower than in well-watered treatments (Fig. 2). Finally, WUEi only showed an effect of drought in LN fertilization treatment, increasing in 111% in drought than in well-watered plants.



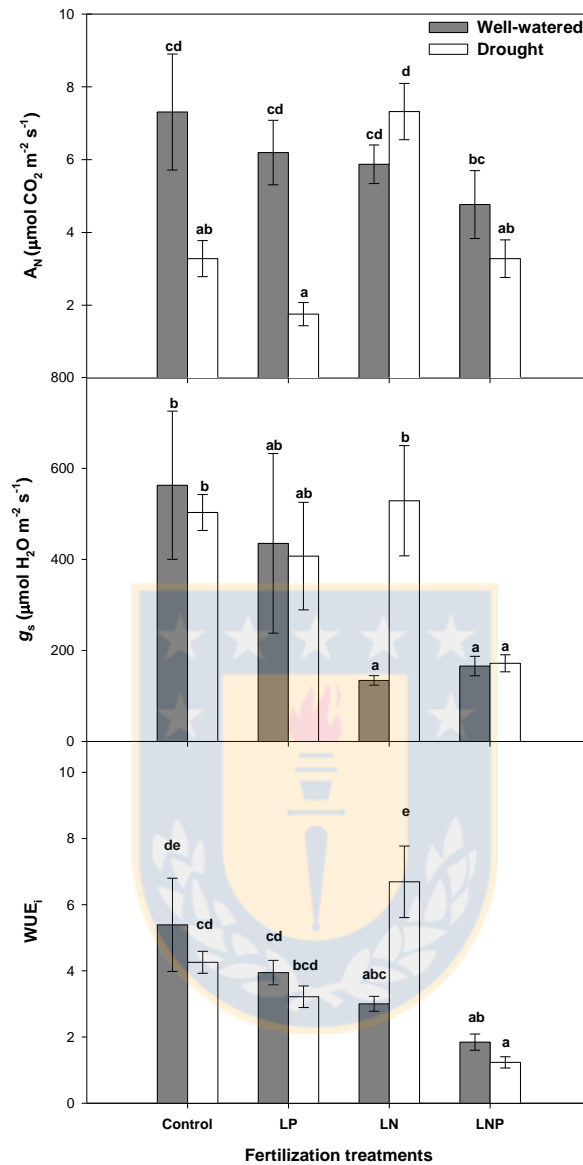


Figure 1. Effect of fertilization and drought on gas exchange parameters of *Cryptocarya alba* seedlings. (a) Net photosynthetic CO₂ assimilation rate (A_N), (b) stomatal conductance (g_s) and (c) instantaneous water use efficiency (WUE_i). Values are means \pm S.E. (n = 5). Different letters indicate statistically significant differences between fertilization and water stress treatments according to Fisher test ($P < 0.05$). Codes for the fertilization treatments as indicated in Table 2.

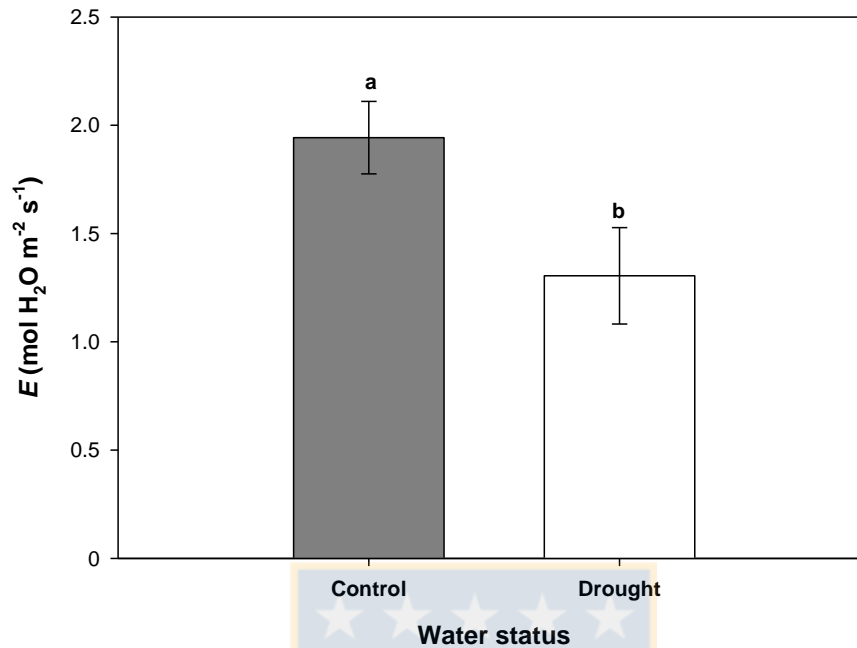


Figure 2. Transpiration rate (E) of well-watered and drought-stressed *C. alba* seedlings during the experimental period. Values are means \pm S.E. (n = 5). Different letters indicate statistically significant differences between fertilization and water stress treatments according to Fisher test ($P < 0.05$).

4. Discussion

Our hypotheses about an association between low soil fertilization and the promotion of traits related to plant water use efficiency and its subsequent effects on seedling performance under moderate drought were fully supported. Our findings illustrate that low soil fertilization during nursery cultivation drove intra-specific changes in above and below-ground traits promoting those that enhance plant water use efficiency in the five native species studied. Additionally, in an experimental greenhouse trail, we found that traits generated in *Cryptocarya alba* seedlings in low nitrogen fertilization enhanced physiological performance, improving water use efficiency under moderate drought.

4.1. Are fertilization treatments driving morpho-physiological traits related with drought tolerance?

Although there is no consensus about the set of traits that can determine a successful establishment in arid or semi-arid ecosystems (Cortina, Vilagrosa, & Trubat 2013, Oliet, Puértolas, & Planelles 2013), several experiences using different doses of fertilization in the nursery have shown that the growth and survival in the field is increased when the amount of nutrients is higher (Puértolas *et al.* 2003; Villar-Salvador *et al.* 2004; Oliet *et al.* 2009). However, plants fertilized with high amounts of nitrogen would increase water consumption in absolute terms (Cortina *et al.* 2008). For this reason, in climates with severe water limitations, a reduction of fertilization during culture period may be beneficial because it produces less development of the aerial part of the plant (Cortina *et al.* 2006; Trubat *et al.* 2011, Ovalle *et al.* 2016), resulting in a reduction of water consumption. Our study supports the idea that low fertilization (mainly low N fertilization) promotes morphological traits related to drought tolerance, increasing those favoring water use efficiency in seedlings. In general, we observed that all the species studied reduced the leaves biomass and area when were subjected low-N and low-P fertilization (Table 3). This response could be due to anatomical changes such as increased cell wall thickness, reduced cell diameter and increased tissue density (Corcuera *et al.* 2002). The change in this leaf trait is one of the factors resulting in lower water loss (Gratani & Bombelli 2001). Furthermore, while root biomass did not augment in low fertilization treatments, the S:R decreased, and root depth per leaf area and the specific root length increased. The observed values of S:R and RDLA were because the reduction of the aerial biomass was more pronounced in the treatments with low fertilization than the increase observed in the root biomass in these same treatments (Table 3). Plants adjust their morphology to an imbalance of resources through the allocation of new biomass to the organs that are involved in acquiring the scarcest resources (Poorter *et al.* 2012). This change in biomass allocation to roots is a widely documented response to nutrient limitation (Poorter & Nagel 2000) and would allow plants to access soil resources, be they water or nutrients (Hernández *et al.* 2009). Low nitrogen and phosphorus concentration in seedlings could result in higher levels of carbon allocated to the root and a decrease in root to shoot biomass ratio (Vance *et al.* 2003; Sánchez-Calderón *et al.* 2006, Ovalle *et al.* 2016).

Similar to other studies, we found a high SRL for all the species in the low fertilization treatments (Trubat, Cortina, & Vilagrosa 2012, Ovalle *et al.* 2016). High SRL can be the result of having a small diameter or a low density of tissue (Wright & Westoby 1999). In our case, in all the species studied, root

length remained constant among treatments while root biomass decreased in low fertilization treatments. Thus, seedlings in low nutrient treatments produced a lower density of roots or thinner roots. Thin roots with high SRL offer less resistance to the radial flow of water, thus increasing radial conductivity (Huang & Eissenstat 2000). Also, plants with high SRL tend to show a high capacity for soil exploration with high specific hydraulic conductance per leaf unit surface area (Pemán *et al.* 2006) or per stem cross-section area (Hernández *et al.* 2010). Consequently, plants with high SRL (considering either the whole root system or only fine roots) show high uptake rates of water (Eissenstat 1991), nitrogen (Reich *et al.* 1998) and phosphorus (Comas *et al.* 2002). These patterns suggest that plant hydraulic capacity is determined by the root system morphology (Hernández *et al.* 2010).

Low fertilization treatments drove intra-specific changes in above, and below-ground traits in the five species studied that could favor the response of plants to drought (e.g., Trubat, Cortina, & Vilagrosa 2012, Cortina, Vilagrosa, & Trubat 2013, Ovalle *et al.* 2016). However, these changes in morphology were not immediately reflected in the water economy of the plants. Measurements of WUE_i done at the end of the fertilization experiment, and in seedlings maintained in a growth chamber in well-watered conditions, were consistently lower in all the species studied and all the low fertilization treatments (Table 4). The low values of WUE_i observed in the low fertilization treatments were due to the low values of A_N in these treatments. Low values of A_N in low fertilization treatments cannot be explained by a reduction on stomatal conductance, because g_s was similar among all fertilization treatments in all the species studied (Table 4). Low values of A_N could be because nutrients such as P and N are fundamental for the photosynthetic machinery and processes (Field & Mooney 1986; Conroy *et al.* 1986). The low P causes a reduction of carbon assimilation through reduced thylakoidal (Conroy *et al.* 1986) and stromal processes (Sivak & Walker 1986). Besides, during photosynthetic carbon assimilation, P is required for the production of ATP from ADP, for the production and export of triose-P and for ribulose-1,5-bisphosphate (RuBP) regeneration (Geiger & Sersvaites 1994). Therefore, P availability has a direct impact on plant function and productivity (Epstein and Bloom 2005). At the same time, Nitrogen limitation is associated with decreased enzyme activities that are required for energy metabolism such as photosynthesis and respiration (de Groot *et al.* 2003), because the majority of foliar N is integral to the proteins of the photosynthetic machinery, especially ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) (Field & Mooney 1986).

4.2. Effects of fertilization treatments on drought tolerance of *Cryptocarya alba* seedlings

Through the evaluation of the combined effect of fertilization and drought, we found that the seedlings that were growing under low soil fertilization, mainly those in low-N, presented morpho-physiological traits that could promote high drought tolerance. Specifically, *C. alba* maintained high rates of carbon assimilation (similar to the well-watered and well nurtured seedlings), and low rates of transpiration, which consequently increased the WUE_i only in the LN treatment under moderate drought. Responses in our study are in agreement with Ovalle *et al.* (2016). They found that seedlings grown without fertilization and under drought maintained the photochemical efficiency in comparison to well-watered plants, whereas fertilized seedlings suffered a drastic decrease in F_v/F_m values under water stress, supporting the idea that small seedling phenotypes exhibit better resistance to an extended drought. As was discussed before, the physiological responses observed under drought were probably related with the morphological traits that were promoted by low fertilization during cultivation in the nursery: low leaf biomass, low leaf area, low S:R and high SRL (Table 3,5). Furthermore, we also found that seedlings held under moderate drought and well nurtured (Control treatment of fertilization) showed a pronounced decline in carbon assimilation (55%). Donoso *et al.* (2011) also found a decrease in carbon assimilation in seedlings of *C. alba* under drought conditions. However, low values of photosynthesis observed in that study were related to low values of stomatal conductance whereas in our study stomatal conductance was similar between treatments. The low photosynthesis observed under drought in our study may be due to an increase in the restrictions imposed by the mesophyll or by biochemical limitation. *C. alba* plants under optimal growth conditions present mesophyll conductance limitations, probably mediated by leaf anatomical traits (Brito *et al.* 2014). It has also been shown that plants which are grown under drought increase mesophyll resistance (Flexas *et al.* 2014). There could also be a biochemical limitation that explains the decrease in photosynthesis (Flexas *et al.* 2014).

Although in our study we did not evaluate field seedling survival, it is important to consider that the morphological traits that were promoted through the use of low doses of fertilization can affect seedling survival under drought conditions. In Andalusia, Spain species with high SRL and high RDLA used soil water in a conservative way (low transpiration rate) and had higher survival under drought (Lopez-Iglesias *et al.*, 2014). Similarly, survival of seedlings during the summer dry season in a Mediterranean community was related to the ability of the species to produce root rather than shoots and leaves (Lloret, Casanovas, & Peñuelas, 1999).

4.3. Implications for restoration of communities in drought-prone environments

Water stress is a major cause of failure in forest restoration projects in Mediterranean ecosystems (Alloza and Vallejo 1999). Functional traits and trait-based community ecology theory can provide a basis for predicting the success of a restoration treatment in a particular community (Sandel, Corbin, & Krupa 2011; Clark *et al.* 2012, Cortina *et al.* 2006), helping to ensure that treatments are only applied where they will be most beneficial. Our results show that promoting the development of traits that increase tolerance to drought through low doses of fertilization (low concentrations of nutrients) during the growth in the nursery may improve the resistance of plants to water stress. Consequently, the consideration of functional traits during cultivation of seedlings may contribute to enhancing species' success when restoring communities in climates with severe water limitations. For dryland reforestation, a relevant nursery decision is the downward adjustment of fertilization doses to obtain seedlings better conditioned to anticipate field moisture stress (Ovalle *et al.* 2016).

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III. CONCLUSIONES GENERALES

En relación a las variables morfológicas, la mayoría de las especies respondieron al tratamiento de baja concentración de nitrógeno, generando una mayor longitud específica de raíz, una baja relación biomasa aérea: biomasa radicular y una disminución del área foliar por unidad de masa bajo riego a capacidad de campo.

Los tratamientos con bajas concentraciones de nutrientes mostraron una disminución en su conductancia estomática y en la EUA cuando son crecidas con riego a capacidad de campo. Los tratamientos con una baja concentración de nutrientes promueven rasgos morfológicos que podrían ser beneficiosos para sobrevivir condiciones de estrés hídrico en campo, pero no promueven rasgos fisiológicos que mejoren la EUA.

Los tratamientos bajos en concentraciones de N y P mostraron una alta eficiencia en el uso del agua para *Cryptocarya alba* bajo condiciones de estrés hídrico moderado, lo cual podría explicarse principalmente por la mayor asignación de recursos a la producción de raíces y la reducción en el tamaño del área foliar.

La aplicación de bajas concentraciones de N y P, durante la fase de crecimiento en vivero podría ser una buena estrategia para la producción de plantas que puedan tolerar condiciones de estrés hídrico en terreno.

La selección de los tratamientos de fertilización para mejorar el desempeño de las plantas en condiciones de sequía debe ser especie-específica.

