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EFECTO DEL RÉGIMEN DE TRANSMISIVIDAD DE LA RADIACIÓN SOLAR Y AMBIENTES DE LUZ CONTRASTANTES EN LA DENSIDAD Y CRECIMIENTO DE LA REGENERACIÓN NATURAL Y ARTIFICIAL EN UN BOSQUE SOBREMADURO DE *Nothofagus dombeyi* (Mirb.) Oerst., EN LA ZONA PRE-CORDILLERANA DE LA REGIÓN DEL BIOBÍO.

Tesis para optar al grado de Doctor en Ciencias Forestales

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DEDICATORIA

“El conocimiento es el eslabón, hacia una sociedad más justa”

Pamela Encina Astudillo

A mi compañero de vidas Rodrigo (Negro).
Por estas dos décadas caminando a mí lado.
En el goce, la alegría y el disgusto.
Gracias por tu amor infinito y soñar junto a mí,
*que lo imposible se puede lograr***.**

A mis hijos Agustín y Simón
Por entregarme sus destellos de plata
e iluminar Cada día de mi vida.

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y su cariño que aun permanece latente.
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RESUMEN GENERAL

La regeneración de *Nothofagus dombeyi* creciendo bajo bosques sobremaduros, en la cordillera de los Andes chilenos, plantea la existencia de una divergencia interespecíficas en relación a la superviencia, el crecimiento y desarrollo de sus renovales, creciendo bajo diferentes regímenes de luminosidad, posterior al disturbio de gran escala. Este estudio plantea la hipótesis, que los patrones de la regeneración de *Nothofagus dombeyi*, dependen del régimen de luz ocasionado por disturbios de pequeña escala, así como la localización de biomasa y variables de intercambio gaseoso, son respuestas a niveles intermedios o bajos de luz, para lo cual se hace necesario aplicar sistemas silvícolas para mantener los atributos del bosque y establecer plantaciones suplementarias con especies capaces de sobrevivir, y desarrollarse en ambientes bajo dosel. Se analizó el régimen de transmisividad de la radiación solar y el efecto del régimen de luz en el crecimiento en diámetro y altura de las plantas que componen la regeneración avanzada de *N. dombeyi*, así también los efectos de la disponibilidad de transmisividad en la distribución de biomasa y en las variables de intercambio de gases; además del comportamiento al establecimiento de tres especies: *Nothofagus nervosa*, *Laurelia philipiana y Podocarpus saligna*, en respuesta a tres condiciones de transmisividad de radiación solar, en un bosque sobre-maduro de *N. dombeyi*. La transmisividad de la radiación solar varió entre 3% a 40%. La densidad de la regeneración natural varió entre 0 y 14 plantas m^{-2}. El incremento radial absoluto (ARG) varió entre 1,20 y 2,22 mm año^{-1} y el incremento en altura (AHG) entre 0,15 y 0,43 mm^{-1}, ARG y AHG mostró una correlación con la transmisividad de la radiación solar directa y global, pero no con la difusa. Estas variables, junto a la edad de la planta, permitieron explicar los patrones de la regeneración natural y crecimiento de *N. dombeyi*. La asignación de biomasa de todos los componentes de *N. dombeyi* mostró una correlación positiva con la edad y se establecieron diferencias significativas en hojas y tallos con respecto a la biomasa total, con una asignación de la hoja al tallo de un 4.1% en luminosidad y una disminución de 5,9% en media sombra; asimismo se detectaron diferencias significativas en los rasgos morfológicos de la longitud de la raíz, número y tamaño de hojas, al comparar la condición de luminosidad con la media sombra. No se observó plasticidad en la asignación de biomasa, pero se detectó plasticidad morfológica. Entre las variables morfológicas y las variables de intercambio de gases no se encontró una correlación significativa. En condiciones de alta luminosidad, el rendimiento fotosintético de *N. dombeyi* mejoró, pero el incremento medio anual MAI en altura (H) se vio limitado por el punto de saturación de luz (LSP). *N. dombeyi* satura la fotosíntesis y aumenta significativamente la eficiencia del uso del agua para mantener el rendimiento fotosintético. El establecimiento de especies nativas, presentó altas tasas de supervivencia y no presentaron diferencias significativas entre ellas. *N. Nervosa* y *L. sempervirens* presentaron mayores incrementos en el diámetro a la altura de cuello (Dac), que *P.saligna* en condiciones de alta transmisividad difusa, el incremento en H fue mayor en *N. Nervosa*. Los incrementos en Dac disminuyeron y no presentaron diferencias significativas entre las tres especies. Por lo tanto, este estudio postula que la dinámica de la regeneración avanzada de *N. dombeyi* responde a pequeños disturbios, y con ello se sugiere la necesidad de establecer un manejo silvícola usando el método de selección en grupo o individuo, con un establecimiento de especies mixtas, con la finalidad de rejuvenecer los bosques sobre-maduros y mantener su equilibrio.

ABSTRACT

The regeneration of *Nothofagus dombeyi* growing under over-ripe forests, in the Chilean Andes, raises the existence of an interspecific divergence in relation to the survival, growth and development of its renewals, growing under different light regimes, following the disturbance of big scale. This study proposes the hypothesis that the regeneration patterns of *Nothofagus dombeyi*, depend on the light regime caused by small-scale disturbances, as well as the location of biomass and gas exchange variables, are responses to intermediate or low levels of light, for which it is necessary to apply silvicultural systems to maintain the attributes of the forest and establish supplementary plantations with species capable of surviving and developing in environments under canopy. The transmissivity regime of the solar radiation and the effect of the light regime on the growth in diameter and height of the plants that make up the advanced regeneration of *N. dombeyi* were analyzed, as well as the effects of the availability of transmissivity in the distribution of biomass and in the gas exchange variables; besides the behavior to the establishment of three species *Nothofagus nervosa*, *Laurelia philipiana* and *Podocarpus saligna* in response to three conditions of transmissivity of solar radiation, in an over-mature forest of *N. dombeyi*. The transmissivity of solar radiation varied between 3 to 40%. The density of natural regeneration varied between 0 and 14 m-2 plants. The absolute radial increase (ARG) varied between 1.20 and 2.22 mm year-1 and the increase in height (AHG) between 0.15 and 0.43 mm-1, ARG and AHG showed a correlation with the transmissivity of direct and global solar radiation, but not with the diffuse, these variables together with the age of the plant, allowed to explain, the patterns of natural regeneration growth of *N. dombeyi*. The biomass allocation of all the components of *N. dombeyi* showed a positive correlation with age and significant differences were established in leaves and stems with respect to the total biomass, with an allocation of the leaf to the stem of 4.1% in luminosity and a decrease of 5.9% in half shade; Likewise, significant differences were detected in the morphological features of the root length, number and size of leaves, when comparing the luminosity condition with the shade half. No plasticity was observed in the biomass allocation, but morphological plasticity was detected. Among the morphological variables and the gas exchange variables, no significant correlation was found. Under high light conditions, the photosynthetic performance of *N. dombeyi* improved, but the average annual MAI increase in height (H) was limited by the light saturation point (LSP). N. dombeyi saturates photosynthesis and significantly increases the efficiency of water use to maintain photosynthetic performance. The establishment of native species, showed high survival rates and did not present significant differences between them, *N. Nervosa* and *L. sempervirens* showed greater increases in diameter at neck height (Dac) than *P. saligna* under conditions of high diffuse transmissivity , the increase in H was greater in N. Nervosa. The increases in Dac decreased and did not present significant differences between the three species. Therefore, this study postulates that the dynamics of the advanced regeneration of N. dombeyi responds to small disturbances, it is suggested the need to establish a silvicultural management using the selection method in group or individual, with an establishment of mixed species, with the purpose of rejuvenating over-mature forests and maintaining their balance.

CAPÍTULO I

INTRODUCCIÓN GENERAL

1.1 Características de los bosques sobremaduros

Los bosques sobremaduros, son regenerados de forma natural, con bajo impacto humano, y dominados por árboles que están cerca de su vida útil biológica, o árboles que han sustituido a la cohorte post-perturbación inicial (Shoorohova et al., 2011). Estos se identifican por ser multietaneos, con presencia de árboles de grandes diámetros, compuestos por especies tolerantes, semitolerantes e intolerantes a la sombra, con árboles muertos en pie, escombros leñosos y con presencia de plantas epifitas e indicadoras (Scott, 2009). De acuerdo a lo anterior, se establece que los bosques sobremaduros se caracterizan en su fase inicial porque en su dinámica de regeneración predomina una cohorte en particular; sin embargo, cuando se presentan perturbaciones parciales pero recurrentes, se estimulan los procesos de mortalidad de árboles favoreciendo la regeneración, lo que conduce a una estructura de edad multimodal en una segunda fase (Shoorohova et al., 2011).

1.2 Dinámica de la regeneración natural en bosques sobremaduros.

Los investigadores han reconocido históricamente la importancia de las perturbaciones naturales en el desarrollo y mantención de la estructura, funciones de los bosques y dinámica de la comunidad de plantas (Attiwill, 1994). Estas perturbaciones al eliminar la vegetación original, dejan espacios abiertos a nivel de rodal, dando origen a los claros (Parhizkar et al., 2011), interviniendo en la regeneración y el desarrollo natural de un bosque, puesto que afectan severamente las condiciones del rodal, alterando la dinámica del microclima y la redistribución de los recursos del sitio. (Lowman y Rinker, 2004) Una de las consecuencias más evidentes de la formación de claros en el sitio forestal, es la del incremento temporal en la disponibilidad de luz (Canham et al., 1990), recurso que varía a nivel de rodal, más que cualquier otro utilizado por las plantas (Martens et al., 2000). Entre los factores más importantes que explican la variación espacial en los niveles de luz en el dosel, se encuentran: la geometría de copas, el tamaño y distribución de árboles vecinos, y la limpidez de la atmósfera (Canham et al.,, 1999). A su vez, la luz es altamente variable en el tiempo, después de la formación de los claros del dosel (Hu y Zhu, 2008). Los cambios temporales y espaciales de la luz, pueden ser esenciales en la supervivencia y crecimiento de las plantas (Kneeshaw y Bergeron, 1998; Mountford et al., 2006). Por lo tanto, la oferta de luz es un factor clave que afecta la dinámica y sucesión de las comunidades de plantas y el espectro de especies en los ecosistemas forestales.

1.3 Caracteristicas morfológicas y fisiológicas de la regeneración avanzada en bosques sobremaduros

Las especies de manera natural tienden a adaptarse a condiciones ambientales cambiantes mediante ajustes en su morfología y fisiología (Wood, 2005; Hernández et al., 2010). En diversos tipos de bosques sobremaduros, las plántulas y árboles jóvenes sobreviven y crecen lentamente durante mucho tiempo bajo el dosel sombreado, lo que origina una regeneración avanzada (Messier, 1999). La falta de luz en el bosque tiene un impacto significativo en la regeneración avanzada, ya que se ha observado una reducción tanto de la tasa de crecimiento como de supervivencia en diversas especies (Pearcy, 2007; Jarčuška, 2009). Por ello, es necesario comprender la ecología de la regeneración avanzada que crece en el bosque sombreado, ya que las plantas para enfrentar la oferta limitada de luz, adaptan sus rasgos en todos los niveles de la organización biológica, tanto a nivel de hoja como de la planta completa (Valladares y Niinemets, 2008).

Los rasgos más característicos que adecúan las plantas a la disminución de la disponibilidad de luz son de carácter: morfológico, anatómico y bioquímico los que se conocen como respuestas adaptativas funcionales fisiológicas (Watt, 1925). A nivel de hoja los rasgos morfológicos más comunes a la adaptabilidad a la sombra son: el aumento del área foliar específica, el área foliar total, la proporción de área foliar (área foliar dividido por la masa seca de toda la planta), la densidad de estomas y las proporciones de clorofila α y β, para que las hojas puedan estar mejor adaptadas a la dinámica del ambiente de luz en el dosel (Valladares et al., 2002). Los plantas que crecen bajo el dosel presentan rasgos morfológicos que responden a la sombra mediante el aumento de sus incrementos laterales de ramas a nivel de la copa, a expensas de incrementos de altura (Stanciou y O'Hara, 2006). Por ende, la luz es el recurso definitorio de adaptación a la sombra y un factor crítico que afecta los rasgos del árbol (Lieffers et al., 1999). Además las plantas están expuestas a un conjunto de condiciones ambientales, como: el movimiento del aire, temperatura, el nivel de CO_2, humedad y nutrientes del suelo (Messier et al, 1999).

Existe una vasta investigación sobre la base fisiológica de adaptación de las plantas a ambientes con altos niveles y bajos niveles de luz; sin embargo, los resultados han sido contradictorios y las conclusiones también han sido diversas (Lusk, 2002). Ello se explica por las diferencias reales entre especies de bosques caducifolios y las especies latifoliadas, (Walters y Reich, 1999) y por cambios ontogénicos en los rasgos de plantas (Poorter, 1998).

Las explicaciones tradicionales se han basado en la teoría del balance de carbono que desarrollan las plantas en respuesta a la luz (Givnish, 1988). Otra explicación, es la relación entre la capacidad fotosintética y las tasas de respiración oscura (Sims y Pearcy, 1991) y la variación interespecífica en los patrones de localización de carbono, los que pueden ser igual o más importantes, que las características de intercambio de gases (Kobe, 1997).

Diversos estudios comparativos han demostrado que las plántulas de las especies demandantes de luz maximizan el potencial de crecimiento mediante el desarrollo de una alta área foliar específica y una alta área foliar total (Kitajima, 1994), para comprometer rápidamente recursos para un nuevo crecimiento, con baja localización de carbohidratos destinados para el almacenamiento y defensa de tejidos (Kobe, 1997). Sin embargo, la alta supervivencia de plántulas en especies en sombra, se ha relacionado con patrones de localización de carbono conservadores, en que se sacrifica el potencial de crecimiento para potenciar rasgos que favorecen la supervivencia (Walters y Reich, 1999). El riesgo de daños por patógenos, herbívoros y estrés físico se reduce por la producción de tejidos más densos, durables y defensivos (Kitajima, 1994) y la recuperación de tales daños es facilitada por la fuerte localización de carbohidratos para el almacenamiento (Kobe, 1997). Al respecto, Lusk (2002) analizando 12 especies chilenas de alta y baja tolerancia a la sombra del bosque templado lluvioso, encontró que las tasas de crecimiento relativo en biomasa aérea en condiciones de altos niveles de luz, presentaron una fuerte correlación con la capacidad fotosintética y que las bajas tasas de mortalidad en condiciones de bajos niveles de luz, tuvieron una fuerte correlación positiva con el punto de compensación de luz y la capacidad fotosintética. De esta forma, se ha concluido la ventaja de supervivencia que presentan especies a condiciones de poca luz, pero presentan desventajas en las tasas de crecimiento, y que las plántulas de especies que requieren luz, crecen más rápido que las especies asociadas tolerantes a la sombra (Walters y Reich, 1999). Por consiguiente, la supervivencia y crecimiento en condiciones de alta o baja disponibilidad de luz, puede atribuirse a diversos factores: la condición de especie tolerante o intolerante a la sombra, transmisividad de la radiación solar a través del dosel, balance de carbono, localización de biomasa, y variables ecofisiológicas como el punto de compensación de luz y capacidad fotosintética.

1.4 Dinámica regenerativa de *N. dombeyi*

En la cordillera de los Andes chilenos, se ha formulado la hipótesis que en los bosques dominados por *N. dombeyi*, su regeneración es enteramente dependiente de la frecuencia de perturbaciones de gran escala: como deslizamientos de tierra desencadenados por sismos, depósitos de inundación, o caídas masivas de árboles por efectos del viento (Veblen et al.,, 1997). Además, en ausencia de tales perturbaciones, especies tolerantes como: *Laurelia sempervirens* (Laurel), y Drymis winteris (Canelo), podrían sustituir a *N. dombeyi*, en la precordillerana de la región del Biobío (Veblen, 1980). Sin embargo, Lusk (2001) ha reportado que en rodales puros, cuando no está presente o dispersos bambúes del género *Chusquea*, los pequeños claros favorecen la regeneración de *N. dombeyi*. Estas perturbaciones de pequeña escala afectan la distribución de la transmisividad de la radiación solar en el interior del bosque y los patrones de regeneración en bosques sobremaduros (Promis et al., 2009). Al respecto, estudios experimentales y ecofisiológicos sugieren la existencia de divergencias interespecíficas con relación a la supervivencia, el crecimiento y desarrollo de renovales de *N. dombeyi* creciendo bajo diferentes regímenes de luminosidad posterior al disturbio (Weinberger y Ramírez, 2001). De esta forma, el aumento del diámetro y el incremento en altura de árboles provenientes de la sucesión de especies intolerantes a la sombra, solo alcanzarán estratos superiores del dosel y competir exitosamente con especies de sombra, si aumenta la disponibilidad de luz (Messier et al., 1999).

La variable autoecológica más relevante de *N. dombeyi* es ser una especie intolerante, logrando su mejor desarrollo en condiciones de mayor luminosidad, por lo que posee un amplio rango de tolerancia a la sombra, creciendo a mayor altura, prefiriendo suelos húmedos y formando bosques puros y en algunas situaciones, asociado a otras especies (Donoso et al, 1991). La propuesta de una menor tolerancia a la sombra en *N. dombeyi*, también es explicada por Lusk and Del Pozo 2002, debido a que las especies intolerantes maximizan su crecimiento inicial bajo altas condiciones de luminosidad, ya que hacen un rápido uso de los recursos energéticos en función del crecimiento. De acuerdo a lo anterior, Dezotti (2008) establece que *N. dombeyi*, no aplica el modelo tradicional de localización de recursos, donde los árboles destinan una fracción más alta en la biomasa aérea, que en biomasa bajo el suelo (Waring, 1998); debido a que sus renovales, acumulan menos biomasa aérea que especies como: *N. alpina y N. obliqua* y que la fracción de biomasa foliar, es equivalente en condiciones de alta y baja luminosidad. Aunque *N. dombeyi* es considerablemente menos tolerante a la sombra que *N. alpina y N. obliqua*, esta especie localiza la mayor cantidad de carbohidratos a las hojas, siguiendo un comportamiento fenotípico (Dezotti, 2008). En general, las especies intolerantes tienden a destinar los recursos adquiridos al nuevo crecimiento, asignando pocos carbohidratos a tejidos de almacenamiento, pues en los ambientes de alta luminosidad, la reposición de tejido perdido, es fácilmente recuperable a partir de altas tasas fotosintéticas (Piper et al., 2007).

Lusk and Del Pozo 2002, demostraron que plántulas de *N. dombeyi* presentan una mayor tasa de mortalidad cuando son sometidas a condiciones de crecimiento de baja luminosidad en condiciones de un experimento controlado. De acuerdo a lo anterior, es necesario considerar el factor lumínico en el análisis de las distribución espacial de *N. dombeyi*, lo que refleja la adaptación diferencial a gradientes de disponibilidad de luz (Piper et al., 2007). En general, los estudios de respuesta de la regeneración a distintos regímenes de luz y condiciones de limpidez de la atmósfera, se han desarrollado principalmente en bosques boreales (Canham et al., 1990; Kneeshaw y Bergeron, 1998; Promis et al., 2009). Sin embargo, la respuesta de la regeneración avanzada al régimen de transmisividad de la radiación solar en bosques sobremaduros de *N. dombeyi*, creciendo en climas templados-mediterráneos, ha sido escasamente estudiada.

1.5 Establecimientos de especies nativas bajo un bosque sobremaduro

Desde el punto de vista del establecimiento de plantaciones con especies nativas, diversos estudios han demostrado que existe un rango de intensidad de luz en el cual sobrevive y se desarrolla mejor una determinada especie, dando como resultado diferentes comportamientos en el patrón de crecimiento de las especies en su etapa de planta o en la adultez (Weinberger y Ramírez, 2001). Por otra parte, la radiación excesiva que reciben las especies plantadas en amplios ambientes lumínicos, como es el caso a campo abierto, puede provocar el cierre de estomas como método de autodefensa de la planta, lo que provoca condiciones fisiológicamente inestables para que estas especies puedan sobrevivir (Weinberger y Ramírez, 2001). Por ello, el establecimiento de plantaciones bajo el dosel de un bosque sobremaduro, podría ser una gran oportunidad para su preservación. Experiencias de estudios de plantaciones realizados a 500 m.s.n.m en un bosque degradado, reportaron buenas tasas de crecimiento, con resultados alrededor de un 100% de supervivencia en especies de *Nothofagus*, como *N. dombeyi* y *N. alpina*, en contraste con una experiencia a campo abierto a la misma altitud, donde casi el 100% de plantación murió por heladas de invierno-primavera y sequías de verano (Soto y Rios, 2009). Otras experiencias de plantaciones con especies nativas, han demostrado que la protección superior o lateral tiene un mejor desarrollo que plantaciones a campo abierto en altitudes > 600 m.s.n.m (Álvarez y Lara, 2008).

Las características de adaptabilidad ambiental de las especies, juega un rol fundamental en el establecimiento de una plantación, por ejemplo: estudios de plantaciones mixtas realizados en la precordillera de la costa de Valdivia, han comprobado que *N. dombeyi* presenta una alta capacidad de adaptación ambiental, a condiciones de sitio desfavorables, permitiendo una mayor supervivencia de esta especie (Soto y Rios, 2009), lo que no ocurre con *N. alpina*, especie en que el crecimiento, se ve restringido por su menor adaptación a condiciones desfavorables de sitio, pero a la vez muy sensible a estímulos nutritivos y a la mejora estructural del suelo (Ríos, 2008). Estas especies nativas del género *Nothofagus*, son las que concitan mayor interés junto con *N. obliqua*, principalmente por sus tasas de crecimiento y el valor de su madera (Donoso et al., 2009). Es importante señalar que las plantaciones mixtas, además de mejorar los indicadores económicos, mejoran la producción potencial del sitio, ya que hacen un uso más eficiente de los recursos (luz, agua, nutrientes) (Donoso et al., 2009). Sin embargo, en Chile no se han desarrollado investigaciones focalizadas en diseños, mezclas de especies y manejo cultural (Donoso et al., 2009).

Las plantaciones bajo protección o en claros de dosel, se están presentando como una gran oportunidad en todos los ecosistemas forestales del centro-sur (Donoso et al., 2009); por ello, es necesario profundizar en estudios tales como: la intensidad lumínica en el desarrollo de plantaciones y el efecto en el desarrollo, lo cual podrá permitir rejuvenecer los bosques sobremaduros en Chile. Debido a la importancia de estos bosques, altamente sensibles para la comunidad, existe una preocupación permanente acerca de su manejo, por lo que se hace necesario un enfoque silvicultural extremadamente cuidadoso en el manejo de estos bosques, que permitan guiar artificialmente la regeneración de bosques sobremaduros de *N. dombeyi*. Por consiguiente, resulta adecuado formular técnicas silvícolas en bosques sobremaduros de *N. dombeyi*, resolviendo los principales factores que explican el manejo de la luz en la supervivencia y crecimiento tanto en la regeneración natural avanzada, como en la utilización de especies para la regeneración artificial.

1.6 HIPOTESIS

Los patrones de regeneración natural en densidad, crecimiento y su desarrollo dependen tanto del régimen de luz ocasionado por pequeños disturbios, así como de la localización de biomasa y variables de intercambio gaseoso, en respuesta a niveles intermedios o bajos de luz. Puesto que para *N. dombeyi* en niveles muy bajos de luz no existe regeneración natural, es necesario desarrollar plantaciones suplementarias, con especies que sean capaces de sobrevivir y desarrollarse en ambientes bajo dosel.

1.7 OBJETIVOS

1.7.1 Objetivo General

Analizar el efecto del régimen de transmisividad de la radiación solar y de la luz en la regeneración natural y artificial en bosques sobremaduros de *N. dombeyi*, en la zona pre-cordillerana de la región del Biobío que permitan formular una técnica de manejo silvícola de esta especie.

1.7.2 Objetivos especificos

- Analizar el efecto de la transmisividad de la radiación solar, en los patrones de regeneración y crecimiento en diámetro y altura de plantas que componen la regeneración avanzada.
- Analizar los efectos de dos ambientes contrastantes de transmisividad de la radiacion solar en la distribución de biomasa y variables morfológicas, en plantas de regeneración natural avanzada.
- Analizar los efectos de dos ambientes contrastantes de luz en varariables morfológicas y variables de intercambio gaseoso, en plantas de regeneración natural avanzada.
- Determinar el comportamiento al establecimiento de tres especies nativas de características intolerantes, tolerantes y semi-tolerantes en respuesta a tres rangos de transmisividad e intercambio gaseoso en dos ambientes contrastante de luz, en un bosque sobre maduro de *N. dombey*i.

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CAPÍTULO II

EFFECTS OF SOLAR RADIATION ON REGENERATION PATTERNS IN A *Nothofagus dombeyi* (Mirb.) Oerst. OLD-GROWTHFOREST IN CHILE'S CENTRAL-SOUTHERN ANDES.

Encina, P., Rodríguez, R., Muller-Using, B., Annighöfer, P., Ríos-Leal, D., Sáez-Carrillo, K., & Sánchez-Olate, M. "Effects of solar radiation on regeneration patterns in a Nothofagus dombeyi (Mirb.) Oerst. old-growthforest in Chile's central-southern Andes". *Gayana Botanica.* Aceptado. 26-09-2018

ABSTRACT

Nothofagus species behave like early successional species that recolonize open sites after of regular and large-scale disturbances. However, has been hypothesized that regeneration is controlled by small-scale disturbances, been necessary the application of a silvivultural systems to maintain old-growth forest attributes. This study analyzed the effects of light regimes on patterns of advanced regeneration dynamics, growth in diameter and height of Nothofagus dombeyi (Mirb.) Oerst. Systematic sampling every 50 m in three stands (7.5 ha) was used. At each point and with the same center, two concentric circular plots of 9.0 m and 1.8 m radius were established. For estimate solar radiation transmissivity in the plots, a solariscope hemispheric photographic camera was used. Diameters at breast height and heights (H) were measured. Then, seedlings and saplings of N. dombeyi were counted and measured. 13 saplings of advanced regeneration were harvested from all gaps to obtain age (E), total height (TH), absolute radial growth (ARG), and absolute height growth (AHG). As results, solar radiation varied between 3 and 40%. ARG varied between 1.20 and 2.22 mm yr-1 and AHG between 0.15 and 0.43 m yr-1. We found correlation for ARG and AHG with direct and global solar radiation transmissivity, but not with diffuse solar radiation transmissivity. The plant age and transmittance of direct and global solar radiation explains the increases in diameter and height. Therefore, transmissivity of solar radiation explain natural regeneration patterns and growth of N. dombeyi.

Keywords: Solar radiation transmissivity, advanced regeneration, disturbance.

2.1 INTRODUCTION

Silviculturalist have recognised the importance of natural disturbances in the development and maintenance of forest structures, functions and community dynamics (Attiwill, 1994). Small-scale disturbances eliminate original vegetation, leaving open spaces in stands which represent canopy gaps (Parhizkar *et al.*, 2011) and facilitate resources such as light, nutrients and water (Valladares & Niinemets, 2008). The temporary increase in light availability below the first canopy layer (Canham *et al.*, 1990) varies at stand level more than for any other plant resource (Martens *et al.*, 2000). The most important factors that explain this spatial variation in understory light levels are canopy shape, size, and distribution of neighbouring trees and local sky brightness distribution (Canham *et al.*, 1999). Light is highly variable in time and space (Valladares & Guzmán, 2006), as conditions change drastically over time and canopy gaps, essential for plant growth and survival, form (Canham *et al.*, 1990; Hu & Zhu 2008; Kneeshaw & Bergeron, 1998; Mountford *et al.*, 2006). Therefore, light is a key factor affecting dynamics and succession of plant communities and the spectrum of species in forest ecosystems.

In central-southern Chile, *Nothofagus* species behave like early successional species that recolonize open sites after prior vegetation removal due to regular and large-scale disturbances such as landslides, material deposits from massive flooding or trees knocked down by strong winds (Veblen *et al.*, 1997). Without subsequent disturbances, later successional species tend to settle under the canopy, replacing shade-intolerant species such as *N. dombeyi (Mirb.) Oerst*., which is key to regeneration after large-scale disturbances (Veblen *et al.*, 1996). Every old-growth forest has certain characteristics, species, processes and interactions that rarely - or not at all - appearing younger forests. Old-growth forests belong to the natural diversity of life on Earth. It depends on our effort to conserve biological diversity from the scale of genes to ecosystems; it is important that we conserve old-growth in its natural spatial pattern, i.e., large, continuous expanses (Lapin, 2005).

Nothofagus species have limited opportunities to recruit even in large canopy gaps (> 1,000 m^2) due to the release of advance regeneration of shade-tolerant trees and the vigorous proliferation of *Chusquea spp*. bamboos (Veblen *et al.*, 1997). Tree-fall gaps are larger and logs more abundant in old-growth *Nothofagus spp.* dominated stands (Schlegel & Donoso, 2008), and these conditions can help *Nothofagus spp.* tree recruitment. *N. dombeyi* and *N. nervosa* can reach over 2 m in diameter at breast height (dbh) and above 50 m in height; both species can grow 10 to 30 m above the main canopy (Donoso & Lusk, 2007; González *et al.*, 2015). However, old-growth *Nothofagus* stands growing in the Andean region of south-central Chile are more affected by small-scale disturbances from *Chusquea culeou* (Desvaux.) bamboo thickets which suppress the regeneration of tree species and develop after canopy gaps formed. Depending on the abundance of *C. culeou* thickets, a biphasic pattern of positive feedback on the dynamics of regeneration of these forests has been suggested. In it, the first regeneration phase of *C. culeou* can give rise to a second phase of *N. dombeyi* regeneration (Lusk, 2001). Winds and snow storms also remove overstory-trees individually or in smaller groups, resulting in small to medium-size canopy gaps that create a favourable environment for more shade-intolerant species. These species maximise their initial growth under higher light conditions, especially when *C. culeou* thickets (an aggressive colonizer) is absent since inhibit regeneration of tree species (Lusk 2001; Lusk & Del Pozo, 2002). But can grow under different light regimes after episodes of bamboo dieback that provide the main opportunities for reestablishment of tall forest (Lusk 2001). Therefore, management of the stand light regime through silvicultural techniques is required to ensure better regeneration of this species (Sola *et al.*, 2016). In our study, *N. dombeyi* in an old-growth forest stand could reach more than 2 m in dbh and above 50 m in height. Tree-falls of this size can create gaps larger than 700 m^2. Canopy gaps formation has been largely recognised as an important process with indifferent forest ecosystems. However, studies on temperate forests of the southern hemisphere are still lacking compared to tropical forests and northern hemisphere temperate forests (González *et al.*, 2015).

We hypothesise that the regeneration is the response to small-scale disturbance, therefore the high spatial variability of all solar radiation transmissivity components inside the forest varies due to the different degrees of canopy openings, which alter light regimes in pure old-growth *N. dombeyi* stands, explaining natural regeneration patterns and growth. Thus, the study objectives are to analyse light regimes in patterns of regeneration dynamics and the effect these light regimes have on diameter and height growth of plants that compose stands of advanced regeneration.

2.2 MATERIALS AND METHODS

2.2.1 Study area

The study took place in three *N. dombeyi* old-growth forest stands near Yungay city, Bio Bio Region in central Chile (Density of 240 trees ha^{-1}, basal area of 56.7 m^2 ha^{-1}). (Figure 2.1). All stands belong to *N. dombeyi* and *Saxegothea conspicua* (Lindl.) bioclimatic area called Andean Mediterranean temperate evergreen forests (Luebert & Pliscoff, 2006).

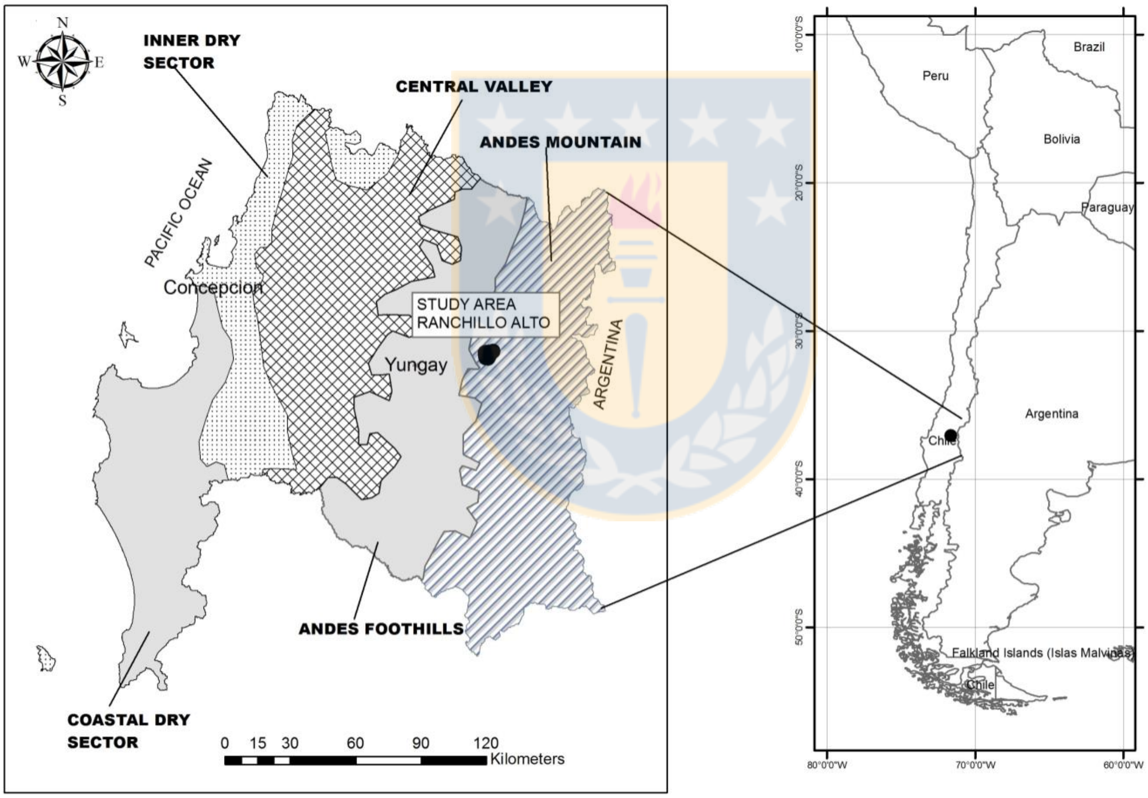

Figure 2.1. Location map of the study area in the Andes Mountains in the Biobío Region, Chile.

The stands are characterised by evergreen forest arboreal layers dominated by *N. dombeyi*, *S. conspicua*, *Podocarpus nubigenus* (Lindl.), *Laureliopsis philippiana* (Looser) Schodde, and occasionally *Weinmannia trichosperma* (Ruiz & Pav.) species in the intermediate layers. However, in a state of old-growth, light conditions below the first canopy layer do often inhibit development of intermediate arboreal strata. The most characteristic geomorphological position of such a forest is in western mid-slopes of the Andes Mountains (Luebert & Pliscoff, 2006). The climate is Mediterranean, with rainfall concentrated during winter and a dry summer lasting three to four months. Study area altitudes (600-1,500 m a.s.l.) correspond to an area with temperate Mediterranean climate as classified by Emberger (Del Pozo & Del Canto, 1999). Average annual rainfall exceeds 1,400 mm, and ice and snowfall can cause disturbances in the native forest, while growing season lasts around three months due to low winter temperatures (Del Pozo & Del Canto, 1999).

Soils originate from volcanic ash, most likely post glacial, resting on a non-related substrate comprising fluvial or glacio-fluvial materials that remain detected due to the depth at which they occur (Kühne *et al.*, 2005). Soil is deep and medium-textured, generally silty loam within the first meter and silty clay loam at depths of 165 cm or more (Kühne *et al.,* 2005).

2.2.2 Seedling and plant density measurements

Field work was carried out in 2015 during Chile's growing season from January to February. To measure density of saplings (lignified) and seedlings (non-lignified), systematic sampling was carried out in three old-growth *N. dombeyi* stands with a total area of 7.5 ha, a 240 trees ha^{-1}density, a basal area of 56.7 m^{2} ha^{-1} and 13 gaps of forest with an area between 45 and 300 m^{2}. The starting position for the systematic grid was determined randomly. With this information and a map of the study site, lines were drawn with a distance of 50 m in a parallel and perpendicular direction, giving rise to a network of 64 points for the three stands; at each point, two concentric circular plots with an only center of radius 9.0 m (large plot) and 1.8 m (regeneration plot) were established (Figure 2.2).

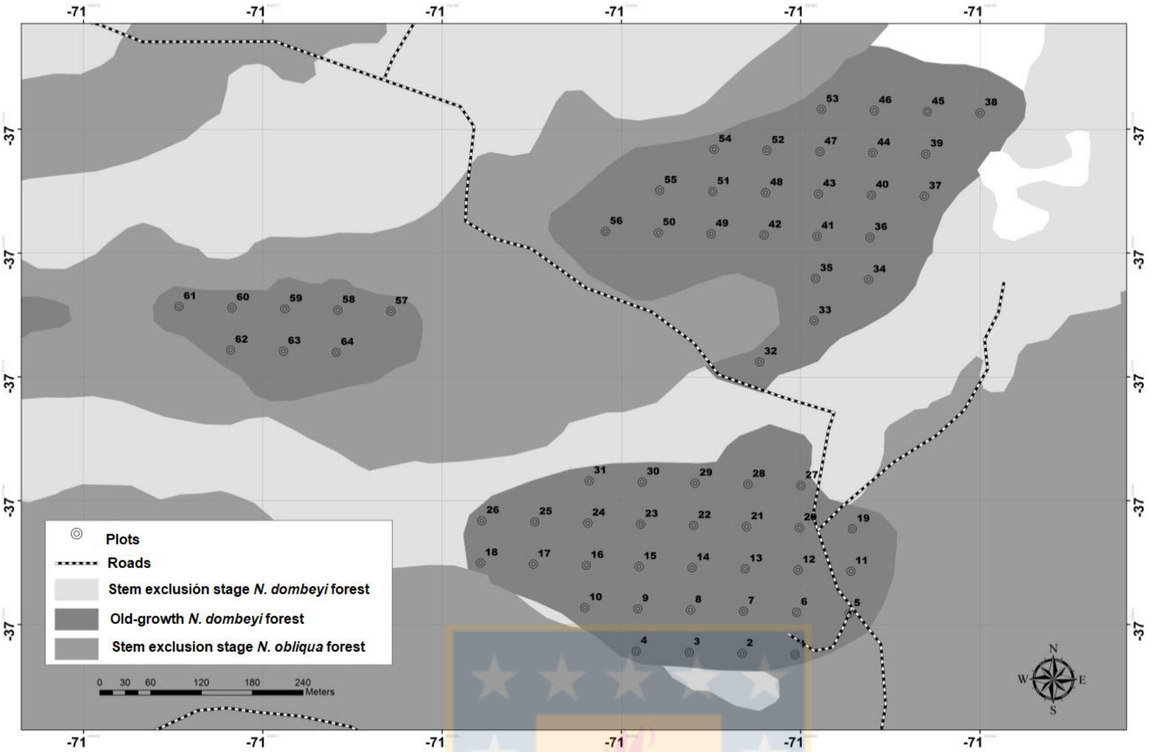

Figure 2.2. Map of the experimental design in the Andes Mountain, Biobío Region, Chile. Numbers refer to plots; at each point, two concentric circular plots of radius of 9.0 m and 1.8 m (regeneration plot) were established, with a total of 64 points.

Within each large plot, adult tree diameter at breast height (dbh) was measured with a caliper and diametric tape in order to derive diameter distributions, basal areas (BA), and analyse their relationship with the occurring regeneration of *N. dombeyi*. In the regeneration plots, the saplings were height measured and counted along with all germinated and non-lignified seedlings of *N. dombeyi*.

Tree seedlings and saplings of *N. dombeyi* were counted and classified as: germinant and non-lignified < 0.05 m, and lignified > 0.051, 0.051 < 0.5, 0.5 < 1, 1 < 1.5, 1.5 < 2, and ≥ 2 m of height. In addition, from each of the 13 plots the highest individual was harvested (i.e. between 3 and 5 meters high).On each individual a first cut was made to ground level and every 1.0 m until the apex. Each disk was divided in four quadrants, and then the distance from the medulla to each ring was measured using a standing digital meter with an accuracy of 0.01 mm. The average of the four quadrants, was considered as the absolute radial growth (ARG). Total plant height and increases thereof were also analyzed obtain absolute height growth (AHG).

2.2.3 Light measurements

Light conditions were measured in the center of each plot and solar radiation transmissivity was obtained for direct (Dir), diffuse (Dif) and global (GL) solar radiation by analysing hemispherical digital photos taken with a Solariscope camera (Behling SOL300, version 1.0). Photographs were taken during January 2015, two metres above ground when solar rays were vertical (between 11:00 and 15:00 hrs) (Vyncke, 1969). Seven photographs were taken in each gap, resulting in 448 images as the best image per plot was visually selected, according to most accurate detection of canopy and sky.

2.2.4 Statistical analysis

To analyse light regimes in patterns of regeneration it is necessary to explore using explanatory variables (Neter *et al.,* 1996). By them, variables were correlated using Spearman's rank correlation coefficient to explore the relationship between varying densities of natural regeneration and solar radiation transmissivity. For natural regeneration density, AHG and ARG correlation with Dir, Dif and GL, Pearson rank correlation was used. To analyse the effect of light regimes on diameter and height growth of plants, generalised linear regression models were used. Tukey test was used to detect significant differences between variables. Data and statistical analyses were performed with significance values of $p < 0.05$ using Statistica v.10 software.

2.3 RESULT

2.3.1 Solar radiation transmissivity

Solar radiation transmissivity ranged from 3 to 39% with an average value of 13% (Figure 2.3). Diffuse solar radiation transmissivity had an average value of 11%, ranging between 3 and 28%, while global radiation transmissivity reached an average of 12%, ranging from 4 to

31% (Figure 2.3).The ranges of variation in solar radiation transmission, whether direct, diffuse or global, were closely related to the different opening levels of the canopy (Table 2.1). Mean values of 8.6, 9.6 and 9.4%, for Dir, Dif and GL solar radiation, respectively, represent a closed canopy, while mean values between 21.3 and 23.6% for Dir, Dif or GL solar radiation represent centre gaps (Table 2.1). However, no significant differences were detected for the border and centre gap, as Dir, Dif or GL solar radiation showed significant differences between gap centre and border centre or closed canopy (Table 2.1).

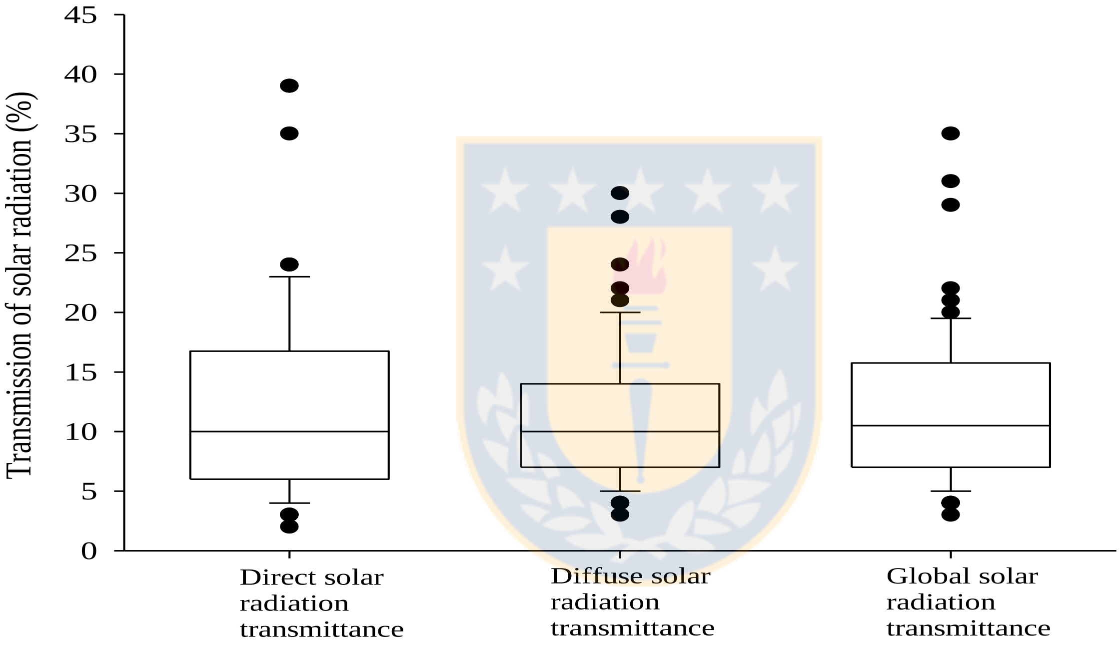

Figure 2.3. Solar transmittance at the 64 points of study: direct, diffuse, and global solar radiation in an old-growth forest of *N. dombeyi* in the Andean central-southern region of Chile.

Table 2.1. Mean values of solar radiation transmittance in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

	Photo location in the plot		
	Centre gap	Border gap	Closed canopy
Variables			
Dir	$23.6^{a} \pm 2.86$	$10.8^{b} \pm 3.08$	$8.6^{b} \pm 1.05$
Dif	$21.3^{a} \pm 1.72$	$10.0^{b} \pm 1.86$	$9.6^{b} \pm 0.64$
GL	$22.6^{a} \pm 2.17$	$10.3^{b} \pm 2.34$	$9.4^{b} \pm 0.80$

Note: Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Rows with different letters indicate significant differences at $p < 0.05$ (Tukey Test).

2.3.2 Influence of solar radiation on regeneration density

Densities of natural regeneration for both seedlings and saplings varied widely within the forest between 0 and 14 plants m^{-2}. Highest densities emerged around the centre gap, varying between 0 and 3 seedlings m^{-2} and 5 and 13 saplings m^{-2}. The density in the border gap was between 1 and 8 seedlings m^{-2} and 2 to 11 saplings m^{-2}. However, under closed canopy, 43% of the plots did not present sapling, whereas in the 57% of the plots, density varied between 0 and 8 plants m^{-2} (Figure 2.4). Seedling density did not correlate with any solar radiation component. However, sapling density related highly significantly to diffuse radiation ($p < 0.0001$) and global solar radiation ($p < 0.0031$) (Table 2.1).

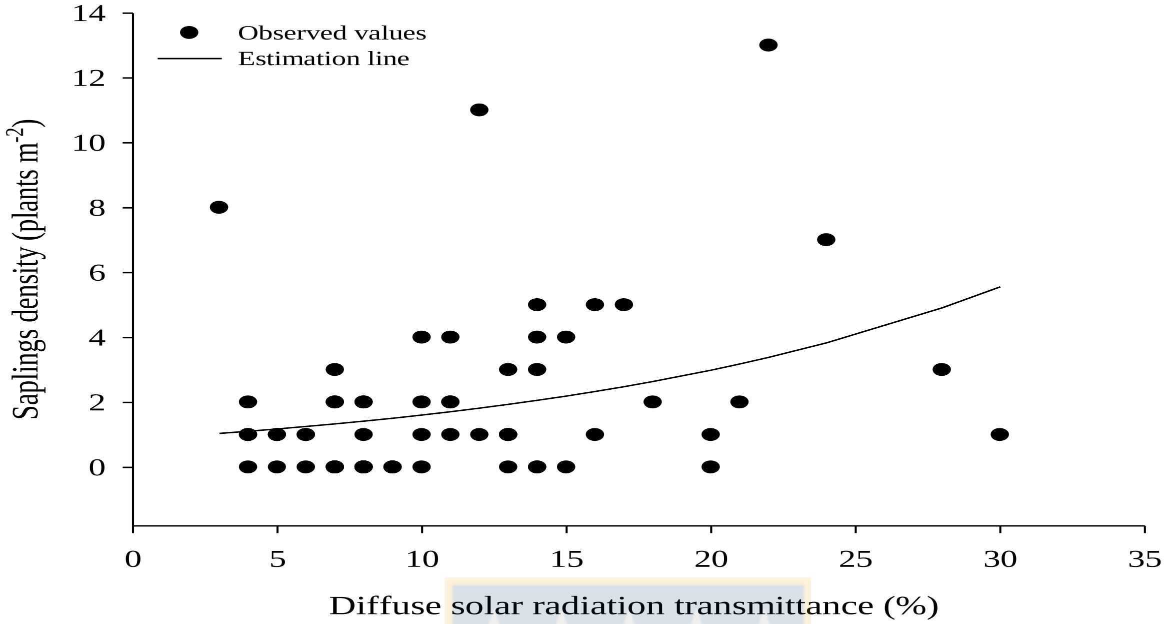

Figure 2.4. Poisson dispersion showing the relationship between diffuse solar radiation transmittance and saplings density ($y = exp^{-0.1404+0.0619x}$; R^2 = 0.26; p = 0.0001) in an old-growth forest of *N. dombeyi* in Chile's central-southern Andean region.

Table 2.2. Spearman's rank correlation matrix for transmittance of solar radiation and natural regeneration density in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

Variables	**SED**	**SAD**	**Dir**	**Dif**	**GL**
SED		0.50*			
SAD	0.50*			0.36*	0.27*
Dir				0.69*	0.95*
Dif		0.36*	0.69*		0.87*
GL		0.27*	0.95*	0.87*	

Note: SED is seedling density; SAD is saplings density; Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Statistically significant correlations are with asterisk ($p \leq 0.05$) (n = 64).

Density of advanced regeneration of *N. dombeyi* increased with rising diffuse radiation (Figure 2.4). Notably, under 3% in diffuse solar radiation transmittance regeneration does not occur and the maximum sapling regeneration density did not exceed 20% in diffuse solar radiation transmittance (Figure 2.4). Considering the natural regeneration of seedlings and saplings, there was no correlation with the stand basal area (Table 2.2). Though the 0.051 to 0.5 m height classes in seedlings and saplings did not show a correlation with any solar radiation component, the remaining height classes showed at least one positive significant correlation (Table 2.3). Particularly sapling density regeneration showed a positive and significant correlation with diffuse and global solar radiation transmissivity (Table 2.3).

Table 2.3. Spearman's rank correlation matrix for natural regeneration density according to height classes in relation to solar radiation transmittances in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

Height classes (m)	Dir	Dif	GL
Seedling	-0.19	0.04	-0.11
Saplings	0.14	0.36*	0.27*
0.051–0.5	-0.04	0.20	0.08
0.51–1.0	0.28*	0.38*	0.37*
1.1–1.5	0.17	0.36*	0.29*
1.51–2	0.19	0.34*	0.29*
>2	0.14	0.36*	0.28*

Note: Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance and GL is global solar radiation transmittance. Statistically significant correlations are with asterisk ($p \leq 0.05$).

2.3.3 Influence of solar radiation on radial increase and plant height

Advanced natural plant regeneration was observed on only 13 plots, which coincided with the borders or centres of canopy gaps in the stand. The average age of the tallest saplings (3-5 m in height) was 23 years (±7.1 SD) and ARG of plants varied between 1.20 and 2.22 mm year^{-1}, with an average increment of 1.52 mm year^{-1}. However, no correlation was observed between increasing radials and stand variables, such as basal area, total tree height and regeneration density. As global solar radiation transmissivity increased, ARG also increased (Figure 2.5 and Table 2.4).

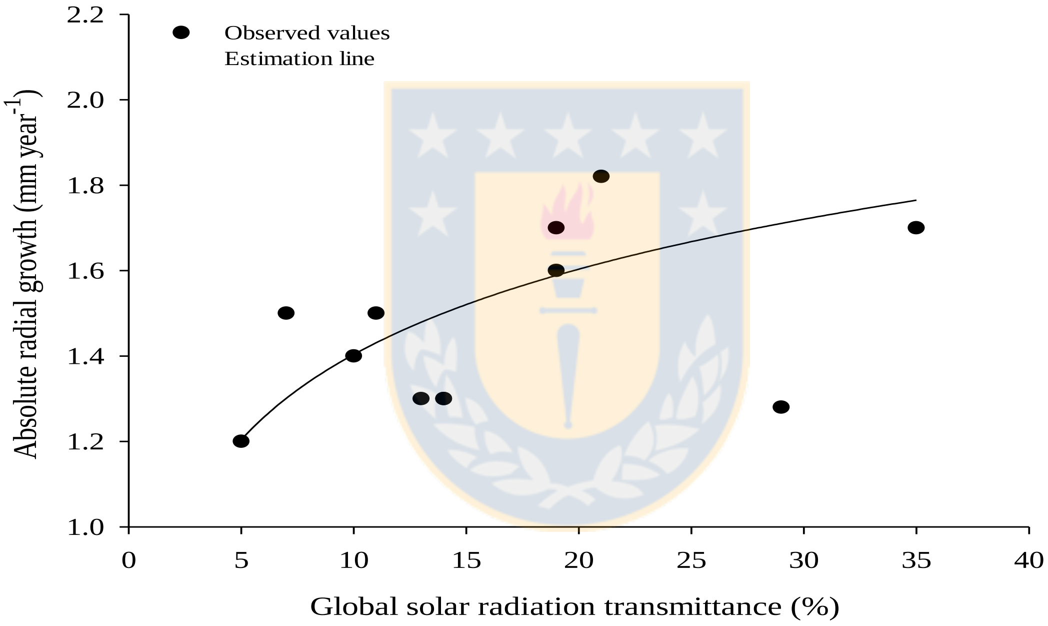

Figure 2.5. Relationship between global solar radiation transmittance and absolute radial growth (ARG = 0.7398 + 0.6638 * log10(x); $R^2 = 0.60$; $p = 0.031$) in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

Table 2.4. Pearson rank correlation for absolute height growth (AHG) and absolute radial growth (ARG) and other measured variables in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

Variables	**AHG**	**ARG**
AHG		0.88*
ARG	0.88*	
E	-0.71*	-0.59*
Dir	0.70*	0.55
GL	0.70*	0.60*

Note: SAD is saplings density; BA is the basal area of stand; TH is total height; E is the age of the highest plant in the plot, Dir is direct solar radiation transmittance; Dif is diffuse solar radiation transmittance GL is global solar radiation. Statistically significant correlations are with asterisk ($p \leq 0.05$) ($n = 13$).

Lowest ARG was observed when solar radiation transmissivity was at 5%, and highest when global solar radiation transmissivity values exceeded 35% (Figure 2.5). Absolute height growth values (AHG) increased from 0.15 and 0.43 m year^{-1}, with an average of 0.22 m year^{-1} (Figure 2.6 and 2.7). No correlation was observed between ARG and stands variables such as basal area or advanced regeneration species density. On the other hand, ARG and AHG shows a significant negative correlation ($p < 0.05$) with age ($r = -0.71$). In addition, it showed a significant positive correlation ($p < 0.05$) with the transmissivity of diffuse radiation ($r = 0.51$; $p < 0.05$).

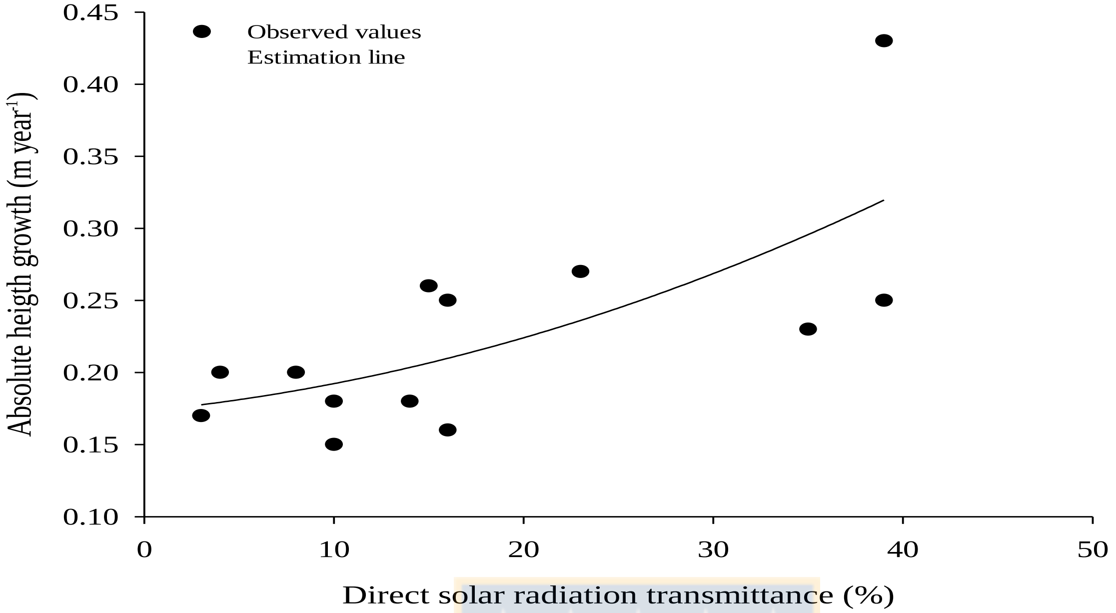

Figure 2.6. Relationship between direct solar radiation transmittance (%) and absolute height increment (AHG = 0.1733 + 0.0013 * x + 6.3677e^{-5} * x^2; R^2 = 0.69, p = 0.0081) in an old-growth forest of *N. dombeyi* in the central-southern Andean region of Chile.

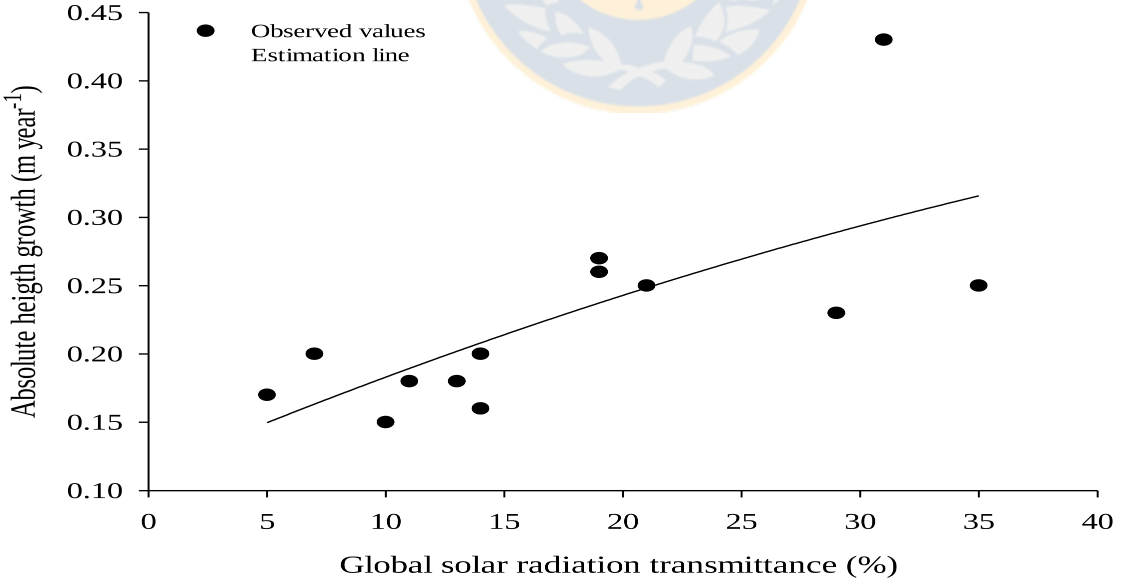

Figure 2.7. Relationship between global solar radiation transmittance (%) and absolute height growth (AHG = 0.1141 + 0.00073 * x – 4.5354e^{-5} * x^2; R^2 = 0.703; p = 0.0073) in an *N. dombeyi* old-growth forest in Chile’s central-southern Andean region.

The adjustment of model solar radiation transmissivity-AHG explains widely and significantly the variance proportion explained by the model Dir-AHG ($R^2 = 0.60$; $p < 0.01$) and GL-AHG ($R^2 = 0.70$; $p < 0.01$). Tests performed in residuals of solar radiation transmissivity and AHG showed independence and normality in its distribution (Figure 2.6 and 2.7). Dif it did not turn out to be significant to explain AHG. Height increase was influenced by the transmissivity of direct and global solar radiation.

2.4 DISCUSSION

2.4.1 Solar transmissivity measurements and differentiation of global, direct and diffuse radiation components

Both intensity and direction of solar radiation transmissivity in forests are constantly changing due to daily and yearly movements of celestial bodies and the Earth in relation to the sun's position and cloud cover (Baldocchi & Collineau, 1994). Considering these factors, we suggested instantaneous measurements of solar radiation around sunrise, because an intense brume covers the canopy, on calm and clear days (in the study area there are no cloudy days in summer). Thus, reflection of the solar radiation in both canopy and stems was avoided. The camera provided seven photographs in each shutter, and the best image was selected according to the criterion that minimizes the presence of red colour in the image and the clearness of canopy. In this form, relative light intensity under the canopy is a function of sun height, measured at the same time as solar radiation intensity at sunrise in an open field (Annighöfer *et al.*, 2015).

When tree canopies, shrubs or herbaceous strata at a particular site vary in size, shape and opacity, the transmissivity of solar radiation penetrating the canopy transforms, creating a wide variation of incoming light in the forest (Lieffers *et al.*, 1999). In our study, stands showed high spatial variability for all transmissivity components of solar radiation inside forests (3 to 40%, Figure 2.3), likely due to different degrees of canopy coverage caused by small-scale disturbance. In this sense, patterns of spatial solar radiation transmissivity observed in the study area are consistent with changes occurring in forests, particularly the presence of different gaps, canopies surface characteristics, and gap size and location (Parker et al., 2002). This has been proven through models (Hardy *et al.,* 2004) showing that spatial changes in solar radiation transmissivity are due to the highly variable nature of light and canopy geometry, particularly discontinuous canopies, as seems to be the case for *N. dombeyi* old-growth forest stands. It is necessary to consider that sunfleck spectra are similar to direct solar radiation transmissivity (Leuchner *et al.*, 2012), which can be physiologically important since plants use this solar radiation in photosynthesis (Dengel *et al.,* 2015). In this sense, under forest understory conditions, leaves are at intermediate induction states of photosynthesis for most of the day and the ability to utilize sunflecks may therefore be strongly influenced by the ability of leaves to maintain relatively high states of induction during long periods of low light (Chazdon & Pearcy, 1986). This explain why shade-tolerant species are, particularly in low light, capable of efficient sunfleck utilization (Rijkers *et al.*, 2000).

It is necessary to refer to the dominant solar environment of *N. dombeyi* old-growth forests, since it corresponds to the growth responses of temperate forests in a Mediterranean climate. It has been reported that diffuse solar radiation can account only 15% of midday radiation coming through the canopy and 40% of the radiation below the shrub layer in deciduous leaf stands, representing between 14 and 41% of canopy transmittance for stands dominated by conifers (Canham *et al.*, 1994); this also explains increases in diffuse light proportions under canopies (Dengel *et al.,* 2015). Sunfleck spectra are similar to incident radiation (Leuchner. *et al.*, 2012) and could also function in areas with transiently higher temperatures, sometimes leading to physiological significance (Dengel *et al.*, 2015), as in the case of the present study area. It is important to note that the transmissivity of diffuse solar radiation enhances terrestrial vegetation photosynthesis (Dengel *et al.,* 2015), while the transmissivity of direct solar radiation can cause photosynthesis saturation in the upper canopy and possibly photoinhibition (Long *et al.,* 1994).

The area under study has been affected to varying intensity and duration by recurring snowstorms and wind (Mitchell, 2013), forming large gaps with a high proportion of surviving trees, creating gaps mosaics (Mitchell, 2013). Wide crowns of *N. dombeyi* retain snow until damage occurs under snow weight pressure, but with more intense storms, a larger number of trees break or are uprooted, which opens the canopies, resulting in gaps, as Mitchell (2013) reported.

2.4.2 Effects of solar radiation transmissivity on natural regeneration density, radial increase and plant height

Gap formation coupled to disturbances provokes a high spatial variability in solar radiation transmissivity, which can satisfactorily explain structural changes and regeneration dynamics (Canham *et al.*, 1994). High spatial variability in solar radiation transmissivity is directly related to small-scale disturbances, which is a characteristic of old-growth forests in the absence of fires (Gauthier *et al.*, 2010), as is the case for the study area for which no fires have been reported over the last 50 years. Moreover, the wide age range between 12 and 40 years of the advanced regeneration in the gaps could explain that saplings are related to the formation and development of various size of gaps in response to small-scale disturbances.

The highest densities for advanced regeneration were observed in 13 from 64 plots, with location at the edges or centres of stand gaps. However, saplings density showed low correlation with diffuse solar radiation transmissivity ($R^2 = 0.26$; Figure 2.4). Our results indicate that until 30% of diffuse solar radiation transmissivity advanced sapling regeneration was highest (5 saplings m^{-2}), and with low levels of diffuse solar radiation transmissivity, under 5%, usually the density of advanced saplings was only 1 sapling m^{-2}, with exception in one plots with 8 saplings m^{-2} (Figure 2.4). These results coincide with a study by Müller-Using (1973), who reported that for *N. dombeyi* regeneration density ranged from 0.08 to 0.8 plants m^{-2} with diffuse solar radiation transmissivity between 1.8 and 7%. The range of spatial regeneration variability in our study was associated with diffuse solar radiation transmissivity between 3 and 40%, values, as reported for European beech (*Fagus sylvatica* L.) (Collet & Chenost, 2006).

In addition, our results are consistent with Saldaña & Lusk (2003), namely that available light explains most variation in advanced *N. dombeyi* regeneration density. Likewise, a controlled experiment found that the scarce regeneration of *N. dombeyi* under canopies of old-growth forests is at least partially attributable to the higher light compensation points (LCP) of this species, -but not for shade-tolerant species. Higher LCP is a typical characteristic of shade-intolerant species qualified as pioneers, such as *N. dombeyi* (Lusk & Del Pozo, 2002).

Besides, site resources, especially water and nutrients in the soil, could be relevant to explain the density of advanced regeneration (Stancioiu & O'Hara, 2006) of pioneer tree species. However, presence or absentia of saplings under the canopy of old-growth forests are not only explained by the level of light at ground level, but also by different factors such as competition from herbaceous plants, bushes and overstory-trees as well as climatic extremes such as drought or frost (Pacala *et al.*, 1994; Stancioiu & O'Hara, 2006). Here, solar radiation transmissivity had no influence on the height of seedlings and saplings under the canopy for the height class shorter than 0.5 m (Table 2.3). This result is consistent with Promis *et al.*, (2010) findings for *Nothofagus betuloides* (Mirb.) Oerst. and could be explained because low-height seedlings and saplings highly depends on other site resources, especially water and nutrients in the soil (Aussenac, 2000; Stancioiu & O'Hara, 2006). Studies developed by Lusk (2004) and Ammer *et al.*, (2008) found the same tends, indicating that size and age might affect plants' growth response to resource availability.

In contrast, both diffuse and global solar radiation transmissivity highly influenced height classes 1 < 1.5 m, possibly reflecting high competition for this resource, forcing saplings to invest more energy in height growth (Table 2.3) especially in understory old-growth forests where light is scarce related to secondary forests. However, diffuse and global radiation influence height plants > 2 m (Table 2.3), due to competition for access to higher proportions of diffuse radiation under the canopy (Lieffers *et al.*, 1999). Müller-Using and Schlegel (1981) found, in a study controlling shade conditions, that *N. dombeyi* height significantly increased with increasing light intensity. In the case of small gaps with a more or less closed canopy, total diffuse light and daily carbon gain is linearly related to total daily PPFD. The proportion of total daily carbon gain during sunflecks ranged from 15% to 60% (Chazdon 1986; Peri *et al.*, 2009), and consequently, may be important for the discovery of regeneration under shaded canopies in *Nothofagus* (Peri *et al.*, 2009). Thus, direct light with higher energy levels, but lower occurrence during the day, stimulates photosynthetic processes leading to higher growth rates. In this respect, it has been reported that the effect of direct and global solar radiation transmissivity on height increment is relevant at levels above 20%, as in the case of *N. betuloides* (Lusk, 2004). However, advanced regeneration in large gaps, AHG are limited by gas exchange that allow inhibition of photosynthesis as consequence of high energy contents if unavailable for long periods of the day (Dengel *et al.*, 2015).

In fact, high light levels in gaps in the Andes may be the cause of severe photoinhibition of *N. dombeyi* saplings (Donoso *et al.,* 2013).

The largest increases in AHG occurred in the 15 to 23% range of direct and global solar radiation transmissivity (Figure 2.6 and 2.7). Factors explaining AHG in the present study were also reported by Lusk (2004), Ammer *et al.,* (2008), and Promis *et al.,* (2010), who see transmissivity of direct and global solar radiation and age as a partial explanation of AHG (R^2 = 0.7; Figure 2.6 and 2.7), because saplings also respond to other available site resources for growth. Therefore, maximum increases in growth do not correlate with the highest light level. An explanation is that competition in the advanced regeneration of *N. dombeyi* excludes other species from the understory; it could therefore be argued that ARG is much more sensitive to intraspecific competition than growth in height (Ammer *et al.,* 2005). The observed AHG patterns suggest that advanced regeneration of *N. dombeyi* compete mainly for light, simultaneously increasing biomass in the stem area in terms of height at the expense of radial growth (Ammer *et al.,* 2005).

Diaci *et al.,* (2007) showed the relative importance of both diffuse and direct radiation transmissivity for the successful regeneration of *F. sylvatica* under canopy openings with diffuse radiation, which coincides with the findings in this study (Table 2.1). However, height classes, ARG, and AHG showed no correlation with diffuse solar radiation transmissivity, likely a response to competition for density and greater access to diffuse radiation under the canopy by light-demanding species (Lieffers *et al.,* 1999).When competing for light, height growth is of prime importance due to mechanical stress, and therefore ARG and AHG are regulated by the local environment (Vanninen & Mäkelä, 2000). In this study, the local microenvironment and site resources, such as water availability, were not analysed, but future studies should take these into account.

However, we found that AHG was negatively affected by sapling age (Table 2.4), what has also been reported for *Fagus sylvatica* L. (Jarčuška & Day, 2013). And, growth decline in AHG may be explained not as effect of age per se, but as indirect age-related effect probably induced through plastic response of saplings to past growth conditions (Jarčuška & Day, 2013).

Under light competition growth allocation between height and diameter is regulated by local conditions, as a result local conditions on growth patterns (Vanninen & Mäkelä, 2000), and decline AHG decay ARG with age. Therefore, plant age and direct and global transmittance of solar radiation through canopy openings explain the increases in diameter and height of saplings, and we recommend that local habitat and total sapling height of surrounding trees play a fundamental role in regulating competition in height growth for regeneration (Annighöfer *et al.*, 2015).

2.4.3 Silvicultural implications

The studied stands correspond to mono-specific old-growth evergreen *N. dombeyi* forests. As no universal definition for old-growth forests exists (Wirth *et al.,* 2009), we used a broader and more pragmatic approach as most suitable definition by Shorohova *et al.*, (2011): old-growth forests as naturally regenerated forests with low human impact and dominated by trees that approach the end of their biological life cycle. This phase is interesting because it opens room for human intervention, such as forest rehabilitation or the practice of close-to-nature silviculture.

For old-growth *N. dombeyi* forests, it has been hypothesised that in the absence of large-scale disturbances, late successional species tend to settle under the canopy and replace early successional species; therefore, regeneration of these species would depend on disturbance frequency (Veblen *et al.,* 1996). However, this hypothesis does not apply to old-growth forests in this study, because old-growth canopy layers of *N. dombeyi* have been primarily affected by small-scale disturbances such as rain and snow pressure, giving rise to differently sized gaps that stimulate natural regeneration in absence of bamboo species such as *C. culeou* (Lusk, 2001). Wind also causes a variety of gap sizes that depend directly on the intensity and duration of storms, site heterogeneity and stand conditions. In this form, overstory gaps vary so much that it is difficult to distinguish between a medium gap with a low proportion of fallen trees and a mosaic of small gaps.

The old-growth *N. dombeyi* stands of this study contained mainly two features. First, the presence of single layered stands, since canopies are fully closed and a geometric extension of canopies largely prevents solar radiation transmissivity, which affects natural regeneration. The second condition was observed in gaps created by small-scale disturbances and consisting of saplings competing for light, since the trees in the upper canopy still reduce light availability in the lower canopy (Oliver & Larson, 1996). Similar to the seedling and sapling regeneration of *N. betuloides* (Promis *et al.,* 2010), regeneration in this study developed slowly in the understory, where saplings needed 20 to 40 years to reach a height of 5 m, without forming a consistent secondary tree layer. From this perspective, it is necessary to recommend a silvicultural system that ensures natural regeneration in an old-growth *N. dombeyi* forest. Silvicultural systems consider multiple and often conflicting management objectives. Due to the high economic and ecologic value of the species presented here, it is necessary to preserve attributes of this forest type (Bauhus *et al.*, 2009). Thus, the group selection method constitutes an appropriate method to promote regeneration, given that trees are removed in small groups (Lindenmayer & Franklin, 2002) and felling can continue at the border of the created gap. This method results in more or less "homogeneous" canopy gap patterns which allow for more resources, especially light, in areas lacking regeneration (Nyland, 2002).

In the case of old-growth forests, no competition with *C. culeou* occurs and gaps are related to small areas on the forest floor where regeneration can develop over several years. However, the demand for light increases with age (Lieffers *et al.*, 1999), making it necessary to expand existing gaps and create new ones to sustain the regeneration of new plants. These new gaps should imitate the collapse of old-growth trees, i.e. gaps should allow for enough light to stimulate regeneration; hence, cutting two to three trees of the overstory could prove useful, as it results in gaps with a diameter of around 30 m (0.07 ha), depending on stand density and tree size (Dezzotti & Sbrancia, 2006). However, it is necessary to adjust silvicultural practices, particularly the level of canopy openings, to maintain species composition unaffected as a key indicator of sustainability at management unit scale (Sola *et al.*, 2015). Likewise, it is necessary to analyse the impact on biodiversity related to this silvicultural regime. The existing gaps are large enough to introduce other tree species, such as *L. philippiana* and *Podocarpus salignus* (D. Don), and *Lophozonia alpine* ((Popp. & Endl.) Heenan & Smissen) which protects against excess lighting in the gap, thus complementing the natural regeneration of *N. dombeyi* (Dezzotti, 2008). Regarding gap size and *N. dombeyi* regeneration, Dezzotti & Sbrancia (2006) found an average of 61.2 plants m^{-2} in gap sizes of 0.15 and 0.4 ha, demonstrating the effectiveness of this approach. These sizes suggest that gaps should have a maximum width of 40 to 60 m in wet temperate climates, preferably with winter rains. To optimize plant natural regeneration throughout the area, gaps should exhibit an elongated shape with a maximum width of 30-40 m which correspond with around one and a half times the height of adjacent adult trees. Under these weather conditions, gaps meet the objective of not creating central areas that are too large for the transmissivity of direct or global solar radiation or for natural regeneration defences against late frosts or desiccation (Dezzotti & Sbrancia, 2006).

In this study, the range of the solar radiation transmissivity spectrum was lower than wet temperate climate zones, expressed in a maximum transmissivity value of 40%. Therefore, gap sizes should be even smaller in areas of Mediterranean climates, and this justifies that we propose a diameter of no more than 30 m for gaps and the study of enrichment techniques using shade-tolerant species.

2.5 CONCLUSION

In the case of old-growth *N. dombeyi* forest, recurrence of wind and snowstorms and the geometry of canopies cause the loss of individual trees if the storms are of low intensity. In cases of intense storms, the loss of a greater number of trees provides more and larger canopy openings. However, the height classes, ARG and AHG did not correlate with the diffuse solar radiation transmissivity, but with the direct and global. Therefore, plant age and direct, and global transmittance of solar radiation through canopy openings explain the increases in diameter and height of saplings, and we recommend that local habitat and total sapling height of surrounding trees play a fundamental role in regulating competition in height growth for regeneration. Our findings suggest that single-tree or group-selection harvests should emulate the small-size gap disturbance as an important regeneration management for *N. dombeyi* old-growth forest.

2.6 ACKNOWLEDGEMENTS

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CAPÍTULO III

EFFECTS OF SOLAR RADIATION ON PLASTICITY OF ABOVEGROUND AND BELOWGROUND BIOMASS ALLOCATION AND MORPHOLOGICAL TRAITS IN ADVANCED REGENERATION UNDER CANOPY OF *Nothofagus dombeyi* (Mirb.) Oerst. OLD-GROWTH FOREST IN THE CENTRAL-SOUTHERN ANDES, CHILE

Encina, P., Rodríguez, R., Muller-Using, B., Annighöfer, P., Mena P & Sánchez-Olate, M. "Effects of solar radiation on plasticity of aboveground and belowground biomass allocation and morphological traits in advanced regeneration under canopy of *Nothofagus dombeyi* (Mirb.) Oerst. old-growth forest in the central-southern andes, chile". *Landscape and Ecological Engineering*. Enviado. 3-10-2018

ABSTRACT

We studied the effects of two luminosity intensities on morphometric traits, morphological plasticity, allocation and biomass partitioning in saplings of N. dombeyi. In three gaps, two circular 2 m-radius plots were established, one in the gap center and another between the gap and the closed canopy. Solar radiation transmissivity was measured in each plot. Biomass of all plant components (leaves, branches, stems, and roots) was obtained, as were age and morphological variables, through destructive sampling. Biomass allocation of all components showed a positive correlation with age. Relative biomass distribution showed significant differences in leaves and stems to total biomass; leaf to stem allocation was 4.1% in light. In medium shade, however, saplings' leaf to stem allocation decreased by 5.9%, showing a low impact. Significant differences were detected in the morphological traits of root length, as well as number and size of leaves when comparing light and medium shade. However, leaf area (LA) and specific leaf area (SLA) did not show significant differences. No plasticity was observed in biomass allocation, but morphological plasticity was detected. We suggest N. dombeyi plant acclimatization to sun and shade conditions is expressed through morphological plasticity in root:shoot, height:diameter, and height:stem mass.

Keywords: morphometric traits, saplings, intolerant, light.

3.1 INTRODUCTION

Forestry studies apply techniques based on biological foundations to direct forest development toward a specific objective, which can be related to individual tree morphology or species composition along other forest functions like biodiversity maintenance (Bauhus et al., 2009).

The concept of old-growth forests has evolved in its definition from a set of static structures and properties to a more dynamic vision with results on multiple scales (Kneeshaw and Gauthier, 2003). Shorohova et al., (2011) define old-growth forests as naturally-regenerated forests with low human impact, dominated by trees close to the end of their biological life span or trees that have replaced the initial post-disturbance cohort. In southern South America, wind and snow storms in the mid-altitudes of the Andes Mountains cause trees to fall individually or in groups, creating small gaps and allowing the establishment of shade intolerant species. Initial growth is maximized under light conditions in the absence of bamboo like C. culeou (Lusk, 2001; Lusk and del Pozo, 2002), which competes for light with tree regeneration in these gaps after small-scale disturbance (Weinberger and Ramírez, 2001).

An obvious consequence of canopy gaps is the temporary increase in light availability (Canham et al., 1990; Lieffers et al., 1999). Light availability possibly varies more in time and space than any other resource (Canham et al., 1990; Hu and Zhu 2008; Martens et al., 2000) and is essential to plant growth and survival (Kneeshaw and Bergeron 1998; Mountford et al., 2006). Therefore, light is a key factor that affects plants in a dynamic succession of conglomerates. This response to light could be viewed as a plastic and morphology adjust¬ment at the individual and species level (Jarčuška and Barna, 2011).

Several studies have used the balanced-allocation hypothesis to analyze the effect of light, water, or nutrient availability on plant plasticity, where the resources from photosynthesis, assigned to a function or organ, are not made available for other structures (Weiner, 2004). These products are stored by plants or are allocated in various ways to the different tissues forming the plant organs (Bloom et al., 1985). However, it has also been reported that plant biomass is constant while allocation to leaves, stems, and roots varies little with light availability (Curt et al., 2005; Kaelke et al., 2001; Machado et al., 2003). Furthermore, some studies suggest that aboveground biomass magnitudes are facilitated by ecologically important subterranean elements which grant access to the mycorrhizal network (McGuire 2007; Teste et al., 2009).

However, at a given irradiance, species that differ in their relative growth rate can be decomposed into a morphological and a physiological component. In this form, a net assimilation rate has been found, showing that large changes in biomass allocation and plant morphology occur jointly at the lower end of the light gradient (Poorter, 1999). Likewise, comparative studies of species morphology have shown that plants maximize their growth potential by developing a large foliage area with a specific leaf area (Kitajima, 1994) under shaded environments to quickly acquire growth resources (Kobe, 1997). It has also been reported that increasing shade level increased SLA a common response of plants to shade that has been well documented in beech and oak (Valladares et al., 2002; Kunstler et al., 2005; Goisser et al., 2013). Similarly, Lth decreased with increasing shade, which has also been reported in other studies (Valladares et al., 2002). Various species exhibited morphological acclimation to increasing levels of shade, such as by increasing SLA and H/Rcd ratios and decreasing leaf thickness and root:shoot ratio. The acclimation of leaves to shade would increase saplings' ability to intercept light, while the changes in H/Rcd and root:shoot ratios suggest that plants allocate more biomass to the aboveground than belowground parts in response to shade (Sevillano et al., 2016). And the strong correlation between Lth and SLA might suggest that Lth could be as useful an indicator as SLA of plant's light-use strategy (Sevillano et al., 2016).

In the case of N. dombeyi, allometric changes or morphological traits in adaptation to light are more important. Our hypothesis is that in Mediterranean environments, with solar radiation and extended droughts in summer, morphological traits become more important than the allometry of plants to explain the survival and growth of saplings.

Due to the importance of N. dombeyi for old-growth forests in Chile, there is a permanent concern about its natural regenerative ability. Therefore, the objective of this study is to analyze the impact of light availability on aboveground and belowground biomass partitioning and morphological traits in advanced natural regenerations under two contrasting light environments in an old-growth forest of N. dombeyi, in Chile’s central-southern Andes.

3.2 MATERIALS AND METHODS

3.2.1 Study area

The study took place in three *N. dombeyi* old-growth forest stands near Yungay city, Bio Bio Region in central Chile (Density of 240 trees ha^{-1}, basal area of 56.7 m^2 ha^{-1}). (Figure 3.1). All stands of *N. dombeyi* belong to bioclimatic area called Andean Mediterranean Deciduous Forests of *Nothofagus obliqua* and *Austrocedrus chilensis* (Luebert & Pliscoff, 2006).

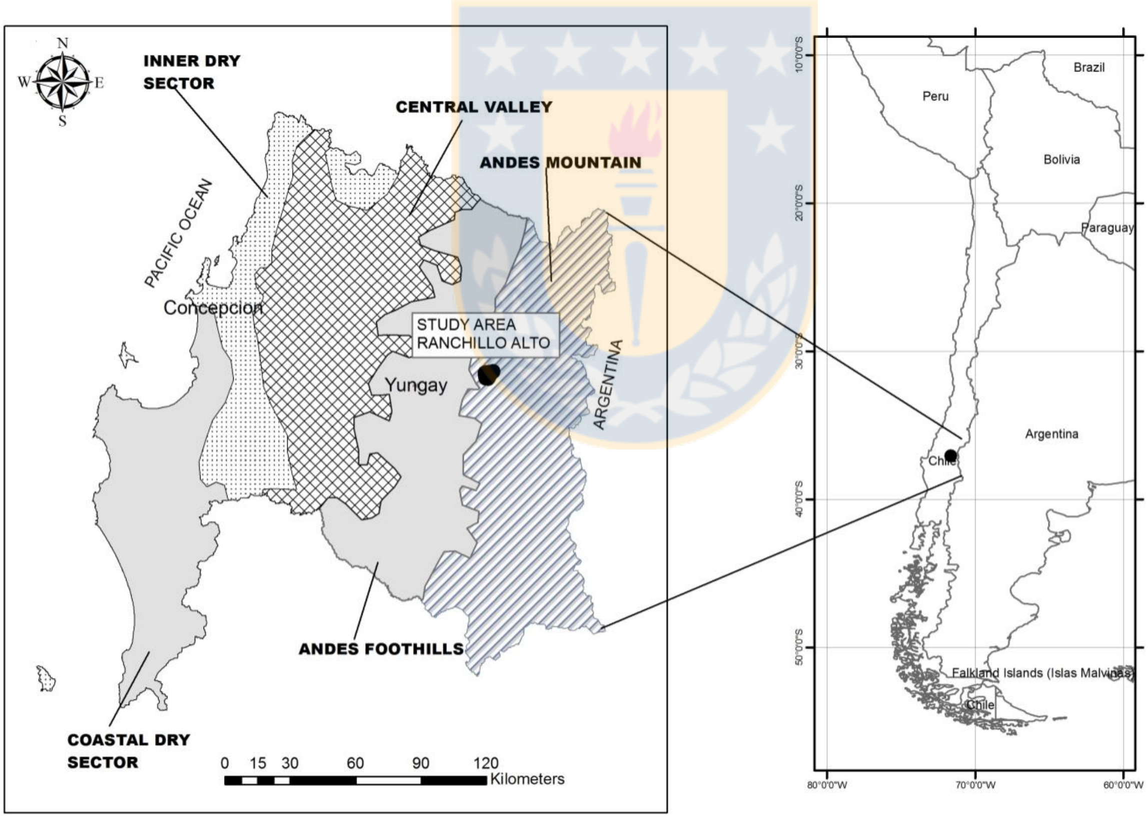

Figure 3.1. Location map of the study area in the Andes Mountains in the Biobío Region, Chile.

The bioclimatic area is characterized by extra zone communities called *Aristotelio-Nothofagetum dombeyi* (ravine), *Kagenekia angustifolia-Guindilia trinervis* (arid slopes) and *Nothofagus dombeyi-Gaultheria phillyreifolia* (water courses). However, in a state of old-growth, light conditions below the first canopy layer do often inhibit development of intermediate arboreal strata. The most characteristic geomorphological position of such a forest is in western mid-slopes of the Andes Mountains (Luebert and Pliscoff 2006). The climate is Mediterranean, with rainfall concentrated during winter and a dry summer lasting three to four months. Study area altitudes (600-1,500 m.a.s.l.) correspond to an area with temperate Mediterranean climate as classified by Emberger (Del Pozo and Del Canto 1999). Average annual rainfall exceeds 1,400 mm, and ice and snowfall can cause disturbances in the native forest, while growing season lasts around three months due to low winter temperatures (Del Pozo and Del Canto, 1999).

Soils originate from volcanic ash, most likely post glacial, resting on a non-related substrate comprising fluvial or glacio-fluvial materials that remain detected due to the depth at which they occur (Kühne et al., 2005). Soil is deep and medium-textured, generally silty loam within the first meter and silty clay loam at depths of 165 cm or more (Kühne et al., 2005).

3.2.2 Sampling

To obtain solar radiation transmissivity measurement three gaps were used. They varied in size between 45 and 300 m2. To characterize light environment inside each plot, the transmittance of direct solar radiation (DSF), transmittance of diffuse solar radiation (ISF), and transmittance of global solar radiation (GSF) were measured. Two circular 2 m-radius plots per gap were used. One plot was established in the gap center, representing light conditions. The other plot representing medium shade conditions, was oriented to the north, and intersected the gap edge and closed canopy. Under the closed canopy (under 3% diffuse solar transmittance), plant recruitment was non-existent (Table 3.1).

Table 3.1. Descriptions of light conditions, stand characteristics, and density of advanced regeneration in an old-growth forest of Coigüe growing in the central-southern Andean region of Chile.

Characteristics	**High light conditions**	**Medium shade**
	Plots	**Plots**
	Centre gap	**Border gap and closed canopy**
Dir	11 (10–13)	3.7 (2–5)
Dif	31.3 (27–37)	8.3 (4–11)
GL	19.7 (19–21)	4 (3–9)
BA	56.7	0
SD	240	0
REG	2.1	1.4
Dbh	5.4	0
H	24.6	0
A	9.4	6.5

Note: Dir is direct solar radiation transmissivity (%), Dif diffuse solar radiation transmissivity (%), GL is global solar radiation transmissivity, BA is Basal area (m^2 ha^{-1}), SD is stand density (trees ha^{-1}), and REG is saplings density (saplings m^{-2}) while Dbh is diameter at breast height (cm), H height (m), and A is age of saplings (years)

In the center of each plot images were taken using a fisheye Solariscope SQL 300 camera (Behling Germany) that was placed 1.5 m above ground (Annighöfer et al., 2015). The Solariscope takes hemispherical photographs and subsequently analyses them for different parameters of interest for users (e.g., direct, diffuse and global solar radiation transmissivity, tree canopy openness, leaf area index). The measurements were taken in November, with cloudy skies, during early morning from 6:00 a.m. to 9:00 a.m., the ideal conditions for taking hemispheric photographs. Thus, reflections of the luminosity in both canopy and stem were avoided. Solariscope provided seven photographs in each shutter and 42 images in total. The best image was selected according to the criterion that minimizes the presence of red color in the image and the clarity of the vegetal cover.

3.2.3 Analysis of plant material and biomass

Individual saplings were sampled in six circular plots within the random gaps (Table 3.1). Sampling was carried out at the end of the growing season in April 2016. Saplings were randomly chosen from the regeneration patches; they had to be undamaged, without symptoms of pathogen attack. Stem length (H) and Root collar diameter (Rcd) were measured before the plant was harvested. Afterwards, all leaves were collected and the wooden parts were separated into stem, branch and roots. Soil samples were taken at depths of 40 cm and were immersed in water to remove remaining soils fragment. In the laboratory, samples were washed again and all roots were sieved, dead roots removed, and the remaining ones were dried at 70° C and weighed to 0.01 g. At the stem base a stem disc was collected from each individual to determine age (A) by counting year rings. Plant compartments were stored in cold chambers at 2 ºC for further analysis. In the laboratory, all plant material was dried at 110 ºC for 24 hours, or longer, until reaching constant weight. Biomass (g) was obtained for leaves (L_{mass}), branches (B_{mass}), stems (S_{mass}), and roots (R_{mass}). Aboveground biomass (A_{mass}), i.e., the sum of biomass of all aboveground compartments and total biomass including root biomass (T_{mass}), was calculated.

A subsample of five leaves was taken for each plant and kept in a cold chamber at 2 ºC. Leaves were photographed using a Nikon Coolpix s7000 camera. The software ImageJ win-32 (rsb.info.nih.gov/ij/) was used to measure the leaf size (L_{size}) (cm^2). Each leaf was then weighed on a precision analytical scale with 0.1 mg resolution. The specific leaf area ($cm\ g^{-1}$) was calculated as the proportion of the measured area of the fresh subsample in relation to leaf dry weight. Leaf area (LA) (cm^2) was calculated as the product of leaf dry mass content (g) and SLA. The number of leaves (L_{num}) was obtained as a product of total leaf biomass ratio to subsample leaf biomass. Height to diameter (H/Rcd ratios, $mm\ mm^{-1}$), height to stem mass ($H{:}S_{mass}$, $mm\ g^{-1}$) and root dry mass to branches + stem dry mass (root:shoot, $g\ g^{-1}$) ratios were calculated from the measurements. Leaf thickness (L_{th}) was estimated by dividing leaf biomass by leaf area ($g\ cm^{-2}$), allowing leaf thickness estimates from easily measured leaf traits (Vile et al., 2005; Pérez-Harguindeguy et al., 2013; Sevillano et al., 2016).

An index of phenotypic plasticity ranging from 0 to 1 was calculated for each variable as the difference between the minimum and the maximum mean values among the light conditions divided by maximum mean value (Valladares et al., 2002; Sevillano et al., 2016); more details in Valladares et al., 2000. This index allowed the comparison of changes in variables expressed in different units.

3.2.4 Statistical analysis

A Pearson correlation matrix was constructed to identify significantly correlated variables, with ratio (r) greater than ± 0.75 (Table 3.2) to further analyze how light affects biomass allocation, partitioning and morphometric variables in advanced natural regeneration. Analysis of covariance (ANCOVA) was used to test treatment effects on biomass components. Analysis of variance (ANOVA) detected significant differences (p-value <0.05) in variables not correlated with age. The general model was:

$$y_{il} = u + t_i + \beta(x_{il} - \overline{x}) + \varepsilon_{il}$$

Where:

y_{ij} is the variable value (biomass component, biomass distribution, and morphometric traits), observed in the l-th experimental unit (stand) of the i-th treatment (light condition),

x_{il} is the covariate value (Rcd2*H and Age),

u the general mean of the random variable,

$\bar{x}$ the average x_{il}value,

t_i is the effect of the i-th treatment,

β the linear regression coefficient ($\beta \neq 0$) and,

e_{il} is the residue of the l-th experimental unit in the i-th treatment.

Normal error distribution and variance homogeneity were evaluated graphically.

Residue data, which did not conform to assumptions of normality and/or variance homogeneity, were transformed using logarithms. All statistical tests were performed using SAS Software v. 9.4.

Table 3.2. Spearman's rank correlation, matrix biomass allocation, and morphological variables for two contrasting light conditions in an old-growth forest of *N. dombeyi* growing in the central-southern Andean region of Chile.

	Rcd	L_{num}	H	LA	Rcd^2*H	A	S_{mass}	B_{mass}	L_{mass}	R_{mass}	T_{mass}	A_{mass}	$H:S_{mass}$
Rcd	1												
L_{numb}	0.9	1											
H	0.84	0.79	1										
LA	0.92	0.97	0.84	1									
Rcd^2*H	0.98	0.89	0.93	0.93	1								
A	0.88	0.8	0.72	0.79	0.85	1							
S_{mass}	0.91	0.88	0.94	0.9	0.96	0.82	1						
B_{mass}	0.92	0.93	0.85	0.93	0.93	0.83	0.92	1					
L_{mass}	0.93	0.97	0.82	0.99	0.92	0.82	0.9	0.94	1				
R_{mass}	0.96	0.9	0.88	0.93	0.97	0.85	0.94	0.93	0.94	1			
T_{mass}	0.95	0.93	0.92	0.95	0.98	0.85	0.98	0.97	0.95	0.98	1		
A_{mass}	0.92	0.93	0.85	0.93	0.93	0.82	0.92	1	0.94	0.93	0.97	1	
$H:S_{mass}$	-0.91	-0.89	-0.86	-0.89	-0.93	-0.83	-0.98	-0.91	-0.89	-0.93	-0.97	-0.91	1

Note: Rcd is root collar diameter, L_{num} number of leaves per sapling, H is height of sapling, LA foliage area, Rcd^2*H is the product of root collar diameter squared and height, A is age, S_{mass} stem mass allocation, B_{mass} is branch mass allocation, while L_{mass} is leaf mass allocation, R_{mass} root mass allocation, T_{mass} total biomass, A_{mass} is aerial biomass per sapling, and $H:S_{mass}$ is height:stem mass ratio. Variables were transformed to natural logarithms. All variables showed significant differences ($p \leq 0.05$). In the table, only $r \geq 0.75$ are shown.

3.3 RESULT

3.3.1 Effects of light conditions on biomass allocation and distribution

The ages of saplings in light were significantly higher than those in medium shade conditions. Full lit saplings averaged 9.4 years of age, between 6 and 22 years. Saplings in medium shade averaged 6.5 years, varying between 4 and 13 years. It is necessary to high light the significant correlation between Rcd and L_{num}, LA and H, and H/S_{mass}. Although results show a negative relation, they were the only morphometric variables and correlated with age (Table 3.2). The biomass of all plant compartments was closely correlated with age (Table 3.2). Therefore, ANCOVA models were used for the Rcd2*H variable, using age as covariate to determine if significant differences in biomass components existed (Table 3.3)

Table 3.3. Terms of error of the covariance analysis (ANCOVA) for foliage, branch, stem, root, aboveground biomass, and total biomass in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Dependent	**Source**	**SS**	**F-value**
L_{mass}	Trat	0.0219	0.6800
	Ln(Rcd2*H)	31.3503	<.0001
	Ln(Rcd^2*H)*Treat	0.0010	0.9313
B_{mass}	Trat	0.0175	0.7354
	Ln(Rcd^2*H)	37.2730	<.0001
	Ln(Rcd^2*H)*Treat	0.0350	0.6329
S_{mass}	Trat	0.0073	0.7965
	Ln(Rcd^2*H)	47.6484	<.0001
	Ln(Rcd^2*H)*Treat	0.0005	0.9452
R_{mass}	Treat	0.0132	0.6739
	Ln(Rcd^2*H)	36.8106	<.0001
	Ln(Rcd^2*H)*Treat	0.0053	0.7900
A_{mass}	Trat	0.0046	0.7878
	Ln(Rcd^2*H)	40.7537	<.0001
	Ln(Rcd^2*H)*Treat	0.0001	0.9746
T_{mass}	Trat	0.0066	0.7208
	Ln(Rcd^2*H)	40.1729	<.0001
	Ln(Rcd^2*H)*Treat	0.0001	0.9581

Note: L_{mass} is leaf mass allocation, B_{mass} branch mass allocation, S_{mass} is stem mass allocation, R_{mass} is root mass allocation, A_{mass} aerial biomass, and T_{mass} total biomass per sapling. Variables were transformed to natural logarithms. All variables showed significant differences ($p \leq 0.05$). Root collar diameter squared multiplied by height (Rcd^2*H) as the covariable was used.

Scatter plots did not detect parallelism for B_{mass} and R_{mass} (Figure 3.3 and Figure 3.5) under both light conditions. ANCOVA confirmed no significant differences in biomass allocation for these components. Scatter plots showed parallelism for L_{mass} and S_{mass} (Figure 3.2 and Figure 3.4), but the differences that emerged were not significant (Table 3.3). Also, dispersion diagrams showed a positive correlation for all biomass components with the variable logRcd2*H, which confirms that it is an important component in all regression models (Figures 3.3, 3.4 and 3.5).

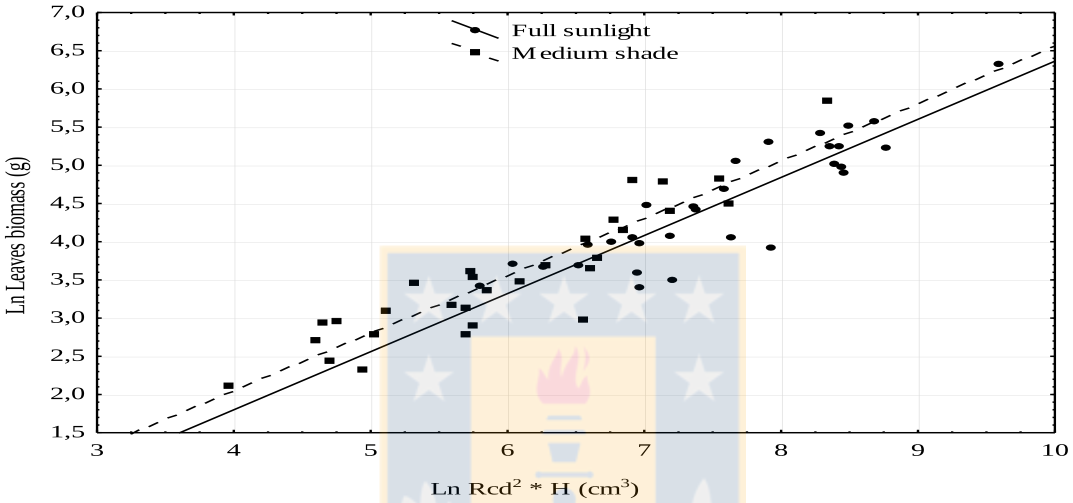

Figure 3.2 Dispersion graphs for allometric relations between Ln of the product of root collar diameter squared and height (H) for leaf biomass of *N. dombeyi* growing in the central-southern Andean region of Chile.

Note: Equation coefficients in high light are Ln leaf biomass biomass (Ln y) = -1.2416 + 0.7604 * Ln x, and $R^2 = 0.79$. Equation coefficients in medium shade are Ln branches biomass (Ln y) =-0.9618 + 0.7521 * Ln x, and $R^2 = 0.84$. Variables were transformed to natural logarithms.

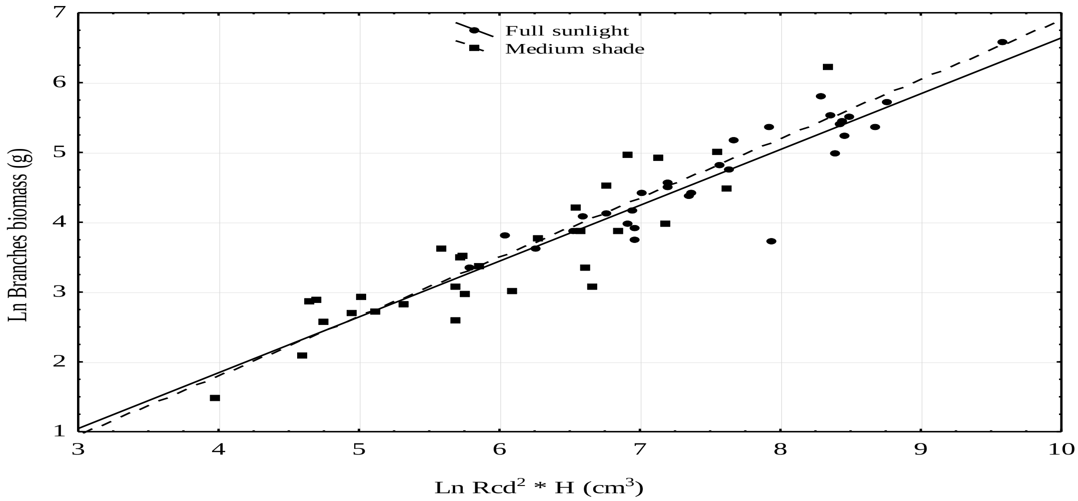

Figure 3.3. Dispersion graphs for allometric relations between Ln of the product of Root collar diameter squared and height (H) for branches biomass of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Note: Equation coefficients in high light are Ln stem biomass (Ln y) = -1.3527 + 0.7994 * Ln x, and R^2 = 0.83. Equation coefficients in medium shade are Ln branches biomass (Ln y) = -1.6025 + 0.8499 * Ln x, and R^2 = 0.81. Variables were transformed to natural logarithms.

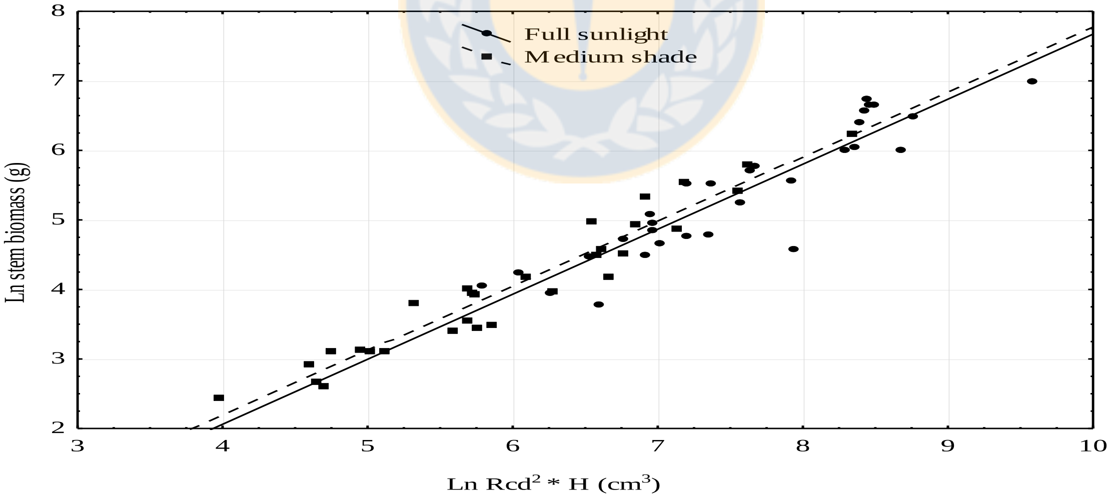

Figure 3.4. Dispersion graphs for allometric relations between Ln of the product of Root collar diameter squared and height (H) for stem biomass of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Note: Equation coefficients in high light are Ln stem biomass (Ln y) = -1.6817 + 0.9354 * Ln x, and R^2 = 0.84. Equation coefficients in medium shade are Ln stem biomass (Ln y) = -1.5201 + 0.9293 * Ln x, and R^2 = 0.93. Variables were transformed to natural logarithms.

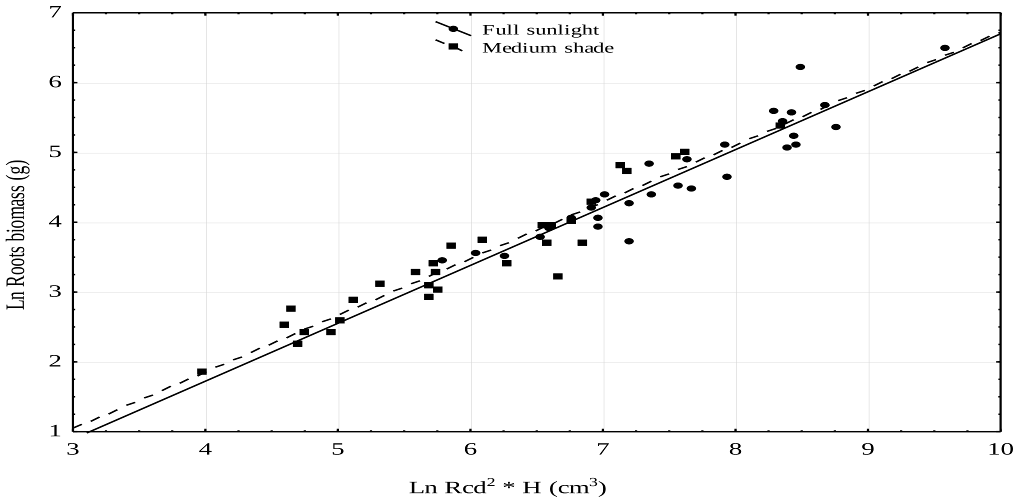

Figure 3.5 Dispersion graphs for allometric relations between Ln of the product of Root collar diameter squared and height (H) for root biomass of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Note: Equation coefficients in high light are Ln root biomass (Ln y) = -1.5942 + 0.8293 * Ln x, and R^2 = 0.89. Equation coefficients in medium shade are Ln root biomass (Ln y) = -1.3775 + 0.8097 * Ln x, and R^2 = 0.91. Variables were transformed to natural logarithms.

There were significant differences in relative leaf and stem biomass distribution (Table 3.4). Leaf biomass was 16.5% under light, and 20.6% in medium shade conditions. Stem biomass allocation was 43.5% for light and 37.6% for medium shade (Table 3.4).

Table 3.4. Mean value for leaf, branch, stem, and root total mass per sapling (g) in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Component	**Full light conditions**		**Medium shade conditions**	
	(g)	(%)	(g)	(%)
L_{mass}	122.2 (110.4)^{a}	16.5^{a}	52.9 (64.6)^{a}	20.6^{b}
B_{mass}	148.9 (140.1)^{a}	20.1^{a}	58.7 (92.9)^{a}	22.8^{a}
S_{mass}	322.9 (288.2)^{a}	43.5^{a}	96.7 (112.9)^{a}	37.6^{b}
R_{mass}	148.2 (142.1)^{a}	19.9^{a}	48.9 (50.5)^{a}	19.0^{a}
T_{mass}	742.2 (633.6)^{a}	100.0	257.2 (204.2)^{a}	100.0

Note: L_{mass} is leaf mass allocation, B_{mass} is branch mass allocation, S_{mass} stem mass allocation, R_{mass} is root mass allocation, and T_{mass} is total biomass per sapling. a: Values in parenthesis indicate standard deviations; b: Rows with different letters indicate significant differences at $p < 0.05$.

3.3.2 Effect of light conditions on morphometric traits

ANCOVA tests applied to LA indicated no significant differences (Table 3.5a). R_{length}, L_{num}, L_{size}, and $H:S_{mass}$ were affected by age. ANOVA was used to detect significant differences, which were revealed for R_{length}, L_{num}, L_{size}, and $H:S_{mass}$ (Table 3.5b). R_{length} was significantly Higher (28%), L_{num} by 49%, and L_{size} by 18% in light conditions with respect to medium shade conditions (Table 3.6). On the other hand, $H:S_{mass}$ was significantly higher (55%) under medium shade conditions compared with light conditions (Table 3.6). However, no significant differences were detected for root:shoot, SLA, LA, or L_{th} H/Rcd (Table 3.6).

Table 3.5a. Terms of error of the covariance analysis (ANCOVA) in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Dependent	**Source**	**SS**	**FValue**	**ProbF**
Ln Leaf	Trat	0.00335032	0.03	0.8709
Ln Leaf area	$\text{Ln}(Rcd^2*H)$	30.59237687	243.30	<.0001
Ln Leaf area	$\text{Ln}(Rcd^2*H)*$Treat	0.00298238	0.02	0.8782

Note: Root collar diameter squared multiplied by height (Rcd2*H) as the covariable was used.

Table 3.5b. Terms of error of the variance analysis (ANOVA) for morphological variables in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Dependent	**Source**	**SS**	**FValue**	**ProbF**
R_{length}	Treat	1.500284	9.98	0.0025
Root:shoot	Treat	0.006152	0.04	0.8376
SLA	Treat	0.000107	0.00	0.9488
L_{num}	Treat	9.033051	13.62	0.0005
L_{th}	Treat	0.055284	1.93	0.1698
L_{size}	Treat	0.432718	9.13	0.0037
H:Rcd	Treat	0.055257	0.88	0.3524
$H:S_{mass}$	Treat	8.737515	20.26	<0.0001

Note: R_{length} is root length, root:shoot is the ratio of root mass to branch mass plus stem mass, SLA is specific leaf area, L_{num} the number of leaves per sapling, L_{th} leaf thickness per sapling, L_{size} is leaf size per sapling, H/Rcd the ratio of height and root collar diameter, and $H:S_{mass}$ is the ratio of height and stem mass. All variables showed significant differences ($p \leq 0.05$).

Table 3.6. Mean value for morphological variables in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Morphological variable	Full light condition	Medium shade condition
R_{length}	0.54 (0.24) ^{a}	0.39 (0.18) ^{b}
Root:Shoot	1.04 (0.41) ^{a}	1.04 (0.45) ^{a}
SLA	131.3 (27.64) ^{a}	129.2 (14.17) ^{a}
L_{num}	4162 (3197) ^{a}	2140 (2309) ^{b}
L_{th}	0.080 (0.014) ^{a}	0.075 (0.012) ^{a}
Lsize	3.77 (0.92) ^{a}	3.14 (0.56) ^{b}
H:Rcd	79.62 (18.00) ^{a}	75.63 (21.56) ^{a}
$H:S_{mass}$	1.24 (0.72) ^{a}	2.75 (1.75) ^{b}

Note: R_{length} is root length (m); root:shoot is the ratio of root mass to branch mass plus stem mass ($g\ g^{-1}$), SLA is specific leaf area ($cm^2\ g^{-1}$), L_{num} the number of leaves per sapling, L_{th} leaf thickness per sapling ($g\ cm^{-2}$), L_{size} is leaf size per sapling (cm^2), H/Rcd the ratio of height and root collar diameter ($mm\ mm^{-1}$), and $H:S_{mass}$ is the ratio of height and stem mass ($mm\ g^{-1}$). All variables showed significant differences ($p \leq 0.05$).

a: Values in parenthesis indicate standard deviations.

b: Rows with different letters indicate significant differences at $p < 0.05$.

3.3.3 Morphology plasticity

No significant plasticity was observed in biomass allocation. On the contrary, morphological plasticity was different in response to light conditions for morphological variables root:shoot ratio, L_{size}, and H/Rcd (Table 3.7). Similar values were found for both light conditions by averaging phenotypic plasticity indices for all variables (Table 3.7).

Table 3.7. Plasticity index in different light conditions in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile

Variable	Full light	Medium shade	Δ light conditions
L_{mass}	0.95	0.97	-0.02
B_{mass}	0.96	0.99	0.02
S_{mass}	0.95	0.98	-0.03
R_{mass}	0.95	0.97	-0.02
R_{length}	0.77	0.78	-0.01
Root:shoot	0.82	0.62	0.20
SLA	0.56	0.50	0.06
L_{num}	0.93	0.95	-0.02
L_{th}	0.50	0.50	0.00
L_{size}	0.63	0.53	0.10
H:Rcd	0.59	0.69	-0.10
H:S_{mass}	0.89	0.93	-0.10
Mean	0.69	0.70	-0.01

Note: L_{mass} is leaf mass allocation, B_{mass} branch mass allocation, S_{mass} is stem mass allocation, R_{mass} is root mass allocation, R_{length} root length; root:shoot is the ratio of root mass to branch mass plus stem mass, SLA is specific leaf area, L_{num} the number of leaves per sapling, L_{th} is leaf thickness per sapling, L_{size} leaf size per sapling, H/Rcd is the ratio of height and root collar diameter, and H:S_{mass} is the ratio of height and stem mass.

3.4 DISCUSSION

3.4.1 Effects of light conditions on biomass allocation and distribution

Saplings grow in changing environmental conditions. A successful strategy in one environment can be disastrous in a different one, which is why saplings use short and long-term allocation mechanisms (Bloom et al., 1985). Applying this principle, it has been hypothesized through plant ecology theory that adaptive strategies allow subordinate late succession and intolerant species and pioneer species settling under canopies. They do so to apply preferential allocation of biomass to the most efficient organs for acquisition of light (Givnish, 1984), water and nutrients (Grime et al., 1988), and phenotypic plasticity, which allows plants to cope under adverse conditions (Messier et al., 1999; Sultan, 2000).

The theory of global allocation for distribution of plant carbohydrates (Kitajima, 1994) assumes that shade conditions give rise to higher relative allocations of stems, constant allocation for leaves, and lower allocation for roots when compared to light conditions. However, in this study, no evidence was found regarding the effect of light on biomass allocation for the analyzed components (leaves, branches, stems, and roots). Considering relative allocation or partitioning, biomass components related to total biomass (Table 3.4), light effects on leaves and stems had a low impact, given that L_{mass} was greater in medium shade conditions by 5%, and S_{mass} by 5.9% (Table 3.4). This finding was also reported by Curt et al., (2005), confirming that allocation is mainly ontogenetic, and therefore presents variability throughout a tree's life (Kitajima, 1994; Gedroc et al., 1996).

Allometric relationships (Figs. 2, 3, 4, and 5) could be the result of size differences (Poorter and Nagel, 2000), given the strong correlation of Rcd and H in biomass components (Table 3.2). These relationships could represent apparent plasticity, which is not actual phenotypic plasticity defined as a change of allometric trajectory in response to variations in environmental conditions (Weiner, 2004). Although the theory of allocation is met in limited terms with respect to aerial biomass, light can have a clear impact on subjacent and underlying morphological variables.

3.4.2 Effects of light conditions on morphometric traits

Leaves play key roles in plant function and long-term adaptation to the environment. Although comprising basically epidermis, stomata, and mesophyll, leaves exhibit apparent differences in area, thickness, and shape among different species as result of adaptation to specific environments (Xu et al., 2008). Some studies have investigated how morphological traits of the leaf's economic spectrum such as leaf area and specific leaf area adapt to environmental factors. In this sense, the present results confirm that light strongly affected saplings growth and morphology. We found that L_{size} was 18% greater in light conditions compared to medium shade conditions, and that L_{num} doubled in light conditions (Table 3.6), showing a strong correlation with LA (Table 3.2). In this regard, these results are based on the fact that leaves respond to different habitats with phenotypic plasticity in leaf morphology, suggesting that this is an important mechanism for saplings to adapt to different environments (Xu et al., 2008). A correlation was found between L_{num} and H (Table 3.2), which was also reported by McGuire (2007) and Teste et al., (2009) where greater plant survival, in terms of leaf height and number, is favored when there is access to vesicular-arbuscular mycorrhiza networks, as has been the case for *N. dombeyi* (Alberdi et al., 2007). In the case of *Nothofagus fusca*, the number of leaves per stem increases with an increase in average solar radiation, therefore variations in leaf number and size may be the result of environmental limitations (Niinemets et al., 2006).

On the other hand, decreased leaf size in shaded conditions plays an important role in crown architectural design and strategies for light capture, since leaf biomass allocation between supporting and functional tissues can alter leaf venation patterns and function in environments with different resource levels (Niinemets et al., 2006). Studies showed that leaf longevity is greater in shade conditions, thus reducing nutrient loss, which contributes to success in environments with limited resources (Lambers and Poorter, 1992). Shadow leaves have usually a longer lifespan than sun leaves, while saplings exposed to light conditions may have higher leaf production rates, compensating for faster leaf deterioration (Pearcy and Sims, 1994). Our data agree with the suggestion of Reich et al., (1998) that leaf, root morphology and growth are closely associated with variation in life-history traits and that variation in leaf and root structure more strongly influences patterns of growth among species and light environments than does biomass partitioning.

Silvicultural implications of this study are that saplings in medium shade conditions can grow and develop just as well as in light conditions, because light only affects plant density (Encina et al., 2017) (Table 3.1). Therefore, the appropriate silvicultural regeneration form for *N. dombeyi* in old-growth forests would be single tree selection of group selection, ensuring a lose canopy coverage according to near-natural forestry principles and dynamics in natural forests.

3.5 CONCLUSION

In this study, age was highly correlated with biomass allocation of all plant components, demanding a covariable and analysis of covariance (ANCOVA). No evidence was found that light affects biomass allocation for the different components analyzed: leaves, branches, stems, and roots. Light had a low impact on stems and leaves related to partitioning. Allometric relationships could be the result of size differences, as in this study, given the correlation of Rcd and H with biomass components. However, it was found that L_{size} was 18% larger in light than in shade conditions. L_{num} doubled for light conditions with respect to shade, and R_{length} was 39% higher in light than in shade conditions. Therefore, saplings' leaf number and size decreased in shade conditions without increasing LA and decreasing R_{length}. However, the opposite occurred in light conditions, although leaf area also increased. *N. dombeyi* has long-lived leaves and increased root length. The specific leaf area did not show significant differences in either light condition, allowing conservation of the same amount of nutrients in both light conditions. Acclimation of leaves and roots to shade would increase sapling ability to intercept light and absorb nutrients, while changes in H:D, $H:S_{mass}$, and root:shoot ratios suggest that saplings allocate more biomass aboveground than belowground, partly in response to shade. Data from this study supports the hypothesis of higher plasticity in shade-intolerant species than in shade-tolerant ones and in leaf and plant morphology than in biomass allocation in response to contrasting light environments.

3.6 ACKNOWLEDGEMENTS

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CAPÍTULO IV

EFFECTS OF TWO CONTRASTING LIGHT ENVIRONMENTS: GAS EXCHANGE AND MORPHOLOGICAL TRAITS CORRELATED IN ADVANCED REGENERATION UNDER CANOPY OF OLD-GROWTH FOREST OF *Nothofagus dombeyi* (Mirb.) Oerst., IN THE CENTRAL-SOUTHERN ANDES, CHILE

Encina, P., Rodríguez, R., Muller-Using, B., Annighöfer, P., & Sánchez-Olate, M. “Effects of two contrasting light environments: Gas exchange and morphological traits correlated in advanced regeneration under canopy of old-growth forest of Nothofagus dombeyi (Mirb.) Oerst., in the central-southern Andes, Chile”. *Annals of Forest Science*. Enviado. 5-10-2018

ABSTRACT

In an environment of Mediterranean climate in the central-south Andes in Chile, the effect light availability has on the survival, development and growth of the advanced natural regeneration in an old-growth forest of *N. dombeyi* was analyzed. Treatments were performed in three gaps, where circular plots with 2 m radius were established in the center of the gap and at the edge of the closed canopy. In each plot and in high and low light conditions, transmissivity of solar radiation was measured, as was gas exchange in 36 plants. In addition, morphological traits were measured in the same plants through destructive sampling. Our results indicate that survival was distributed along the central axis of shade tolerance, which allows surviving in different light conditions. In response to the increase in Root collar diameter (Rcd) and Height (H), a correlation between morphological and gas exchange variables in which Rcd is highly dependent on light was found. But the mean annual increment (MAI) in height is only slightly dependent on light. In conditions of high light, photosynthetic performance of *N. dombeyi* improved, but MAI in H was limited by light saturation point (LSP). In low light conditions, *N* maintains specific leaf area (SLA) values similar to the high light condition, ensuring the availability of nutrients and the modification of the H/Rcd ratio to increase height and opportunities of light capture. In addition, *N. dombeyi* saturates photosynthesis and significantly increases the efficiency of water use to maintain photosynthetic performance. According to this study, it is suggested that appropriate

silvicultural management corresponds to the method of selection by groups, using gaps of light between 20 and 30 m in diameter, irregularly scattered.

Keywords: *Morphological traits, gas exchange, Nothofagus dombeyi, high light, low light.*

4.1 INTRODUCTION

Old-growth forests regenerate naturally with low human impact and dominated by trees that are close to the end of their biological life span or trees that have replaced the initial post-perturbation cohort (Shorohova et al., 2011). This type of tree presents no natural regeneration under its canopy and its generating dynamics are characterized by small disturbances inside the forest, creating gaps where seedlings and saplings survive and grow slowly for a long time in a light gradient from the gap to the shady canopy. This is known as advanced regeneration (Messier et al., 1999). Therefore, an understanding of the ecology of advanced regeneration that grows in the old-growth forest is necessary and useful for silvicultural management (Valladares and Niinemets, 2008). One approach that allows explaining growth and development of plants is the morphological adaptation to different light conditions (Messier et al., 1999). Saplings that grow in these light gradients present morphological traits that respond to the shade condition through the increase of their side increments of branches at canopy level at the expense of height increases (Stanciou and O'Hara, 2005).

The survival of seedlings in shade species has been related to carbon localization patterns where growth potential is sacrificed to enhance traits that favor survival (Walters and Reich, 1999). Therefore, light is the defining resource of adaptation to shade and a critical factor that affects tree traits. Light availability also crucially affects plants in the dynamics and succession of communities and in plasticity and morphology at individual and species scale (Jarčuška and Barna, 2011). The existence of plant species in an environment with variable light supply depends on their specialized adaptation to different light conditions or to capacity to adapt their phenotypes to the predominant conditions (Valladares et al., 2000; Valladares and Niinemets, 2008). Using an ecophysiological approach, Lusk and Del Pozo (2002) studied 12 species of high and low tolerance to shade of the rainy, temperate Chilean forest. In the present work, it was found that the rates of relative growth in aerial biomass in conditions of high levels of light presented a strong correlation with photosynthetic capacity and low mortality rates in conditions of high levels of light. On the other hand, the low mortality rates in conditions of low light levels showed strong correlation with the light compensation point and photosynthetic capacity. According to the above, the survival of tolerant species in conditions of low light levels presented disadvantages in relation to their growth rates, unlike seedlings of species that require more light, which grow faster (Walters and Reich, 1999). Therefore, survival and growth in conditions of high and low light availability can be attributed to various factors such as the level of shade tolerance of species, transmissivity of solar radiation through the canopy, carbon balance, location of biomass, and gas exchange variables like the light compensation point (Lusk and Del Pozo, 2002).

The most characteristic features regarding light availability are of morphological, anatomic and biochemical nature and are known as functional and physiological adaptive responses (Watt, 1925). In the leaf, the most common morphological traits are shade adaptability, total leaf area and the proportion of leaf area (leaf area divided by the dry mass of the entire plant), density of stomata and the proportions of chlorophyll α and β, so that the leaves can better adapt to the dynamics of the light environment in the canopy (Valladares et al., 2002). Therefore, the species naturally tend to adapt to changing environmental conditions through adjustments in both morphology and gas exchange (Wood, 2005; Hernández et al., 2010).

Although there is vast research on the physiological basis of plants' adaptation to environments with high and low levels of light, the results have been contradictory, inevitably leading to diverse conclusions (Lusk, 2002). This is explained by the real differences between deciduous forests and hardwood species (Walters and Reich, 1999), as well as ontogenetic changes in the features of plants (Poorter, 1999). Nothofagus dombeyi (Mirb.) Oerst, is normally a shade intolerant species that develops best in conditions of greater light. However, it tolerates shade better when growing at higher altitudes, preferring humid soils, forming pure forests, and in some situations is associated to other species (Donoso et al., 1991).

But saplings of *N. dombeyi* present a higher mortality rate when subjected to low light conditions (Lusk and Del Pozo, 2002). Accordingly, the light gradient determined the spatial distribution of *N. dombeyi* in which a differential adaptation of this species is reflected (Piper et al., 2007). Therefore, both survival and growth of *N. dombeyi* in conditions of high or low light availability is attributed to different factors, such as the condition of shade tolerant or intolerant species, light gradient between gaps and closed canopy, carbon balance, location of biomass and gas exchange variables; particularly the light compensation point and photosynthetic capacity (Donoso et al., 1991; Lusk and Del Pozo, 2002; Piper et al., 2007).

Our hypothesis establishes that the response of the advanced regeneration of *N. dombeyi* to growth in contrasting light environments presents changes in its morphological and physiological features especially in foliage and gas exchange, which explains its adaptation over long periods to the prevailing light conditions. Therefore, this study i) analyzes the impact of light availability on survival and development of advanced natural regeneration in two contrasting light environments, and ii) determines the relative importance of the morphological traits and gas exchange as correlates that explain the increase in Root collar diameter, height and survival of advanced natural regeneration of an old-growth forest of *N. dombeyi* in the central-southern area of the Andes in Chile.

4.2 MATERIALS AND METHODS

4.2.1 Study area

The study took place in three *N. dombeyi* old-growth forest stands near Yungay city, Bio Bio Region in central Chile (Density of 240 trees ha^{-1}, basal area of 56.7 m^2 ha^{-1}). (Figure 4.1). All stands of *N. dombeyi* belong to bioclimatic area called Andean Mediterranean Deciduous Forests of *Nothofagus obliqua* and *Austrocedrus chilensis* (Luebert & Pliscoff, 2006).

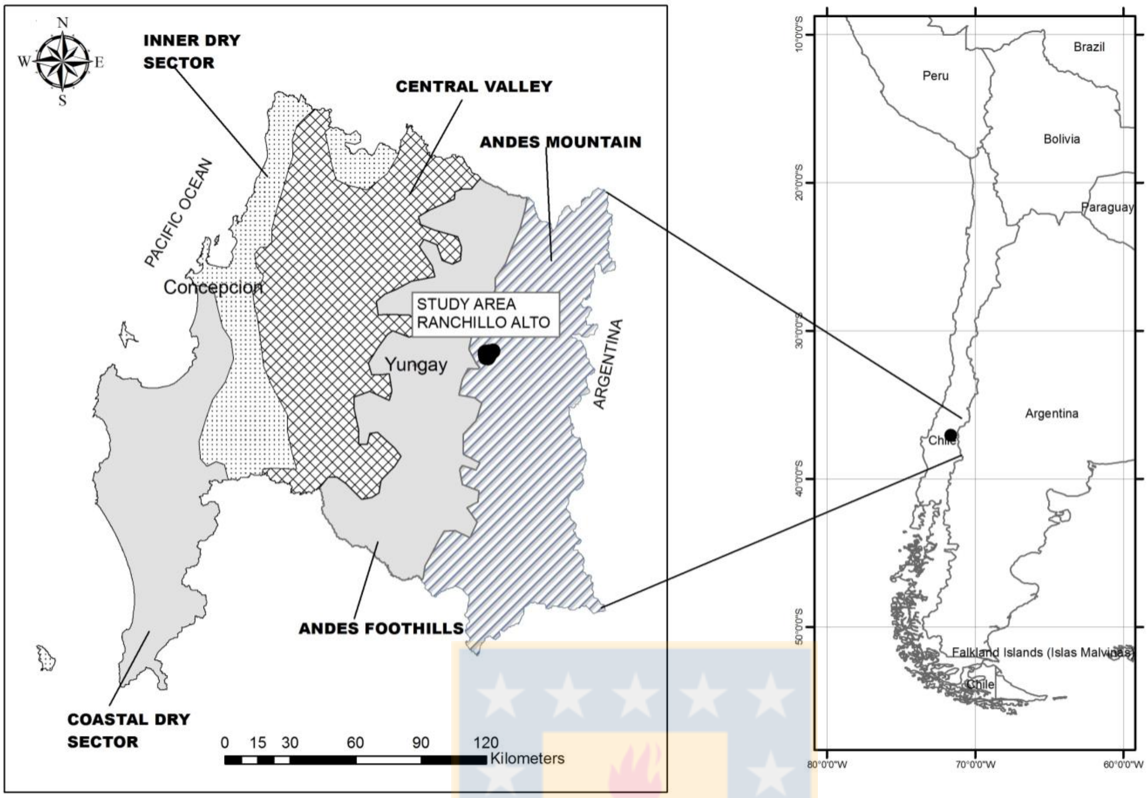

Figure 4.1. Location map of the study area in the Andes Mountains in the Biobío Region, Chile.

The bioclimatic area is characterized by extra zone communities called *Aristotelio-Nothofagetum dombeyi* (ravine), *Kagenekia angustifolia-Guindilia trinervis* (arid slopes) and *Nothofagus dombeyi-Gaultheria phillyreifolia* (water courses). However, in a state of old-growth, light conditions below the first canopy layer do often inhibit development of intermediate arboreal strata. The most characteristic geomorphological position of such a forest is in western mid-slopes of the Andes Mountains (Luebert and Pliscoff, 2006). The climate is Mediterranean, with rainfall concentrated during winter and a dry summer lasting three to four months. Study area altitudes (600-1,500 m.a.s.l.) correspond to an area with temperate Mediterranean climate as classified by Emberger (Del Pozo and Del Canto, 1999). Average annual rainfall exceeds 1,400 mm, and ice and snowfall can cause disturbances in the native forest, while growing season lasts around three months due to low winter temperatures (Del Pozo and Del Canto, 1999).

Soils originate from volcanic ash, most likely post glacial, resting on a non-related substrate comprising fluvial or glacio-fluvial materials that remain detected due to the depth at which they occur (Kühne et al., 2005). Soil is deep and medium-textured, generally silty loam within the first meter and silty clay loam at depths of 165 cm or more (Kühne et al., 2005).

4.2.2 Experimental design

The study was carried out on the basis of two contrasting regimes of solar radiation transmissivity, using three gaps that varied in size between 45 and 300 m2. In total, three circular plots with a radius of 2 m were randomly established. The center of gap represented the environment of high transmissivity of solar radiation (31.3 of diffuse solar radiation transmissivity) (Table 4.1). The other plots were in the interception of the edge of the gap and under the closed canopy (between 4% and 11% of diffuse solar radiation transmissivity) (Table 4.1). Under the closed canopy, no regeneration occurred (less than 3% of solar radiation transmissivity).

Table 4.1. Descriptions of light conditions, stand characteristics, and density of advanced regeneration in an old-growth forest of *N. dombeyi* growing in the central-southern Andean region of Chile.

Characteristics	**Full light conditions**	**Medium shade**
	Plots	**Plots**
	Center gap	**Border gap and closed canopy**
Dir	11.3 (10–13)	3.7 (2–5)
Dif	31.3 (27–37)	8.3 (4–11)
GL	19.7 (19–21)	4 (3–5)
BA	0	56.7
SD	0	240
REG	2.1	1.4

Note: Dir is direct solar radiation transmissivity (%), Dif is diffuse solar radiation transmissivity (%), GL is global solar radiation transmissivity, BA is Basal area (m^2 ha^{-1}), SD is stand density (trees ha^{-1}), and REG is saplings density (saplings m^{-2}).

4.2.3 Gas exchange measurements

A total of four plants of N. dombeti were randomly selected in the six circular plots established, giving 24 samples of individual plants in the growing season. Measurements of the photosynthetic rate were performed with an infrared gas analyzer (IRGA, CIRAS I, PPSystems, UK) at the end of the vegetative rest (Spring, 2016). Measurements were performed during the morning, between 9 and 11 hrs. Curves of response to light were obtained at room temperature and 3900 (with reference to CO2) and established in nine steps: 2,000, 1,500, 1,000, 500, 200, 100, 50, 20 and 0 μmol m^{-2} s^{-1} PAR. With the gas analyzer, the maximum photosynthetic capacity (A_{max}), stomatal conductance (gs), light compensation point (LCP), light saturation point (LSP) and water use efficiency (WUE) were determined.

4.2.4 Measurement of morphological features

After measuring the individual gas exchange, individual seedlings were sampled in six circular plots within the random gaps (Table 4.1). Sampling was carried out at the end of the growing season, in April 2016. Saplings were randomly chosen from the regeneration patches; they had to be undamaged, with no symptoms of pathogen attack. Height (H) and Root collar diameter (Rcd) were measured before the whole plant was harvested. After harvest, at the stem base a stem disc was collected from each individual to determine plant age (A) by counting year rings. Mean annual increment (MAI) for each plant was estimated by dividing H and Rcd by A. Plant compartments were stored in cold chambers at 2 ºC for further analysis. In the laboratory, all plant material was dried at 110 ºC for at least 24 hours, until reaching constant weight. A subsample of five leaves was taken from each plant and kept in a cold chamber at 2 ºC. Leaves were photographed using a Nikon Coolpix 7000 camera, and ImageJ win-32 software (rsb.info.nih.gov/ij/) was used to measure the size of the leaves (L_{size}) (cm2). Each leaf was then weighed on a precision analytical scale with 0.1 mg resolution. Specific leaf area (SLA) (cm2 g-1) was obtained from the ratio of leaf area and dry weight. Leaf area (LA) (cm2) was calculated as the product of leaf dry mass content (g) and SLA. The number of leaves (L_{num}) was obtained as a product of total leaf biomass ratio to subsample leaf biomass. Height to diameter ratio (H/Rcd, mm mm-1), and root dry mass to branches + stem dry mass (root/shoot, g g−1) ratios were calculated from the measurements. Leaf thickness (L_{th}) was estimated by dividing leaf biomass by leaf area, allowing thickness estimates from easily measured leaf traits (Vile et al., 2005; Pérez-Harguindeguy et al., 2013; Sevillano et al., 2016).

The plasticity index (from 0 to 1) was determined for variables studied during the growing season prior to harvest (growth, biomass, and foliage characteristics). It was calculated as the difference between maximum and minimum mean values for two treatments with light difference, divided by maximum mean value (Valladares et al., 2002; Sevillano et al., 2016). This index allowed the comparison of changes in variables expressed in different units.

4.2.5. Statistical analysis

To explore the relation between variables of natural regeneration density, morphological variables and gas exchange of the plants with light levels were correlated through the Spearman correlation coefficient. To analyze the effect of light level on the morphological variables of the plants and gas exchange, ANOVA and MANOVA were used:

4.3 RESULT

4.3.1 Effects of light on morphological features

As expected, the response of the morphological ranges studied to the light conditions was different. According to results of ANOVA and Tukey's test in high light conditions, LA was significantly higher (41%), L_{num} 48.3%, L_{size} 8.5% and L_{th} 8.8%, compared to low light conditions (Table 4.3). On the other hand, no differences were detected for SLA, root/shoot ratio and H/Rcd features (Table 4.2).

Table 4.2. Mean values for morphological and physiological variables in advanced regeneration for two contrasting light condition of old-growth forest of *N. dombeyi* growing in the central-southern Andean region of Chile.

Variable	High light	Low light
SLA	120.9 (19.72)^{a}	128.8 (14.37)^{a}
LA	19.04(14.58)^{a}	7,82(8.14)^{b}
L_{num}	5162 (3594)^{a}	2491 (2572)^{b}
L_{th}	0.086 (0.012)^{a}	0.076 (0.012)^{b}
L_{size}	3.67 (0.89)^{a}	3.13 (0.61)^{b}
Root/Shoot	0.35 (0.10)^{a}	0.33 (0.09)^{a}
H/Rcd	76.80 (19.73)^{a}	75.99 (22.95)^{a}
Amax	4.02 (1,29)^{a}	2.64 (0,81)^{b}
LCP	27.37 (18.21)^{a}	16.591(13.18)^{a}
LSP	160.72 (5.97)^{a}	110.67 (7.81)^{b}
WUE	85.08 (26.58)^{a}	61.50 (28.73)^{b}
Density	2.10 (1.02)^{a}	1.43(0.48)^{b}
MAI in Rcd	3.39(0.66)^{a}	2.90(0.61)^{b}
MAI in H	25.99(8.15)^{a}	21.95(6.98)^{a}

Note: SLA is specific leaf area; LA is leaf area; L_{num} is number of leaves per sapling; L_{th} is leaf thickness per sapling; L_{size} is leave size per sapling; Root/shoot is ratio root mass with branch mass plus stem mass; H/Rcd is height to root collar diameter ratio; A_{max} is maximum photosynthetic capacity; LCP is light compensation point; LSP is light saturation point and WUE is water-use efficiency; density in number in the plots; MAI is annual increment in root collar diameter and height, respectively.

a: Values in parenthesis indicate standard deviations.

b: Rows with different letters indicate significant differences at $p < 0.05$.

In turn, the non-parametric test of Spearman correlation indicates that in conditions of high levels of light density did not positively correlate with H/Rcd (0.57) (Table 4.3). In turn, MAI in Rcd was not correlated with any morphological feature, whereas MAI in H positively correlated with H/Rcd (0.8) and SLA (0.74), and negatively with L_{th} (-0.71) (Table 4.3). On the other hand, in low light conditions density correlated only with LA (0.47). In turn, Rcd positively correlated with LA (0.63) and L_{num} (0.63 and with no other morphological feature (Table 4.3)). In turn, MAI in H was positively correlated with H/Rcd (0.80).

Table 4.3. Spearman rank significant correlations of Rcd and H MAI in low and high light with morphological and gas exchange traits in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Phenotypes expressed in high light	r
Density:	
Height to root collar diameter ratio	0.57
Rcd MAI:	
Light saturation point	0.58
H MAI:	
Height to root collar diameter ratio	0.80
Specific leaf area	0.74
Leaf thickness	-0.71
Phenotypes expressed in low light	
Density:	
Leaf area	0.47
Light saturation point	0.51
Rcd MAI:	
Leaf area	0.63
Number of leaves	0.63
Light saturation point	0.61
Water-use efficiency	0.50
H MAI	
Height to root collar diameter ratio	0.80

4.3.2 Effects of light conditions on gas exchange

In this study, only IMA in Rcd was correlated with LSP in high light conditions. In turn, the density of advanced natural regeneration and MAI in H only responded to morphological features. In fact, the IMA in Rcd presents higher values in high light conditions that low light and both IMA in Rcd in high and low light increases as LSP increases (Figure 4.2).

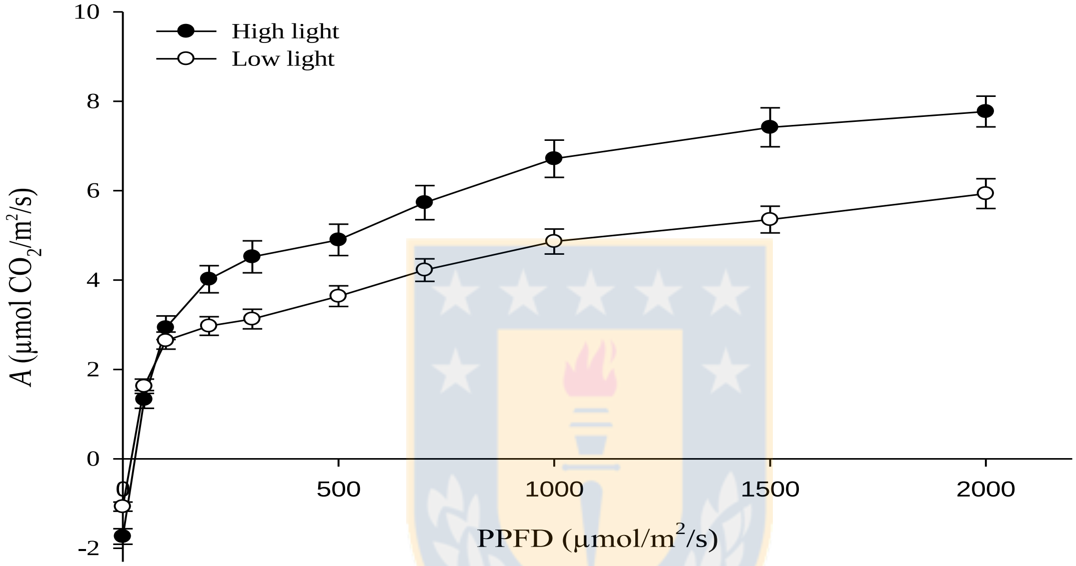

Figure. 4.2 Net photosynthesis rate (A) at different light intensities (photosynthetic flux densities, PPFD) for *N. dombeyi* leaves.

Note: Bars indicates standard error of means (s.e.m)

4.3.3 Morphological plasticity and gas exchange

Morphologic plasticity was observed in response to light conditions for the morphological variables L_{th} (-0.2) and H/Rcd (-0.12) (Table 4.4). In turn, the plasticity in gas exchange in response to light conditions were WUE (-0.11) and LSP (-0.07). By averaging phenotypic plasticity and gas exchange indices, similar values were found in both light conditions of 0.6 in high light conditions and 0.65 in low light conditions (Table 4.4).

Table 4.4. Plasticity index for morphological and gas exchange traits in different light conditions in advanced regeneration of *N. dombeyi*, growing in the central-southern Andean region of Chile.

Variable	High light	Low light	Δ light conditions
SLA	0.36	0.31	0.05
LA	0.94	0.96	-0.01
L_{num}	0.93	0.95	-0.02
L_{th}	0.30	0.50	-0.20
L_{size}	0.59	0.57	0.02
Root/shoot	0.65	0.68	-0.03
H/Rcd	0.55	0.67	-0.12
A_{max}	0.61	0.66	-0.05
LCP	0.92	0.90	0.02
LSP	0.08	0.15	-0.07
WUE	0.65	0.76	-0.11
Mean	0.60	0.65	-0.05

Note: SLA is specific leaf area; LA is leaf area; L_{num} is the number of leaves per sapling; L_{th} is leaf thickness per sapling; L_{size} is leaf size per sapling; Root/shoot is the ratio of root mass to branch mass plus stem mass; H/Rcd is the ratio of height and root collar diameter; A_{max} is maximum photosynthetic capacity; LCP is light compensation point: LSP is light saturation point and WUE is water-use efficiency.

4.4 DISCUSSION

4.4.1 Effects of light conditions on morphological features

Saplings compete for light, soil moisture and nutrients (Cannell and Grace, 1993; Nambiar and Sands, 1993), although evidence from temperate forests suggests that light has a stronger influence on growth and survival of young trees (Pacala et al., 1994). Several observations have been reported that the amount of light received by the undergrowth is a significant issue for establishment, survival and growth of saplings (Coates, 2002; Claveau et al., 2002; Kobe and Coates, 1997; Saldaña and Lusk, 2003). In this study, significant differences were found in the density of natural regeneration. These are attributable to the different light conditions, which in the highest density were found in conditions of high light with 2.1 plants m-2, and with respect to low light conditions with 1.43 plants m-2 (Table 4.1). These results are more or less consistent with a study by Müller-Using (1973), who reported values of natural regeneration that varied from 0.08 to 0.8 plants m-2 in low light conditions. Our results are supported by the theory of classical exchange, which suggests that the survival strategy of a species is defined by its high light growth rate and the capacity of a plant to survive in low light conditions. This allows that the density of species is distributed along a shade tolerance axis, which is only affected by the size of the saplings (Kunstler et al., 2009). This should be related with the traditional distinctions in tolerance to shade of the species (Baraloto et al., 2005).

We also found that the MAI in Rcd was higher by approximately 85.6% in high light conditions with respect to low light conditions, whereas no significant differences were found in MAI in H (Table 4.2). These results coincide with those reported in a controlled experiment of artificial establishment of *N. dombeyi*. In this study it was observed that the increase in Rcd is highly dependent on light, while growth in height is barely dependent on light (Donoso et al., 2015; Soto et al., 2014). This pattern has also been reported in evergreen and shade intolerant species (Valladares and Niinemets, 2008) such as *N. dombeyi*.

We found that in high light conditions, MAI in Rcd presented a positive and significant correlation with H/Rcd and SLA (Table 4.3). The correlation of H/Rcd is explained because height and Rcd are size components fundamental for the processes that range from individual behavior to the function of an entire ecosystem. The height of the sapling plays a significant role in the mechanical support (Niklas, 1993; Lundqvist and Valinger, 1996) found in the present study and reflects the interchange between growth and survival (King et al., 2006). The positive correlation between MAI in Rcd and SLA is sustained by a detailed study that has found a close relation between the potential growth rate of a species and its SLA. Therefore, this feature can be considered as the main issue that determines the interspecific variation in the growth rates for the different species since it concentrates the supply of nutrients in plants (Lambers and Poorter, 1992).

In this regard, leaves of *N. dombeyi* are structurally heavier, with a large leaf mass, which allows concentrating high levels of N and P. This is retained during most of the leaf’s life span of around four years (Hevia et al., 1999). Therefore, by presenting low dependence on life span, the IMA in H depends on the capacity of *N. dombeyi* to maintain its economy of leaf nutrients in conditions of a Mediterranean climate (Hevia et al., 1999) and the longevity of its leaves, since they avoid the loss of nutrients in habitats with limited nutrient (Lambers and Poorter, 1992). However, L_{th} was 8.8% higher in high light conditions with respect to low light conditions, and MAI in H was negatively correlated with L_{th} in high light conditions (Table 4.3). This could be explained by the high risks of photoinhibition.

It has been reported that photoinhibition reduces carbon gains of the treetops of high light, affecting more significantly more shaded leaves of a sapling than the leaves exposed to direct solar light in Mediterranean environments (Valladares et al., 2005). To decrease risks to photoinhibition, saplings increase thickness of the leaf in high light conditions, compared to low light, due to epidermal expansion (Ptushenko, 2016) to be adapted to the availability of water and longevity of the leaves. In order to achieve this, the species seem to use different photoprotective mechanisms to overcome unfavorable drought during dry season (Ishida et al., 2013).

These hypotheses are in line with the present study, with observations that indicate that interaction between low temperatures at high light levels in gaps in the Andes may be the cause of severe photoinhibition of *N. dombeyi* saplings (Donoso et al., 2013). This has showed better photosynthetic performance accompanied by a greater accumulation of photoprotective pigments in the xantophyll cycle under conditions of greater light intensity, temperature and drier conditions (Zúñiga et al., 2006).

Our study showed that LA is lower in low light conditions, due to the dramatic decrease in the number of leaves (Table 4.2), though both variables are significantly and positively correlated with IMA in Rcd. It has been reported that SLA and the concentration of N are important characteristics for relative growth rate and leaf gas exchange (Garnier et al., 2001). These authors also describe the area of light capture displayed per unit of leaf mass (Wright and Westoby, 2001). However, SLA increases as the thickness of the leaf decreases (Meziane and Shipley, 2001).

In the case of *N. dombeyi*, it has been reported that concentration of N in the leaf plays a significant role in the radial growth of different species in terms of use of resources. Likewise, this is strongly related to the growth of trees of shade intolerant species and with N availability at both high and low light levels (Soto et al., 2017). Since LA is a product of SLA for leaf mass, it is suggested that in order to maintain the supply of nutrients to the plant, these decrease AF by means of decreasing the dry mass, L_{size} and L_{th} (Meziane and Shipley, 2001). Therefore, SLA values were similar to those observed in high light conditions (Table 4.2). The fact that H/Rcd relations were similar in contrasting light environments, could suggest that saplings under low light conditions prioritized the allocation of biomass at IMA with H, at the expense of the IMA in Rcd and constitute a mechanism in which under competition for light, the increase in height is of main importance due to mechanical stress. For this reason, the H/Rcd ratio is regulated by local environmental conditions, mainly water stress (Lundqvist and Valinger, 1996; Vaninen and Mäkelä 2000; Rodríguez et al., 2003).

This hypothesis is supported by the fact that species of advanced regeneration in the shade compete especially for light, thus reducing the increase in biomass, though available carbohydrates are allocated to the increase in H, at the expense of growth in Rcd (Prévosto and Balandier, 2007; Einhorn et al., 2004; Ammer et al., 2005). Root:shoot ratios presented no significant differences in response to light conditions (Table 4.3), which supports this hypothesis since plants respond rather to their environment in such a way to optimize the use of resources (Bloom et al., 1985). Thus, the response to nutrient availability is an expression of such optimization between shoot and root (Ågren and Franklin, 2003), which in the case of *N. dombeyi*, depends on SLA (Hevia et al., 1999).

4.4.2 Effects of light on variables related to gas exchange

The photosynthetic rate of individual leaves of Nothofagus decreased as PPFD decreased (Figure 4.2). In addition, the maximum values of A observed in high light conditions reached significant values compared with evergreen and conifer species (from 5.0 to 12.5 µmolCO2/m2/s) and deciduous broadleaves (from 5.4 to 13.8 µmolCO2/m2/s) reported by Reich et al., (1995). Results in Zúñiga et al., (2006) are surprisingly similar to our study. These authors reported values from 6.0 to 6.1 in nursery plants (16.8 µmolCO2/m2/s) for midday conditions in spring, the same we measured in this study. Likewise, these values coincide with those reported by Lusk and Del Pozo (2002) of 6.1 (µmolCO2/m2/s) using values of 150 PPFD (high light conditions) in nursery plants transplanted into the Valdivian forest (2002).

However, a positive linear correlation has been reported between A and gs in response to water stress and where light is not a limiting factor (Peri et al., 2009). This contributed to the fact that maximum values of A for N. pumilio and N. antartica can be the result of a higher amount of RuBisCo and therefore a greater activity that is consistent with greater concentration of N in the leaf (Reich et al., 1995). In the present study, A always increased, but gs varied positively or negatively (Figure 4.3). Therefore, our data are based on the fact that photosynthetic yield in *N. dombeyi* is attributed to a higher accumulation of photoprotective pigments in the xanthophyll cycle (Zúñiga et al., 2006). LCP values in high light conditions differ greatly from those reported by Lusk and Del Pozo (2002) of 15.0 with respect to 27.37, but are similar to the 16.6 of our study in low light conditions. This can be explained by the PPFD levels used in both studies.

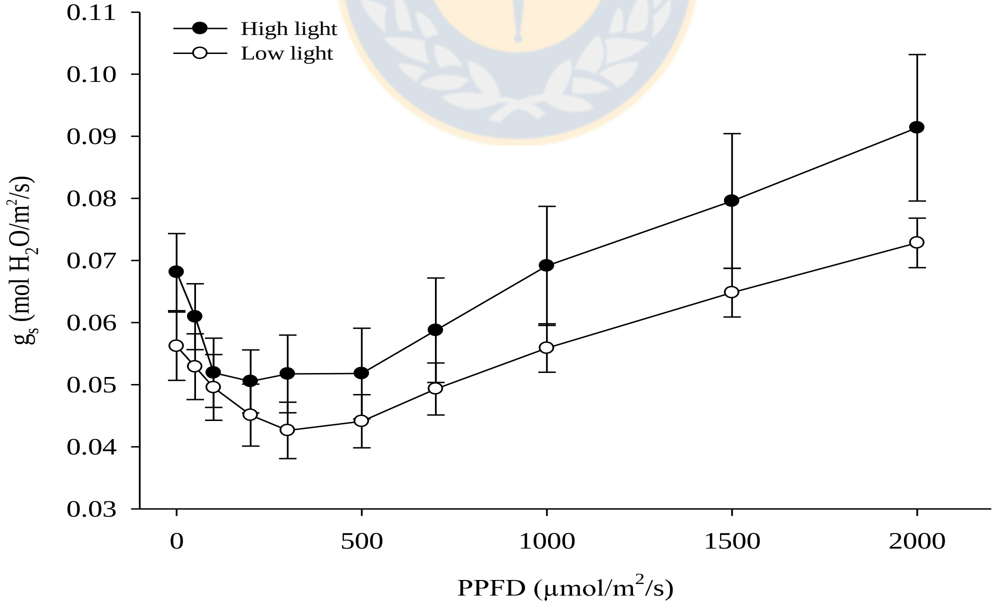

Figure 4.3 Stomatal conductance (g_s) at different light intensities (photosynthetic flux densities, PPFD) for *N. dombeyi* leaves.

Note: Bars indicates standard error of means (s.e.m)

The relation between LSP on IMA in Rcd suggests a limiting factor in the light that influences growth (Figure 4.4). Features of gas exchange emphasize the differences between conditions of high light and plants adapted to low light. An excess of light inhibits growth, changes external morphology and modifies the structure of the chloroplasts.

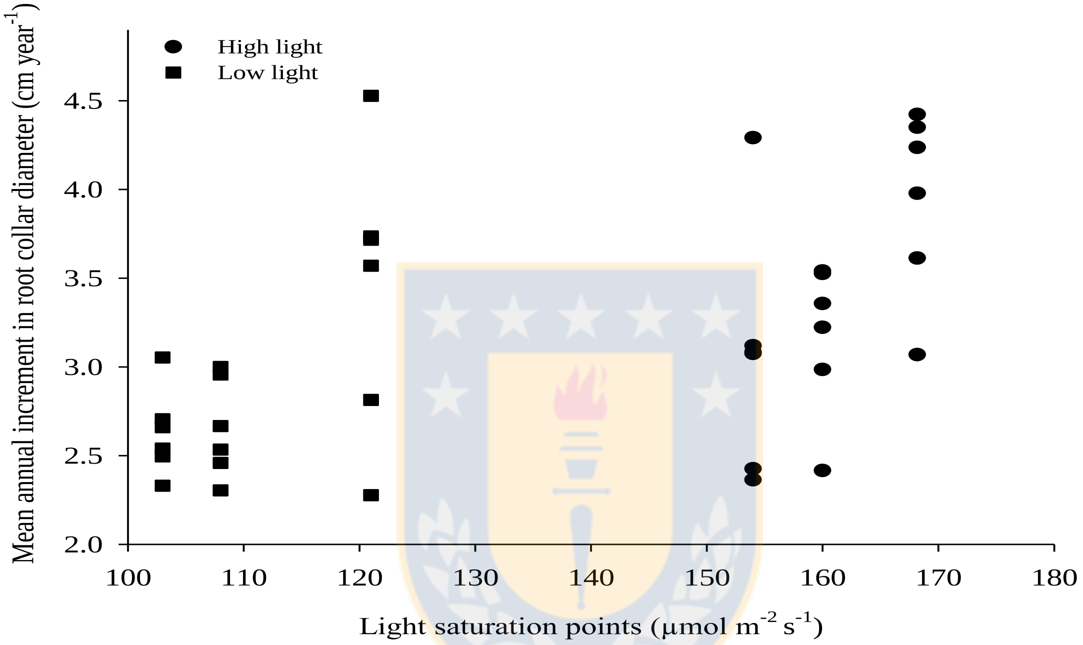

Figure 4.4 Relation between photosynthetic light saturation points of *N. dombeyi* trees in high light, low light (μmoles m^{-2} s^{-1}), and mean annual increment (mm year^{-1}) in root collar diameter. Non-parametric correlation statistics appear in Table 4.3. In high light (r = 0.58; p-value = 0.01), in low light (r = 0.61; p-value = 0.006).

Therefore, it has been suggested that the photosynthetic functions supported by grana are involved in the luminous function of photosynthesis in low light conditions (Mache and Loiseaux, 1973). In fact, the harmful effect of an excess of light has been already mentioned. However, Gauhl (1976) observed no symptoms of photoinhibiton when a plant adapted to shade. On the other hand, *N. dombeyi* has a relatively high point of photosynthetic saturation and it is possible that the excess of energy may have been insufficient for active thermal dissipation at water potentials above -2.5 MPa in high light conditions (Piper et al., 2007). However, when the saturation point of photosynthesis decreased with the intensity of drought, adjustments in the photosynthetic system occurred (Zúñiga et al., 2006). Another possible explanation is the relation of MAI with Rcd that positively correlated with WUE, which depends on the content of soil moisture only under low light conditions (Figure 4.5).

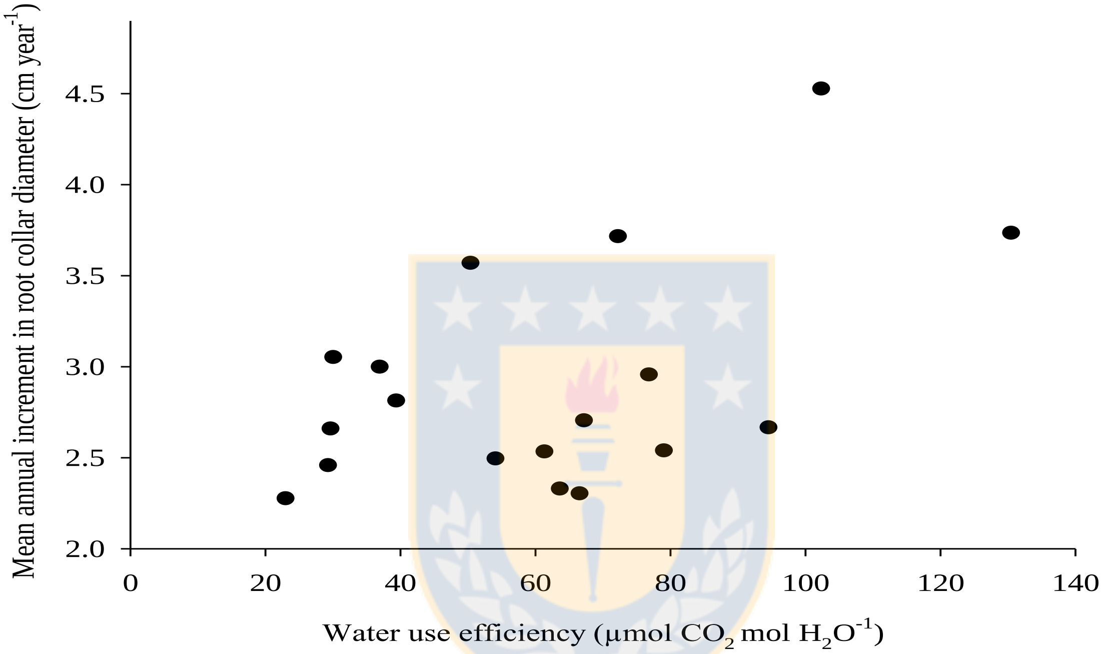

Figure 4.5 Relation between use-efficiency in low light (µmol CO^2 mol H_2O^{-1}) and mean annual increment (mm $year^{-1}$) in root collar diameter. Non-parametric correlation statistics appear in Table 4.3. (r = 0.50; p-value = 0.03)

In this regard, differences in WUE in both light conditions seem to be promoted mainly by differences in the photosynthetic rate (Figure 4.2), according to other studies (Dudley, 1996; Valladares et al., 2016) and in contrast to others that attributed variations in WUE to differences in the stomatal conductance (Read and Farquhar 1991; Zhang et al., 1997; Anev et al., 2016). Features of gas exchange seemed more important than morphological features as determinants of interspecific variation in terms of growth and survival of saplings in a Mediterranean environment. However, survival in high light conditions was strongly correlated with only one morphological feature (Rcd), though in low light conditions, only with LSP (Table 4.3). Therefore, our data suggest an intimate metabolic connection between photosynthesis, carbohydrate capacity and the maintenance of respiratory rates, which constitutes one of the main causes of trade-off. This is frequently cited to privilege growth in high light conditions and survival under low light (Baraloto et al., 2005).

Consequently, a high potential metabolism is an advantage to promote rapid growth in open habitats or gaps, especially in Rcd, but a sacrifice in the IMA in H, in environments where carbon gain is severely restricted by light, water, and nutrient conditions (Grime, 1965; Loach 1967; Givnish 1988; Reich et al., 1998). Results showed that under higher light intensity *N. dombeyi* performs better photosynthesis (Figure 4.2), and the data are consistent with the pioneer capacity of this species and the properties of semi-tolerance to shade (Zúñiga et al., 2006). However, the success of a plant in low levels of light not only depends on the efficiency of the photosynthetic process, but also on the photosynthetic surface that is receiving light and that contributes to the production of carbohydrates (Florence, 1996).

4.4.3 Morphological and gas exchange plasticity

To adapt from high to low light conditions, morphological plasticity was associated to L_{th} and H/Rcd, which is explained by the need to maintain high values of SLA (Lambers and Poorter, 1992) and the need to locate growth in response to environmental stress and especially in the competition for light. This is a result of the close relation between the potential growth rate of a species and the SLA (ibid.), which constitutes an acclimatization of leaves to shade. This allows saplings to increase their capacity to intercept light. In addition, the gas exchange variable LSP and WUE showed a significant plasticity in response to light levels (Table 4.4), which also reveals the semi-tolerant properties to shade. Therefore, it is observed that *N. dombeyi* has developed gas exchange and/or morphological mechanisms that allow it saturating photosynthesis before risks of photoinhibition emerge or use thermal dissipation in the face of excess energy (Piper et al., 2007). This occurs in high light conditions (Figure 4.4) to develop economical use of water during water deficit periods (Dudley, 1996; Valladares et al., 2016). Thus, photosynthetic behavior would be improved (Figure 4.5), as well as a potentially higher net productivity achieved in these conditions than species that close their stomata in response to relatively small water deficits. Therefore, the hypothesis can be formulated that saplings of species in Mediterranean environments, where the warmest months are usually the driest, develop gas exchange and morphological mechanisms that allow them to adapt to different ranges of light and soil water availability.

4.4.4 Silvicultural implications

The amount of light transmitted to the undergrowth is crucial to determine the dynamics of regeneration and growth of saplings in early stages of natural regeneration development (Sevillano, 2016). In the case of some silvicultural systems such as selection in groups or individuals, they can be used to provide continuous cover forestry (CCF) (Hawe and Short, 2012) and are valuable tools to provide structural diversity of species while remaining part of the existing canopy (Brang et al., 2014).

Considering the study background, regeneration of *N. dombeyi* clearly shows that it has adapted to a variety of light ranges, capable to behave like shade intolerant species in high light conditions and semi-tolerant ones in shady conditions. However, advanced regeneration in gaps and the annual increase in height are limited by gas exchange and/or morphological mechanisms that allow the species to saturate photosynthesis before risks of photoinhibition occur (Donoso et al., 2015), or use thermal dissipation in the face of excess energy (Piper et al., 2007). In low light conditions, *N. dombeyi* is limited in its annual growth in diameter, since morphological mechanisms such as SLA and H/Rcd and gas exchange must be developed, such as saturating photosynthesis and substantially increase the efficiency of water use. This will allow the increase in height and the possibilities of light capture.

In according our findings, future studies on size and frequency of gaps should focus not only on the survival of saplings, but also on how to influence development in sapling size through management of light in an old-growth stand of *N. dombeyi*. Among the different reasons for the silviculturalist to favor the process of natural regeneration of a given forest, is to optimize the relationship between the light demands of the species with the level of luminosity that is offered through the management of the canopy in the strata above it. This task is not the same for different climatic zones. In the case of our study, there is an offer of solar radiation over very high crowns in absolute terms, given the geographical location that places it in an area of Mediterranean climate. Although the transmissivity of *N. dombeyi* canopy with their evergreen and not very transparent leaves absorbs incident light at 34% in the centers and 8% at the edges of the gaps under study, this effect still offers, in absolute terms, a luminosity to the advanced regeneration of *N. dombeyi*, which guarantees the establishment and - despite a high mortality in the first years - an acceptable survival of (18,000 saplings ha^{-1}). If this were the silviculturist's only goal, it could be limited to small-scale interventions, such as the perennial foot-harvest of mature trees or a small-group selection method. However, in the case of our study it is about a mature forest. These forests are already in a process of collapse that with the advance of time is accentuated and the cost/benefit ratio of forest management is decreasing more and more. Furthermore, by not advancing in the rejuvenation of that forest, its quality as a net carbon emitter is perpetuated, an effect that must also be taken into account. The values of accumulation of biomass, found at high levels of light, which is expressed in a higher density and foliage twice as many as in low light conditions, play, therefore, in favor of somewhat larger gaps. Photo-inhibition in these conditions is not as strong as speaking of a harmful luminosity. It has also been reported in the case of *N. nitida* during development, changes the balance of light energy utilization and photoprotective mechanisms, supporting a phenotypic transition from shade to sun during its early ontogeny (Coopmann et al., 2008). Another argument to work with larger gaps than merely necessary for the establishment of young plants is that with it there are not so many old trees left if a complete regeneration, which when harvested later, causes considerable damage in the undergrowth. It is concluded, therefore, that a harvest by gaps of light between 20 and 30 m in diameter is a good compromise that does not contradict the results of our study.

4.5 CONCLUSION

Survival was distributed along the axis of shade tolerance, which allows survival in different light conditions. This survival strategy of *N. dombeyi* follows the theory of classic exchange, which privileges growth rate in high light conditions and capacity of natural regeneration to survive in low light conditions. In response to the increase in Rcd and H, a correlation between morphological and gas exchange variables emerged, in which Rcd is highly dependent on light, but growth in height is only slightly dependent on light. Thus, in high light conditions *N. dombeyi* showed better photosynthetic performance, though MAI in H is limited by gas exchange mechanisms that allow saturating photosynthesis before risks of photoinhibition occur. However, in low light conditions, *N. dombeyi* develops mechanisms of morphological plasticity associated to L_{th} and H/Rcd to maintain SLA values related to the supply of nutrients and the modification of the H/Rcd ratio to increase its height and the chances to capture light. In addition, *N. dombeyi* saturates photosynthesis and significantly increases the efficiency of water use to maintain photosynthetic performance. According to this study, it is suggested that appropriate silvicultural management corresponds to the method of selection by groups, using gaps of light between 20 and 30 m in diameter, irregularly scattered.

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CAPÍTULO V

EFECTOS DE LA TRANSMISIVIDAD DE LA RADIACIÓN SOLAR Y EL RÉGIMEN DE LUZ EN EL ESTABLECIMIENTO Y CRECIMIENTO DE TRES ESPECIES NATIVAS EN DIFERENTES RANGOS DE TOLERANCIA A LA SOMBRA, EN UN BOSQUE SOBREMADURO DE *Nothofagus dombeyi* (Mirb.) Oerst., EN EL CENTRO-SUR DE LOS ANDES, CHILE

Encina, P., Rodríguez, R., Muller-Using, B., Annighöfer, P., & Sánchez-Olate, M. “Effects of solar radiation transmissivity and light regime on the establishment and growth of three species with different ranges of tolerance to shade, under canopy of old-growth forest of *Nothofagus dombeyi* (Mirb.) Oerst., in the central-southern Andes, Chile”. (En preparación)

RESUMEN

Se reconoce la necesidad de establecer plantaciones suplementarias para mejorar la provisión de servicios ecosistémicos y la productividad de bosques sobremaduros mono específicos. Sin embargo, se desconoce el comportamiento de las nuevas especies a la variabilidad de rangos de luz de estos bosques. Bajo un bosque sobremaduro de *Nothofagus dombeyi*, se establecieron nueve parcelas cuadradas cercadas de 5×5 m en la cual se plantó la especie intolerante *N. Nervosa*, la especie semitolerante *L. sempervirens* y la especie tolerante *P. saligna*. La especies se establecieron en tres niveles de Dif, en claros (32%), Valores medios de Dif (19%) y bajos niveles de Dif (7%), medidos mediante cámara tipo fisheye (Solariscope®). Además, mediante un medidor de gases (IRGA, CIRAS I, PPSystems, UK), se midieron por cada especie 5 plantas en luz y 5 plantas en sombra en la que se obtuvo Amax, LSP, LCP, g_s y WUE. Se midieron durante tres períodos de crecimiento la supervivencia, Dac (diámetro a la altura del cuello) y H (altura), de las cuales se obtuvieron Dac e incremento en H. Se presentaron altas tasas de supervivencia y no presentaron diferencias significativas entre especies ni rangos de Dif. Bajo alta luminosidad, el mayor incremento en Dac se presentó en *N. nervosa* y los más bajos se presentaron en *P. saligna*, atribuible al comportamiento fotosintético de las especies. En condiciones de baja luz el diámetro a la altura del cuello (Dac) y la altura (H) disminuyeron dramáticamente y no se presentaron diferencias significativas entre las tres especies. Sin embargo, en *N. nervosa* en condiciones de baja luz, se encontró una estrecha relación entre el incremento en Dac y LSP, revelando riesgos de inhibición asociados a altos niveles de luz. *P. saligna* presentó una estrecha relación con g_s, revelando la sensibilidad de la especies a estrés hídrico. En este estudio se sugiere que es útil el empleo de la mezcla formada por *N. nervosa*, *L. sempervirens* y *P. saligna*, para la provisión de servicios ecosistémicos y aumento en la productividad del bosque sobremaduro, para lo cual se debe intervenir utilizando el método de selección en grupos, utilizando claros de pequeño tamaño, no mayor a 30 m de diámetro y separados a 30 y 40 m. La plantación puede ser factible con un 20% de transmisividad de radiación difusa.

Keywords: Bosque sobremaduro, Establecimiento, Especies-Mixtas

5.1 INTRODUCCIÓN

El valor de conservación o las posibilidades del desarrollo de técnicas silvícolas de los bosques sobremaduros, depende del estado actual de los bosques, los que han sido afectados tanto por prácticas de manejo, decisiones que se han tomado anteriormente para su protección y el uso histórico de las tierras. Finalmente, el contexto socio-económico dado por la presencia de las comunidades dependientes de estos recursos, es esencial para determinar las posibilidades futuras tanto de manejo como de conservación de bosques sobremaduros (Spies, 2004).

En el caso de Chile, se han observado que en bosques sobremaduros de *N. dombeyi* con disturbios de pequeña escala, cuando no está presente o en baja densidad una especie de bambú nativo del género *Chusquea*, los pequeños claros favorecen la regeneración de *N. dombeyi* (Lusk 2001; Encina et al., 2018). Estas perturbaciones a pequeña escala afectan la distribución de la radiación solar en el interior del bosque y los patrones de regeneración en bosques sobremaduros (Promis et al., 2010; Encina et al., 2018). Sin embargo, estudios experimentales, ecofisiológicos y poblacionales indican la existencia de divergencias interespecíficas con relación a la supervivencia, el crecimiento y desarrollo de renovales de *N. dombeyi* creciendo bajo diferentes regímenes de luminosidad posterior al disturbio (Weinberger y Ramírez, 2001). Así, el aumento del tamaño y el incremento en altura de plantas provenientes de la sucesión de especies intolerantes, solo alcanzarán estratos superiores y competirán exitosamente con especies de sombra, solo si aumenta la disponibilidad de luz (Messier et al., 1999).

De acuerdo a observaciones en la región del Biobío, la dinámica regenerativa de *N. dombeyi* creciendo en la zona precordillerana del Centro-Sur de Chile, no están en fase de equilibrio, ni en la fase óptima de productividad (Veblen, 1979). Por otra parte, las estructuras y comportamiento de especies tolerantes como *Laurelia philipiana* y *Drymis winterii*, sugieren que en ausencia de disturbios de gran escala, estas especies podrían sustituir a *N. dombeyi*, en la zona precordillerana de la región del Biobío (Veblen et al., 1980).

Por tanto, es posible copiar la dinámica natural mediante el reemplazo de una cubierta vegetal compuesta por una sola especie a una mezcla de especies, lo que puede contribuir a cumplir diversos objetivos de manejo como es la protección de la biodiversidad, mantener la belleza escénica o la producción de agua (Nyland, 2002). En esta perspectiva, las prácticas silvícolas pueden contribuir a la regeneración bajo dosel compuesta por una sola especie, mediante el manejo de las estructuras del dosel con el objetivo de regenerar y reasignar espacios de crecimiento para especies deseadas (Puettmann et al., 2008), especialmente la regeneración artificial compuesta por una mezcla de especies. La regeneración artificial permite el empleo de numerosas técnicas silvícolas que no son posibles o viables en un bosque puro, ya que el establecimiento de muchas especies, que no pueden sobrevivir en ambientes de radiación solar directa, requiere de árboles de refugio, para acondicionar el microclima, el control de vegetación indeseada y favorecer la regeneración natural (Larjavaara, 2008).

Las preguntas sobre qué niveles de recursos o factores ambientales influyen más significativamente en la supervivencia de las plántulas ha sido un tema de las últimas décadas (Walters y Reich, 1997, Kobe, 2006). Además, en climas de tipo mediterráneo, las plantas suelen ser sometidas a estrés hídrico y térmico durante el verano. La escasez de precipitaciones durante esta temporada se asocia generalmente con una alta frecuencia de días claros, lo que se traduce en grandes cargas de radiación solar (Larcher, 1995). Por ello, las plantas adoptan estrategias preventivas en ambientes de recursos limitantes (Valladares y Pearce, 1997). Aun así, la luz es el recurso definitorio de adaptación a la sombra y un factor crítico que afecta los rasgos de plantas juveniles (Lieffers et al., 1999), además de un conjunto de condiciones ambientales, como el movimiento del aire, temperatura, el nivel de CO_2, humedad y nutrientes del suelo (Messier et al., 1999; Valladares et al., 2000; Valladares and Niinemets 2008). Al respecto, Lusk (2002) analizando 12 especies chilenas de alta y baja tolerancia a la sombra del bosque templado lluvioso, encontró que las tasas de crecimiento relativo en biomasa aérea en condiciones de altos niveles de luz, presentaron una fuerte correlación con la capacidad fotosintética y que las bajas tasas de mortalidad en condiciones de bajos niveles de luz tuvieron una fuerte correlación positiva con el punto de compensación de luz y capacidad fotosintética. Por tanto, la supervivencia y crecimiento en condiciones de alta o baja disponibilidad de luz puede atribuirse a diversos factores, la condición de especie tolerante o intolerante a la sombra, transmisividad de la radiación solar a través del dosel, balance de carbono, localización de biomasa y variables de intercambio gaseoso (Lusk y Del Pozo, 2002).

La teoría de la tolerancia a la sombra sugiere que hay especies con adaptaciones fisiológicas y específicas de crecimiento que influyen en su capacidad para sobrevivir y crecer a diferentes niveles de luz. Por ejemplo, en baja luz especies tolerantes a la sombra crecen pero reducen la altura y diámetro y presentan una baja mortalidad, pero este comportamiento no necesariamente puede ser para especies intolerantes a la sombra (Kobe y Coates, 1997). Tales diferencias resultan en diferencias interespecíficas en respuestas a la luz, relacionadas con el crecimiento. Una posibilidad es que especies tolerantes a la sombra mantengan una ganancia de carbono positiva con poca luz, pero muestran una ganancia menor de carbono en condiciones de alta luminosidad que especies exigentes intolerantes a la sombra (Bazzas, 1979).

Debido a la importancia del bosque sobremaduro, los que son altamente sensibles para la comunidad, en que además existe una preocupación permanente acerca del manejo de ellos, se hace necesario un enfoque silvicultural extremadamente cuidadoso del manejo de estos bosques, que permitan guiar artificialmente la regeneración natural y artificial mediante mezcla de especies. Nuestra hipótesis es que es necesario utilizar el disturbio natural y artificial, para favorecer el establecimiento de mezclas de plantaciones suplementarias, en que se pueden encontrar especies adecuadas para crecer y sobrevivir en rangos apropiados de transmisividad de radiación solar y que tienen mecanismos para adaptarse a la luz, creciendo en bosques sobre maduro de *N. dombeyi*. Por tanto, los objetivos de este estudio son analizar el efecto de diferentes niveles de transmisividad de radiación solar y evaluar la importancia de intercambio gaseoso en los patrones de establecimiento en supervivencia, crecimiento en diámetro y altura de plantas durante tres períodos en *Nothofagus nervosa*, especie intolerante a la sombra; *Laurelia sempervirens*, especie semi-tolerante a la sombra y *Podocarpus saligna*, especie tolerante a la sombra, establecidas en mezcla creciendo bajo dosel de rodales sobremaduros de *N. dombeyi*.

5.2 MATERIAL Y METODOS

5.2.1 Area de estudio

El estudio se llevó a cabo en tres rodales forestales de *N. dombeyi* en la Región del Biobio en la ciudad de Yungay, en el centro-sur de Chile (densidad de 240 árboles ha-1, área basal de 56.7 m2 ha-1). (Figura 5.1). Todos los rodales de *N. dombeyi* pertenecen al área bioclimática llamada Bosques caducifolios del Mediterráneo andino de *Nothofagus obliqua* y *Austrocedrus chilensis* (Luebert & Pliscoff, 2006).

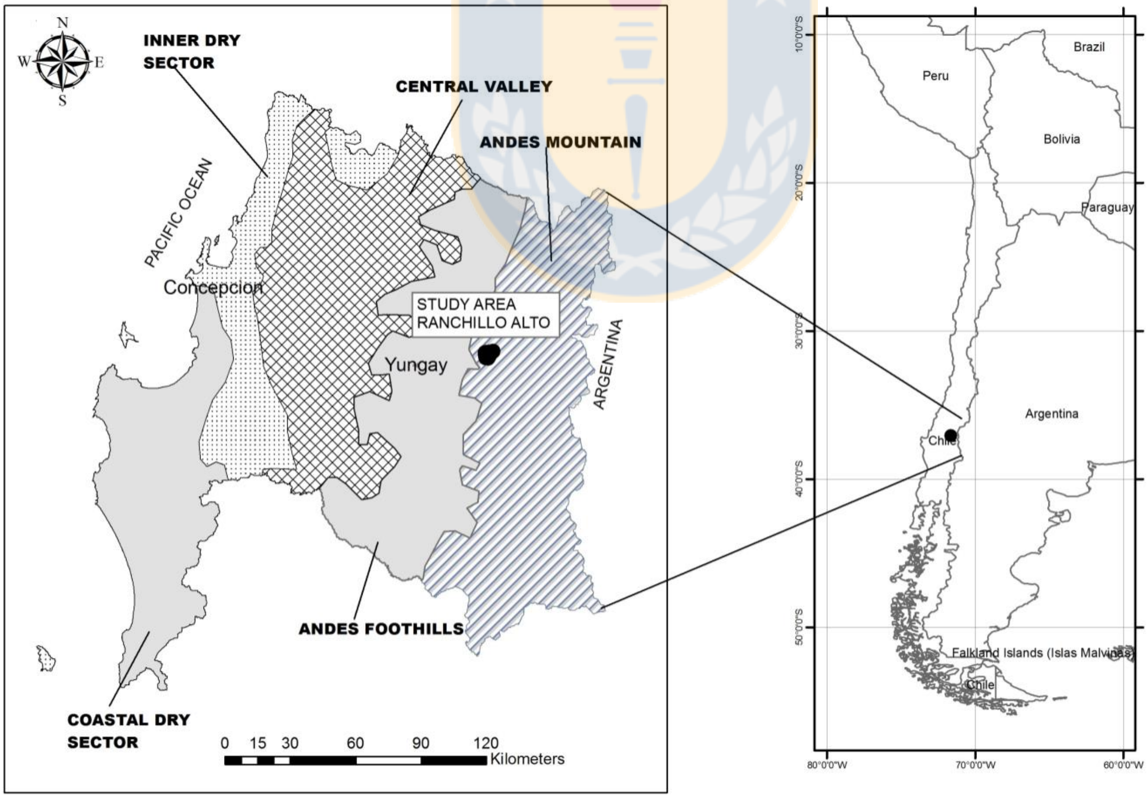


Figura 5.1. Mapa de ubicación del área de estudio en la Cordillera de los Andes en la Región del Biobío, Chile.

El área bioclimática se caracteriza por comunidades extras de zonas adicionales llamadas *Aristotelio-Nothofagetum dombeyi* (barranco), *Kagenekia angustifolia-Guindilia trinervis* (pendientes áridas) y *Nothofagus dombeyi-Gaultheria phillyreifolia* (cursos de agua). Sin embargo, en un estado sobremaduro en condiciones de luminosidad, debajo de la primera capa del dosel a menudo se inhibe el desarrollo de los estratos arbóreos intermedios. La posición geomorfológica más característica en bosques de este tipo se encuentra en la parte media occidental de las laderas de los Andes (Luebert y Pliscoff, 2006). El clima es mediterráneo, con precipitaciones concentradas durante el invierno y un verano seco que dura entre tres y cuatro meses. Las altitudes del área de estudio (600-1,500 m.s.n.m.) corresponden a un área con clima mediterráneo templado según la clasificación de Emberger (Del Pozo y Del Canto, 1999). La precipitación promedio anual supera los 1,400 mm, y el hielo y las nevadas pueden causar disturbios en el bosque nativo, mientras que la temporada de crecimiento dura alrededor de tres meses debido a las bajas temperaturas invernales (Del Pozo y Del Canto, 1999).

Los suelos se originan a partir de cenizas volcánicas, probablemente post glaciales, que descansan sobre un sustrato no relacionado que comprende materiales fluviales o glacio-fluviales que permanecen detectados debido a la profundidad a la que ocurren (Kühne et al., 2005). El suelo es profundo y de textura media, generalmente franco limoso dentro del primer metro y franco arcillo limoso a profundidades de 165 cm o más (Kühne et al., 2005).

5.2.2 Diseño experimental

Bajo un bosque sobremaduro de *N. dombeyi*, se establecieron nueve parcelas cuadradas cercadas de 5×5 m en tres niveles de transmisividad de radiación solar (alta, media y baja). En cada parcela se eliminó toda la vegetación competitiva arbustiva y se incluyó una zona central de 4×3 m rodeada por una zona de amortiguación de 3 m. La zona central se subdividió en una distancia de plantación entre y sobre la hilera de 0,5 m (Figura 5.2). En cada parcela se establecieron tres especies nativas en mezcla, 21 plantas por cada especie, de raíz cubierta de dos años (*Nothofagus nervosa*, *Laurelia sempervirens* y *Podocarpus saligna*), adquiridas por un vivero local, las plantas se distribuyeron en forma alternada dentro de cada parcela, estableciéndose en noviembre del año 2015 (Figura 5.3)

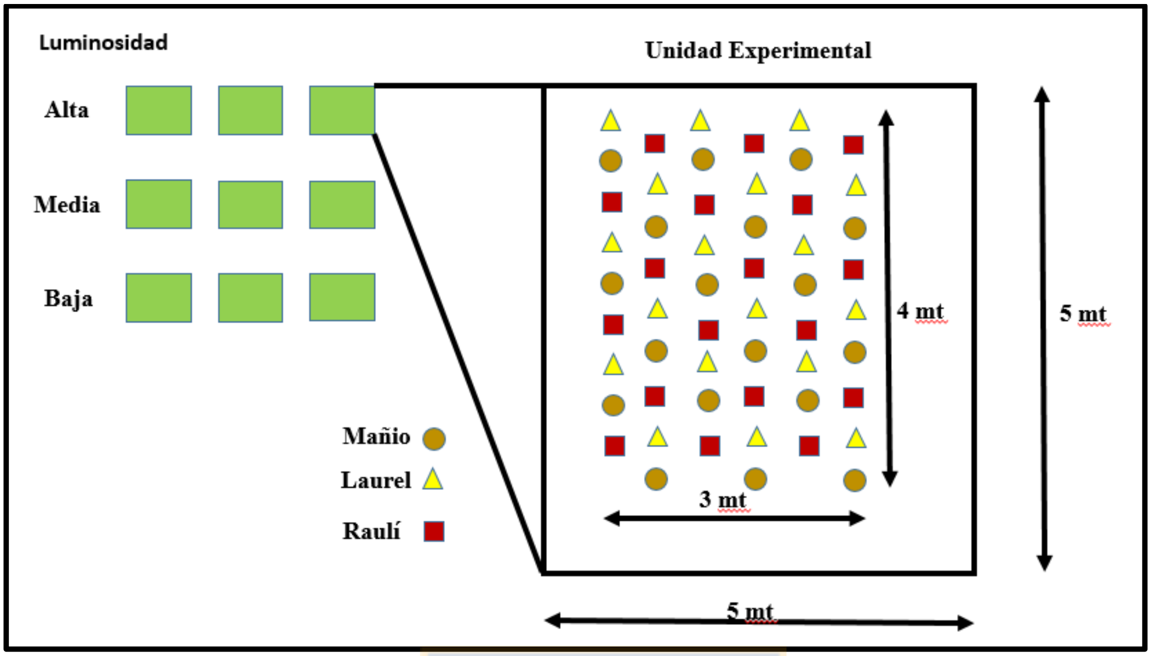


Figura 5.2 Diseño de experimental en tres niveles de luminosidad, al establecimiento de *N. nervosa*, *P. saligna*, *L sempervirens*.

Figura 5.3 Establecimiento de *N. nervosa*, *P. saligna*, *L sempervirens*, año 2015 y año 2018, en condición de alta luminosidad.

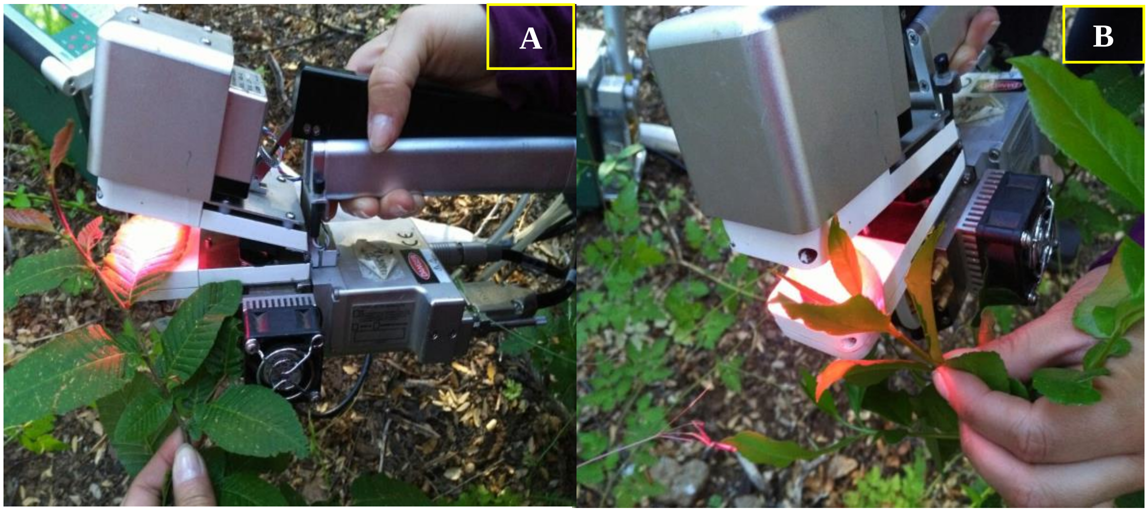
5.2.3 Mediciones de transmisvidad de la radiación solar

Las mediciones fueron realizadas durante tres temporadas en plantas vivas (figura 5.3). En cada planta fue medido el Dac y H por temporada y se contaron las muertas. Para caracterizar el ambiente lumínico al interior de cada parcela, se midió en el vértice de la parcela, la transmisión de radiación solar directa (Dir), transmisión de radiación solar difusa (Dif) y transmisión de radiación solar global (GL), a la altura de 2 y 0.4 m, utilizando una cámara fotográfica hemisférica Solariscope (Behling SOL300, versión 1.0).

Las mediciones se realizaron en el mes de noviembre, con un cielo con nubosidad, durante la madrugada desde las 6:00 a.m. a las 9:00 hrs, condición ideal para la toma de fotografías hemisféricas, evitando el reflejo de la luminosidad en las copas y los fustes de los árboles. La cámara entregó 7 fotografías en cada obturación y 168 imágenes en total. Para elegir la mejor imagen, se seleccionó de acuerdo al criterio que minimiza la presencia del color rojo en la imagen y la nitidez de la cobertura vegetal.

5.2.4 Mediciones de intercambio de gases

Se seleccionaron aleatoriamente un total de cinco plantas de cada especie, de dos parcelas establecidas en alta y baja luminosidad, que dieron 30 muestras de plantas individuales en la temporada de crecimiento. Los valores de los parámetros de intercambio de gases, fueron determinados a través de la medición de asimilación neta de CO_2, en hojas bajo diferentes intensidades lumínicas (2,000, 1,500, 1,000, 700, 500, 200, 100, 50, 20 y 0 µmol fotones m^{-2} s^{-1}) con un IRGA (LI-6400, Li-COR Inc., bioscience, Nebraska, EUA) (Figura 5.4). La concentración de referencia de CO_2 será de 400 ppm (Genty et al., 1989), con un flujo de 300 mL min^{-1}, un 45±5% de humedad relativa al interior de la cubeta y una temperatura de la muestra de 21°±2° C. Todas las mediciones se realizarón entre las 09:00 h. y 13:00 h. Los parámetros de la curva de luz, como la capacidad fotosintética (A_{max}), la conductancia estomática (gs), el punto de compensación de la luz (LCP) y el punto de saturación de luz (LSP) se determinaron, ajustando las curvas de luz mediante la función Solver del software Microsoft Excel (Lobo et al., 2013). La eficiencia del uso del agua (WEA) (1) se obtuvo mediante la relación entre A_{max} y g_s .



(1)

Figura 5.4 Medición de asimilación neta de CO_2, en hojas de *N. nervosa* (imagen A) y *L. sempervirens* (imagen B)

5.2.5 Análisis estadístico

Para analizar el efecto de la luz y de la vegetación competidora en los incrementos el Dac y H de las cuatro especies, se utilizó un modelo de ANOVA. Para construir el modelo de ANOVA solo se utilizaron todas las de la parcela para evaluar la supervivencia. El modelo general fue:

$$y_{ijk} = u + \beta_{ij} + \beta_{ij} * Sp_{jk} + Dif_{ij} * Sp_{jk} + Dif_{jk} * Sp_{jk} + \varepsilon_{ijk} \qquad (2)$$

Donde:

y_{ijk} Respuesta de las plantas a la supervivencia y al incremento en diámetro y altura.

i, j, k i-ésima observación en la planta del j-ésimo bloque y de la k-ésima parcela, respectivamente

Sp Especies *N. nervosa*, *P. saligna y L sempervirens*

Dif Radiación solar indirecta o difusa

ε_i Errores aleatorios para las diferentes variables de respuestas.

La distribución normal de los errores y la homogeneidad de varianza se evaluaron gráficamente. En los datos con residuos que no se ajustaron a los supuestos de normalidad y/o homogeneidad de varianzas se utilizaron transformaciones logarítmicas. Todos los análisis se realizaron por separado para cada especie. Todas las pruebas estadísticas se realizaron mediante el software SAS v. 9.4.

5.3 RESULTADOS

5.3.1 Efectos de la transmisividad de la radiación solar sobre la supervivencia y el incremento del Dac y H de las plantas.

Puesto que no se presentaron diferencias significativas entre los distintos componentes de la radiación solar transmitida, en los análisis se utiliza solo la radiación solar difusa (Tabla 5.1) En condiciones de alta radiación solar difusa transmitida el promedio de 32.4% variando de 30.3 a 33.3, en condiciones media de radiación solar difusa transmitida el promedio fue de 19.4% variando entre 17.7 y 23.0% en tanto que en condiciones de baja radiación solar difusa transmitida el promedio fue de 6.9% y varió entre 4 y 9.3% (Figura 5.5).

Las tasas de supervivencia de plantas para las diferentes especies ensayadas no fueron afectadas por las condiciones de transmisividad de la radiación solar (Tabla 5.1) y no se presentaron diferencias significativas entre las diferentes especies en las tasas de supervivencia (test de Tukey), las que variaron de 41.3 a 88.9% en *L. sempervirens*, 44.4 a 68.3% en *N. nervosa* y 36.5 a 42.9 % en *P. saligna* (Figura 5.6).

Tabla 5.1. Fuente de variación, valor-p para un ANOVA de una vía para la transmisividad de la radiación solar difusa (Dif), el incremento en diámetro (Dac) e incremento en altura (H) y sus interacciones en plantas de *L. sempervirens*, *N. nervosa* y *P. saligna,* creciendo bajo dosel de bosques sobremaduros de *N. dombeyi* (Mirb.) Oerst., en la zona centro-sur de los Andes, Chile

Fuente	G.l.	Supervivencia Valor-p	Incremento en Dac Valor-p	Incremento en H Valor-p
Especie	2	0.1371	0.0429*	0.152
Dif	7	0.0779	0.0147*	0.0798
Dif * Especie	14	0.6835	0.2203	0.8912

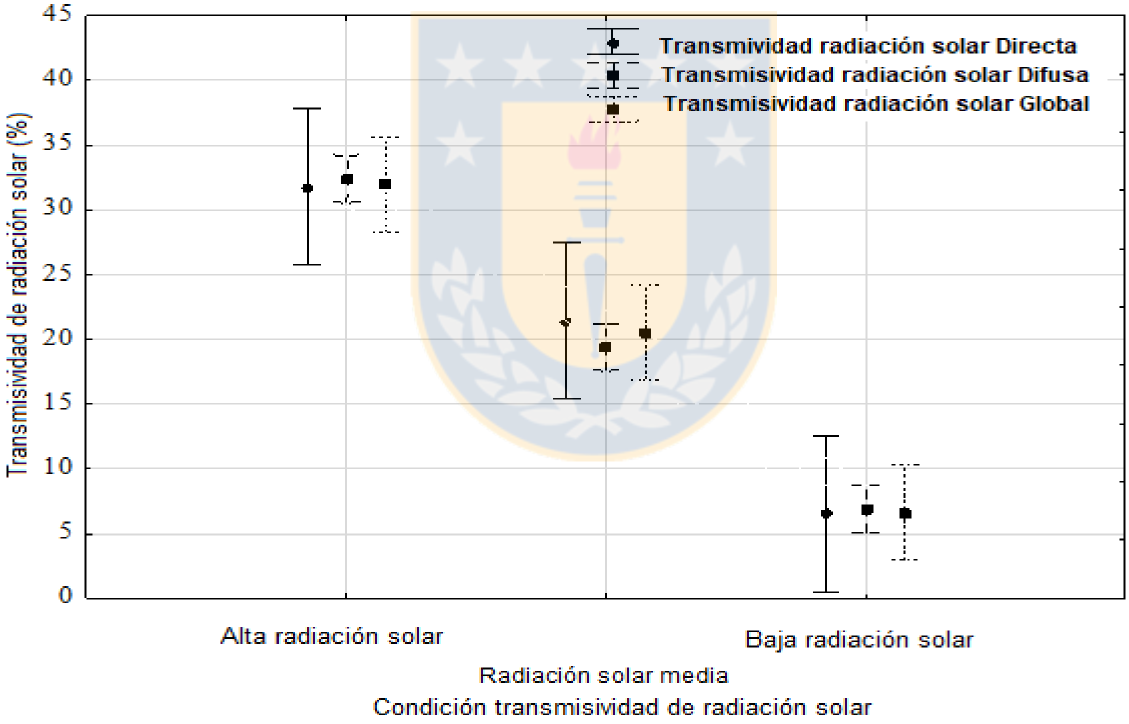


Figura 5.5. Transmisividad de radiación solar en las parcelas de estudio: transmisividad de radiación solar directa, difusa y global en un bosque sobremaduro de *N. dombeyi* en la región centro-sur andina de Chile. El símbolo ■ significa valores medios. Las medias observadas en la figura entre las condiciones muestran diferencias significativas en P <0.05 (prueba de Tukey).

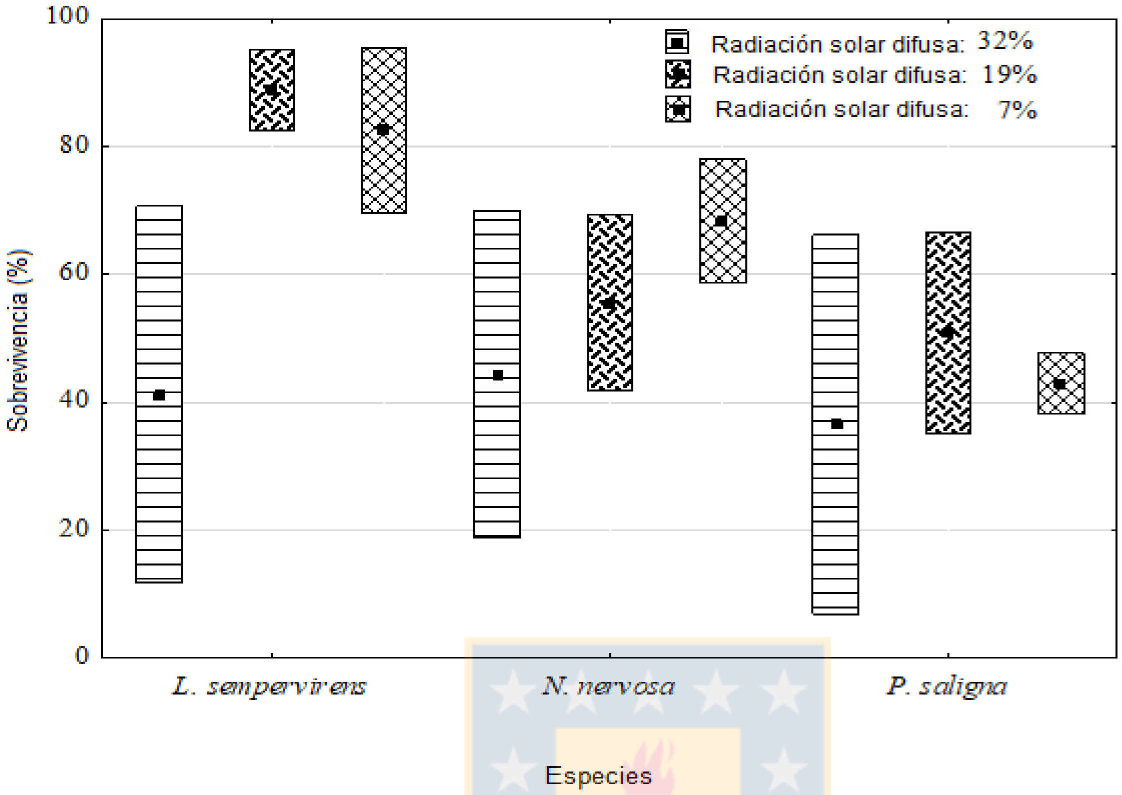


Figura 5.6 Efectos de la transmisividad de la radiación solar difusa (Dif) sobre la supervivencia de *L. sempervirens*, *N. nervosa* y *P. saligna* a un promedio de 32%, 19% y 7% de radiación solar difusa. El símbolo ■ significa valores para la supervivencia de las plantas, y la barra es el error estándar. Los promedios observados en la figura no mostraron diferencias significativas a P <0:05 (prueba de Tukey).

Se observó que *P. saligna* presenta diferencias significativas de menor incremento en Dac con respecto *N. Nervosa* y *L. sempervirens* en condiciones de altos niveles de Dif. En condiciones de niveles intermedios de Dif no se presentaron diferencias significativas entre especies y en bajos niveles de Dif, *N. nervosa* presentó incrementos significativamente mayores que *P saligna* y *L. sempervirens*. A su vez, el incremento en H fue significativamente mayor en N. nervosa con respecto a *L. sempervirens* y *P. saligna* en condiciones de altos niveles de radiación Difusa (Tabla 5.2), en niveles intermedios y bajos de Dif no se observaron diferencias significativas entre especies.

Tabla 5.2. Valores de las medias para el incremento en diámetro a la altura de cuello (Dac) y altura (H) en *N. nervosa*, *P. saligna* and *L. sempervirens* en respuesta a la transmisividad de la radiación solar difusa (Dif), en plantas creciendo bajo dosel de bosques sobremaduros de *N. dombeyi* (Mirb.) Oerst., en la zona centro-sur de los Andes, Chile.

Species	Incremento en Dac (mm año^{-1})			Incremento en altura (cm years^{-1})		
	Promedio Dif 32 (%)	Promedio Dif 19 (%)	Pomedio Dif 7%	Promedio Dif 32 (%)	Promedio Dif 19 (%)	Promedio Dif 7%
N. nervosa	1,18^{a} (0.08)	0.69^{a}(0.07)	0.76^{a} (0.07)	11.91^{a} (0.67)	5.10^{a} (0.64)	5.22^{a} (0.62)
P. saligna	0.67^{b} (0. 08)	0.62^{a} (0.08)	0.42^{b} (0.08)	7.30^{b} (0.65)	4.23^{a} (0.65)	3.57^{a} (0.67)
L. sempervirens	0.92^{a} (0.08)	0.64^{a} (0.07)	0.57^{b} (0.07)	5.57^{b} (0.67)	3.89^{a} (0.57)	3.00^{a} (0.59)

Nota: Dac es el incremento en diámetro a la altura de cuello (mm año^{-1}), H es la altura (cm año^{-1}) y Dif es la transmisividad de la radiación solar difusa (%).
a: Valores en paréntesis indican la desviación estándar.
b: Columnas con diferentes letras indican diferencias significativas a $P < 0:05$ (Prueba de Tukey).

5.3.2 Efecto de las condiciones de luz en el incremento del Dac y H de las plantas.

Se observó que en baja luminosidad LCP no presentó diferencias significativas entre *L. sempervirens* y *N. nervosa*, pero fue significativamente mayor que *P. saligna*. En cambio en baja luminosidad, los valores de LCP presentaron valores que fueron significativamente mayores en *L. sempervirens* y *P. saligna* que *N. nervosa*. En cambio en alta luminosidad y baja luminosidad *N. nervosa* presentó valores de LSP significativamente mayores que *L. sempervirens* y *P. saligna*. Los valores de A_{max} en alta luminosidad fueron significativamente mayores en N. nervosa que *L. sempervirens* y *P. saligna*, en cambio en baja luminosidad P. saligna presentó valores de A_{max} significativamente menores que *L. sempervirens* y *N. nervosa*. Los valores de g_s en alta luminosidad no presentaron diferencias significativas entre especies, en tanto que en baja luminosidad N. nervosa presentó valores de g_s significativamente mayores que *L. sempervirens* y *P. saligna*. Los valores de WUE en alta luminosidad fueron significativamente menores en N.

nervosa que *L. sempervirens* y *P. saligna*, en cambio en baja luminosidad *L. sempervirens* presentó valores significativamente mayores que *N. nervosa* y *P. saligna* (Tabla 5.3).

Tabla 5.3. Valores de las medias para las variables de intercambio gaseoso para las especies de *N. nervosa*, *P. saligna* y *L. sempervirens* en respuesta a la disponibilidad de luz en plantas creciendo bajo dosel de bosques sobremaduros de *N. dombeyi* (Mirb.) Oerst., en la zona centro-sur de los Andes, Chile.

	Intercambio gaseoso									
Especies	LCP		LSP		A_{max}		g_s		WUE	
	Alta luz	Baja luz	Alta luz	Baja luz	Alta luz	Baja luz	Alta luz	Baja luz	Alta luz	Baja luz
N. nervosa	31.9^{a}	13.5^{a}	210.1^{a}	259.4^{a}	5.1^{a}	7.3^{a}	0.10^{a}	0.34^{a}	53.8^{a}	45.4^{a}
P. saligna	10.7^{b}	27.7^{b}	126.0^{b}	121.6^{b}	3.7^{b}	1.9^{b}	0.05^{a}	0.07^{b}	69.3^{b}	35.4^{a}
L. sempervirens	29.9^{a}	21.5^{b}	134.6^{b}	176.8^{a}	2.8^{b}	4.1^{a}	0.06^{a}	0.04^{b}	64.0^{b}	101.7^{b}

Nota: A_{max} es la máxima capacidad fotosintética (µmoles m^{-2} s^{-1}); LCP es el punto de compensación de la luz (µmoles m^{-2} s^{-1}); LSP es el punto de saturación de la luz (µmoles m^{-2} s^{-1}) y WUE es la eficiencia en el uso del agua (µmol CO^2 mol H_2O^{-1}).
Columnas con diferentes letras indican diferencias significativas a *P* < 0:05 (Prueba de Tukey).

La especie *L. sempervirens* no mostró respuesta a ninguno de los niveles de luz medidos en este estudio. En el caso de *N. nervosa* Dac estuvo positiva y significativamente correlacionado con LSP en alta luminosidad (r = 0.97, p = 0.01) (Figura 5.8). También LSP estuvo positiva y significativamente correlacionado con el incremento en Dac en alta luminosidad (r = 0.86, p = 0.02) (Figura 5.9). Además, *N. nervosa* estuvo negativamente y significativamente correlacionada en alta luminosidad con A_{max} (-0.91, p=0.02) (Figura 5.7).

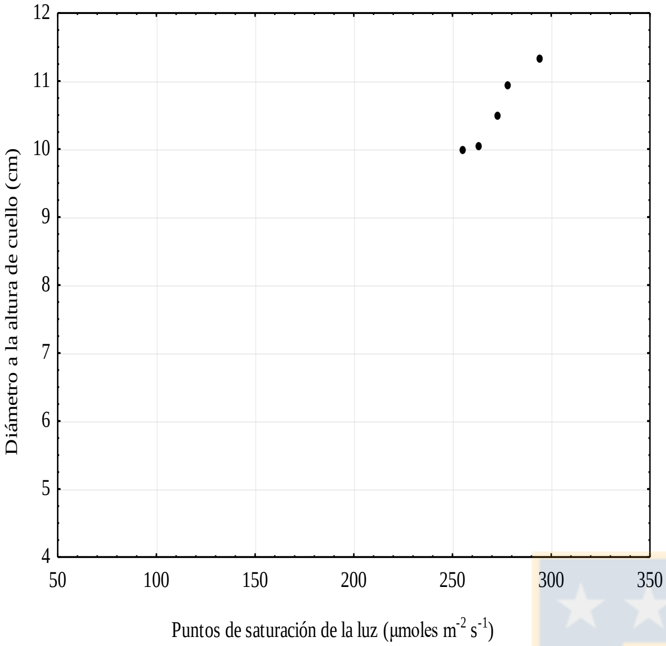


Figura 5.8 Relación entre los puntos de saturación de la luz (µmoles m^{-2} s^{-1}) y diámetro a la altura de cuello (mm) en plantas de *N. nervosa* en condiciones de alta luminosidad.
(r = 0.97; valor-p = 0.01).

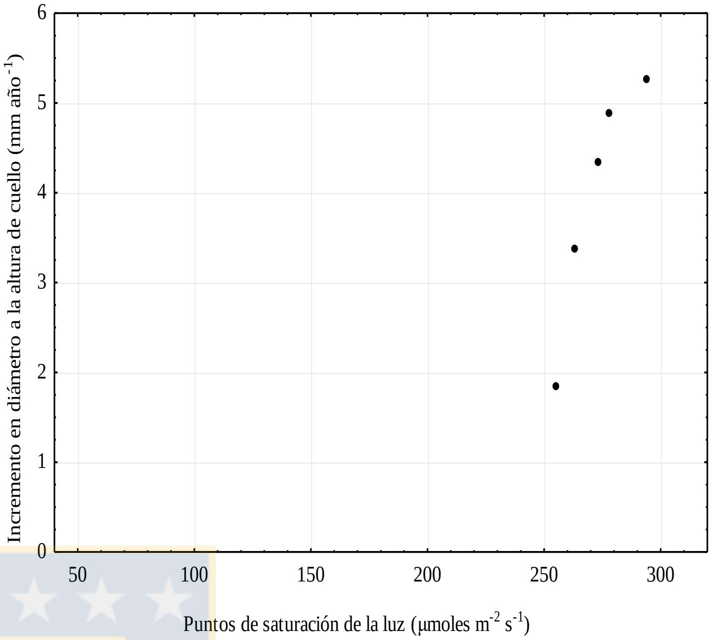


Figura 5.9 Relación entre los puntos de saturación de la luz (µmoles m^{-2} s^{-1}) y el incremento en diámetro a la altura de cuello (mm $año^{-1}$) en plantas de *N. nervosa* en condiciones de alta luminosidad.
(r = 0.86; valor-p = 0.02).

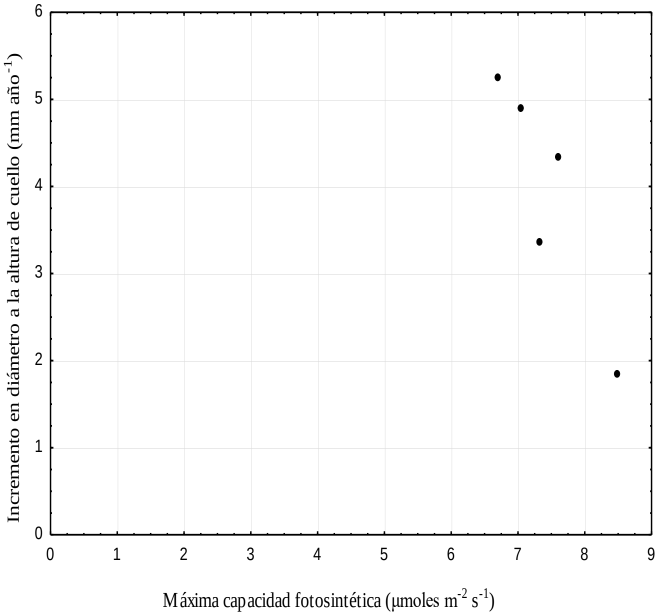
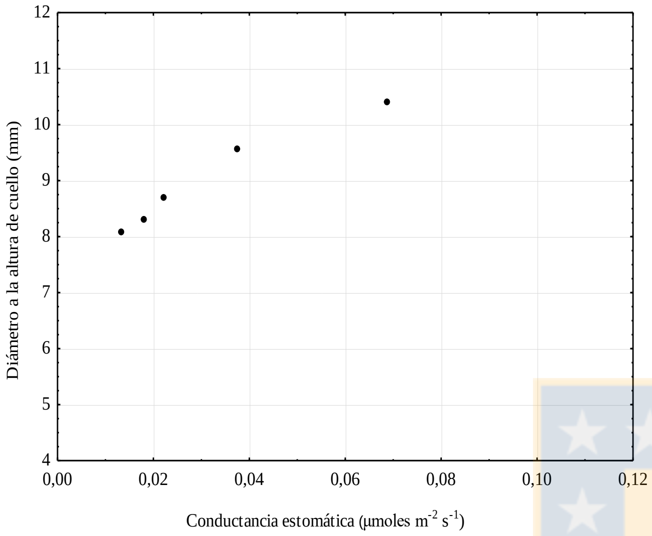


Figura 5.7. Relación entre la A_{max} (µmoles m^{-2} s^{-1}) e incremento en diámetro a la altura de cuello (mm $año^{-1}$) en plantas de *N. nervosa* en condiciones de alta luminosidad.
(r = -0.91; valor-p = 0.02)

Finalmente, la especie *P. saligna* se presentó significativamente correlacionada en Dac con gs (r = 0.97, p = 0.004) en alta luminosidad (Figura 5.10) y el incremento en Dac (r = 0.9, p = 0.01) (Figura 5.11).



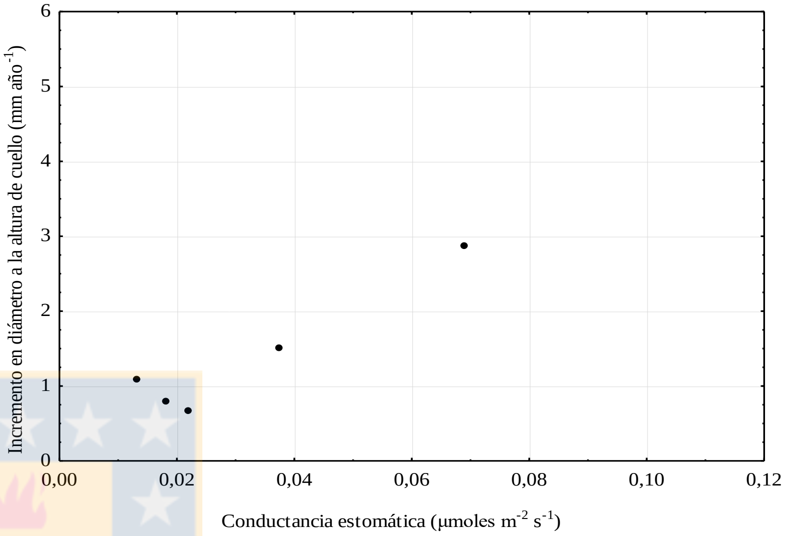


Figura 5.10 Relación entre la conductancia estomática (µmoles m^{-2} s^{-1}) y el diámetro a la altura de cuello (mm) en plantas de *P. saligna* en condiciones de alta luminosidad.
(r = 0.97; valor-p = 0.004)

Figura 5.11 Relación entre la conductancia estomática (µmoles m^{-2} s^{-1}) y el incremento en diámetro a la altura de cuello (mm año^{-1}) en plantas de *P. saligna* en condiciones de alta luminosidad.
(r = 0.97; valor-p = 0.004)

5.4 DISCUSIÓN

5.4.1 Efectos de la transmisividad de la radiación solar en la sobreviencia e incremento en Dac y H de las plantas.

En este estudio nos planteamos un primer aspecto, analizar el efecto de diferentes niveles de transmisividad de radiación solar en la supervivencia de plantas nativas. Al respecto, no encontramos diferencias significativas entre estas especies entre los distintos rangos de transmisividad de radiación solar y la supervivencia (Tabla 5.1; Figura 5.5). El hecho que en nuestro estudio especies con diferentes grados de tolerancia a la sombra, presenten similares altas tasas de supervivencia coinciden con otras especies que pueden sobrevivir a la tolerancia a la sombra y estrés hídrico (Lawson y Michler 2014) y se elimina la competencia con especies herbáceas, en contraste con la situación prevaleciente en condiciones naturales (Collet et al., 2014). Nuestros resultados coinciden además con lo reportado por Sandoval (2017), al comparar especies con distintos rangos de tolerancia a la sombra, tanto exóticas como nativas creciendo bajo dosel de *Eucalyptus globulus-Acacia melanoxylon*. En general, se ha reportado que para condiciones de clima mediterráneo, la tolerancia a la sombra no afecta la supervivencia de plantas y para ello las especies adoptan diferentes estrategias funcionales, morfológicas y fisiológicas para sobrevivir en un ambiente de estrés hídrico y competencia con la vegetación circundante, para una misma condición de sombra (Givnish, 1988; Sack et al., 2003). Nuestros resultados se apoyan en la teoría del intercambio clásico, que sugiere que la estrategia de supervivencia de una especie se define por su tasa de crecimiento de alta luminosidad y la capacidad de una planta para sobrevivir en condiciones de baja luminosidad, lo cual explica que la densidad de las especies se distribuya a lo largo de un eje de tolerancia de la sombra, lo cual solo es afectada por el tamaño de las plántulas (Baraloto et al., 2005; Kunstler et al., 2009).

El hecho que *N. Nervosa* y *L. sempervirens* presentaran mayores incrementos en Dac que *P. saligna* en altos niveles de Dif, se revela que en niveles intermedios de Dif no existen diferencias significativas entre estas especies con el incremento en Dac. Estos resultados coinciden con otros estudios en que Dac es mayor en condiciones de mayor luminosidad (Álvarez and Lara 2008), debido a las características auteocológicas de *N. Nervosa* y *L. sempervirens*, como es la intolerancia a la sombra y su rápido crecimiento inicial, comportamiento predominante en especies intolerantes y semi-tolerantes a la sombra, patrón que ha sido reportado en especies de hoja perenne e intolerantes a la sombra (Valladares and Niinemets, 2008). La especie tolerante *P. saligna* presento las menores tasas de incremento en Dac, lo que se explica porque su estrategia de regeneración en claros con altos niveles de Dif es más bien episódica, asociada a un denso establecimiento inicial y una alta mortalidad posterior, donde solo unos pocos individuos logran establecerse (Donoso and Utreras, 2006; Muñoz and González, 2009). A su vez, el incremento en H fue significativamente mayor en N. nervosa con respecto a *L. sempervirens* y *P. saligna* en condiciones de altos niveles de Dif (Tabla 5.1). Al respecto, se ha reportado que la relación entre incremento en altura en plantas jóvenes y el grado de tolerancia a sombra juega un papel importante en las plantaciones mixtas (Menalled et al., 1998), ya que especies intolerantes crecen rápidamente en altura, asignando más crecimiento al tallo, ramas y poseen copas con baja área foliar, como es el caso en este estudio de *N. nervosa* (Canham et al., 1994; Sheil et al., 2006; Hosseini et al., 2010). Sin embargo, en condiciones medias y bajas de Dif no se observaron diferencias significativas entre las tres especies, que presentaron un comportamiento de especies semitolarantes a tolerantes a la sombra. En el caso de *N. nervosa*, se ha reportado que que puede aprovechar la protección natural de la regeneración natural de individuos en el dosel superior (Donoso, 1993) que brinda el bosque sobremaduro de *N. dombeyi* y presenta un nivel de tolerancia a la sombra mayor que otros *Nothofagus* (Read y Hill, 1985). En este estudio podemos confirmar que N. nervosa, tiene buen crecimiento bajo una condición de media a alta luminosidad, aunque pudiera observarse la existencia de un efecto de la exposición en el establecimiento de plantaciones y la respuesta en crecimiento (Alvarez and Lara, 2008). *L. sempervirens* es considerada como una especie que se adapta fácilmente a zonas templadas y de humedad media siendo de tolerancia media a la sombra (Donoso, 1993). Se ha reportado que en condiciones de sombra o bajo dosel, el crecimiento es altamente influenciado por el área potencialmente aprovechable, ya que los individuos al verse privados de luz directa, comienzan a competir fuertemente por nutrientes y agua, es decir, radicularmente (Uteau and Donoso, 2009). Sin embargo, durante los primeros años de crecimiento, el espacio radicular del cual disponen las plantas para crecer, son de poca importancia ya que fue eliminada la competencia con arbustos y herbáceas. *P. saligna* presenta características de especie tolerantes a la sombra, que utiliza la protección brindada por el dosel superior impidiendo el efecto temperaturas altas o muy bajas (Uteau and Donoso, 2009).

Considerando las tasas de supervivencia y el crecimiento de las tres especies se puede considerar que presentaron una estrategia de claros, esto es que se caracterizan por una marcada y constante respuesta en las tasas de crecimiento al aumentar la luz. A la sombra, mostraron plasticidad para sacrificar tasas de crecimiento beneficiando la supervivencia, probablemente por el aumento del área foliar para mejorar la intercepción (Petritan et al., 2008). Estos resultados están de acuerdo con la visión clásica del impacto de las compensaciones de crecimiento-supervivencia en la dinámica forestal: las posiciones de las especies a lo largo del trade-off impulsan su capacidad para establecerse en alta o con poca luz (Kobe 1999). De esta forma, las mayores tasas de crecimiento en Dac y H en condiciones de alta y media radiación solar se ordenaron de acuerdo al rango de tolerancia. En condiciones de baja radiación solar presentaron las mismas tasas de incremento en Dac y H. De esta forma, se cumple la clásica teoría del trade-off, en que la estrategia de una especie se define por su tasa de crecimiento de alta luz, porque la capacidad de una planta para sobrevivir en la sombra está negativamente correlacionada con su tasa de crecimiento de alta luz, lo que explica que las especies sobreviven y crecen a lo largo de un eje de tolerancia de la sombra, a condición que el tamaño de las plantas no influya en el trade-off (Kunstler et al., 2009). Estas respuestas específicas de las especies se pueden usar para permitir el control en el desarrollo de la regeneración artificial de mezclas de especies en el manejo silvícola utilizando el método de selección por individuos o grupos (Petritan et al., 2009).

5.4.2 Efecto de las condiciones de luz en el incremento en Dac y H de las plantas

La especie intolerante a la sombra *N. nervosa* presentó los mayores valores de A_N, seguida por la semitolerante *L. sempervirens* y la especie tolerante *P. saligna* (Tabla 5.3). Sin embargo, el fuerte incremento de *N. nervosa* con la intensidad de luz explica las tasas muy superiores en incremento en Dac y H con el aumento de PPDF (Figura 5.12) con respecto a las especies restantes. Por tanto, en la medida que aumenta en A_N con el incremento en PPDF, sirve como factor ordenador en la tolerancia de las especies en condiciones de sombra (Figura 5.12) y explica las tasas de incremento en Dac y H, de acuerdo con la teoría de la tolerancia a la sombra (Kobe and Coates, 1997) y que las diferencias en A_N resultan en respuestas a la luz relacionadas con el crecimiento y que especies tolerantes a la sombra mantengan una ganancia de carbono positiva aún con poca luz (Bazzas, 1979).

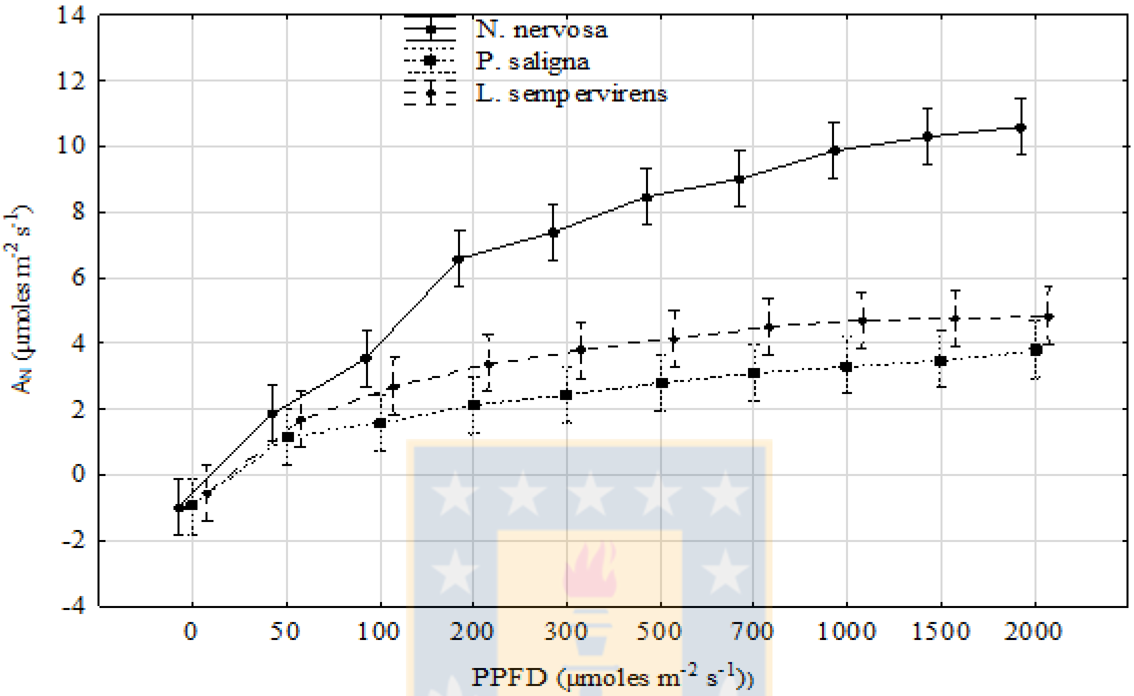


Figura 5.12 Tasa de fotosíntesis neta (A_N) a diferentes intensidades de luz (densidad de flujo fotosintético, PPFD) en hojas de *N. nervosa*, *L. sempervirens* and *P. saligna*.

Nota: Las barras indican el error estándar de la media.

Considerando que g_s no presentó diferencias significativas entre especies con diferentes rangos de tolerancia a la sombra (Tabla 5.3) puede explicar que a mayores valores de A_N, les especies intolerantes pueden sobrevivir y potencialmente crecer en claros de mayor tamaño que las especies semitolerantes y tolerantes (Peri et al., 2009). Sin embargo, *N. nervosa* presentó una relación negativa de A_{max} con el incremento en Dac (Figura 5.7) y una relación positiva y significativa encontrada entre Dac y el incremento en Dac con LSP (Figura 5.8; Figura 5.9). Este hecho puede sugerir que los rasgos de intercambio de gases ilustran acerca de las diferencias entre especies que son capaces de adaptarse a condiciones de alta luminosidad respecto de plantas adaptadas a baja luminosidad (Poorter, 1999). Sin embargo, se conoce que un exceso de luz inhibe el crecimiento, debido a que cambia la morfología externa de la hoja y modifica la estructura del cloroplasto, que está involucrado en la saturación luminosa de la fotosíntesis en condiciones de alta luminosidad (Mache y Loiseaux, 1973). Al respecto, se ha reportado que la mayor tasa fotosintética de *N. dombeyi* le permite destinar carbohidratos al incremento en Dac ya que el incremento en H es limitado por mecanismos de intercambio gaseoso y/o morfológicos que le permiten saturar la fotosíntesis ante riesgos de fotoinhibición (Donoso et al., 2015). A su vez, otras especies como *Austrucedrus chilensis* emplea otra estrategia en que el riesgo de fotoinhibición o daño celular debido al sobrecalentamiento aumenta debido a condición de alta luminosidad, adopta un cierre estomático temprano para evitar daños en las hojas o en la base del tallo por sobrecalentamiento (Gyenge et al., 2007), limitando el incremento en Dac. Por tanto, en este estudio se observa que *N. nervosa* ha desarrollado mecanismos fisiológicos y/o morfológicos que le permiten saturar la fotosíntesis ante riesgos de fotoinhibición (Figura 5.8), de esta forma al disminuir el incremento del Dac le permite destinar los recursos al incremento en H, lo que permite desarrollar una economía en el uso del agua durante los períodos de déficit hídrico (Dudley, 1996; Valladares et al., 2016) y mejorar el comportamiento fotosintético (Tabla 5.3) para mantener así una productividad neta potencialmente más alta en condiciones de alta luminosidad.

Por otra parte, *P. saligna* presentó los valores más bajos de g_s en condiciones de alta luminosidad y positivamente correlacionado con Dac y el incremento en Dac (Figura 5.12; Figura 5.11), en que la fuerte correlación con g_s resulta en un incremento en Dac (Figura 5.11), siendo mayor en un 63% en alta luminosidad que en baja luminosidad (Tabla 5.2). Al respecto, se ha reportado que las relaciones entre la fotosíntesis y la conductancia estomática son casi lineales, por lo cual las diferencias en la reacción de la fotosíntesis a la conductancia estomática, se constituyen en un buen indicador de la adaptabilidad de las especies a la sequía estival (Anev et al., 2016). En *P. saligna* esta hipótesis puede ser válida por dos razones. En primer lugar, porque presenta el mayor valor en WUE en condiciones de alta luminosidad en todas las especies, lo que le permite adaptarse a la sequía estival. Por tanto, el mejoramiento de WUE, relación de la ganancia de carbono en relación al agua transpirada, es una respuesta común en plantas expuestas a la sequía (Valladares et al., 2005). En segundo lugar, porque se ha reportado que una alta colonización de hongos micorrícicos vesículo-arbusculares promueven el crecimiento y la fotosíntesis al reducir LCP (Shi et al., 2017). Es natural en todos los *Podocarpus* la formación de nódulos radicales fuertemente colonizados y de un extraordinario desarrollo de micelio extrarradical (Godoy et al., 1993), lo que pudiera explicar por qué *P. saligna* puede enfrentar exitosamente las sequías de verano e incrementar Dac.

5.4.3 Implicancias silvicolas

En general las especies tolerantes presentan buenas tasas de crecimiento, en tanto que entre las especies semitolerantes del bosque nativo, entre otras especies, *L. sempervirens*, y *P. saligna* se consideran con buenas tasas de crecimiento. Estas características reflejan que el desarrollo de bosques establecidos en mezclas de especies nativas representa una alternativa favorable desde el punto de vista ecológico, ambiental e incluso estético, así como con respecto a la productividad. Es posible lograr una mayor productividad en los bosques mixtos con estructuras y especies que permitan un uso complementario de los recursos, en comparación con los bosques puros (Lusk y Ortega, 2003).

Entre los distintos razonamientos del silvicultor para favorecer el proceso de la regeneración artificial de un bosque, se encuentra el de optimizar la relación entre la demanda de luz de la especie a tratar con el nivel de luminosidad que se le ofrece a través de claros naturales o del manejo del dosel. Las decisiones no son iguales en zonas climáticas diferentes. En el caso de este estudio se cuenta con una oferta de alta radiación solar sobre las copas muy altas, dada la ubicación geográfica que lo sitúa en una zona de clima mediterráneo de montaña.

Por tanto, es necesario ajustar las prácticas silvícolas, particularmente el nivel de apertura del dosel, para que la mezcla de especies no sea afectada, como un indicador clave de sostenibilidad a escala de la unidad de manejo (Sola et al., 2015). De la misma manera, es necesario analizar el impacto en la biodiversidad relacionada con este régimen silvicultural. Los claros existentes en bosques sobremaduros de *N. dombeyi* son lo suficientemente grandes como para introducir otras especies de árboles que complementan la regeneración natural con especies tolerantes a la sombra, como *L. sempervirens* y *P. saligna*, que se protegen contra el exceso de iluminación del claro con el dosel del bosque (Dezzotti, 2008). En este estudio, en el rango del espectro de transmisividad de la radiación solar se encontró que el valor máximo de transmisividad es de 40%. Por otra parte, *N. nervosa* presenta riesgos de inhibición en condiciones de alta luminosidad en tanto que *L. sempervirens* y *P. saligna* presentan bajos valores de tasas fotosintéticas aunque aumente la disponibilidad de luz. Por lo tanto, se sugiere intervenir el bosque sobremaduro utilizando el método de selección en grupos, en que el tamaño de los claros no debe ser superior a 20 y 30 m y con distancias entre 1 y dos veces la altura de árboles sobremaduros, esto es entre 30 y 40 m. Bajo estas condiciones climáticas, los claros cumplen el objetivo de no crear áreas centrales que sean demasiado grandes para la transmisividad de la radiación solar directa o global o para las defensas de regeneración artificial contra las heladas tardías o la desecación (Dezzotti y Sbrancia, 2006) cuando se usan especies semitolerantes como *L. sempervirens* o *P. saligna*.

5.5 CONCLUSION

En este estudio se cumplió la clásica teoría del trade-off, en que la estrategia de una especie se define por su tasa de crecimiento de alta luz y la capacidad de las especies para sobrevivir en la sombra está negativamente correlacionada con su tasa de crecimiento en alta luz. Por tanto, las especies sobreviven y crecen a lo largo de un eje de tolerancia de la sombra. La especie intolerante a la sombra *N. nervosa* presentó los mayores valores de A_{max}, seguida por la semitolerante *L. sempervirens* y la especie tolerante *P. saligna*. Sin embargo, el fuerte incremento de *N. nervosa* con la intensidad de luz explicó las tasas muy superiores en incremento en Dac y H con el aumento de PPDF, comparado con *L sempervirens* y *P. saligna*. Sin embargo, *N. nervosa* presenta riesgos de fotoinhibición, por lo cual satura la fotosíntesis lo que le permite desarrollar una economía en el uso del agua durante los períodos de déficit hídrico, de tal forma que incrementa Dac y H. A su vez, *P. saligna* presentó los valores más bajos de g_s en condiciones de alta luminosidad y positivamente correlacionado con el Dac y el incremento en Dac; además de una fuerte correlación con g_s lo que resultó en un incremento en Dac en alta luminosidad con respecto a baja luminosidad. Se postula que ante la sensibilidad de esta especie a sequías de verano, mejora WUE y posiblemente una alta colonización de hongos micorrícicos vesículo-arbusculares en condiciones naturales.

En este estudio se sugiere que es útil el empleo de la mezcla formada por *N. nervosa*, *L. sempervirens* y *P. saligna*, para la provisión de servicios ecosistémicos y la productividad del bosque sobremaduro, para lo cual se sugiere intervenir el bosque utilizando el método de selección en grupos, utilizando claros de pequeño tamaño y separados a 30 y 40 m. Otra alternativa silvícola es la práctica de *underplanting*, utilizando la mezcla estudiada, pero estableciéndola a niveles sobre 20 % de Dif.

5.6 AGRADECIMIENTOS

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CAPÍTULO VI

DISCUSION GENERAL

La transmisividad de la radiación solar, en los bosques cambia constantemente debido a los movimientos de la tierra en relación con la posición del sol y la nubosidad existente (Baldocchi y Collineau, 1994). Los árboles, arbustos o los estratos herbáceos van creando una amplia variación de la luz entrante en el bosque (Lieffers et al., 1999). En nuestro primer objetivo de estudio, los rodales mostraron una alta variabilidad espacial para todos los componentes de transmisividad de la radiación solar dentro del bosque (3 a 40%, Figure 2.3), probablemente debido a los diferentes grados de cobertura del dosel causados por perturbaciones a pequeña escala, donde los patrones de la radiación solar espacial observados en el área de estudio son consistentes con los cambios que se producen en los bosques, en particular por la presencia de diferentes claros (Parker et al., 2002).

Los bosques primarios de *N. dombeyi* presentan la misma respuesta al crecimiento que los bosques templados de climas mediterráneo, donde se ha establecido que la radiación solar difusa puede representar solo el 15% de la radiación solar del mediodía, la que llega a través del dosel y el 40% de la radiación bajo el dosel de arbustos en rodales de hojas caducas, lo que representa entre el 14 y el 41% de la transmisividad solar del dosel en rodales dominados por coníferas (Canham et al., 1994). Es importante establecer que la transmisividad de la radiación solar difusa mejora la fotosíntesis de la vegetación terrestre (Dengel et al., 2015), mientras que la transmisividad de la radiación solar directa puede causar la saturación de la fotosíntesis en el dosel superior y posiblemente fotoinhibición (Long et al., 1994). La alta variabilidad espacial en la transmisividad de la radiación solar, está directamente relacionada con las perturbaciones a pequeña escala, la cual es una característica de los bosques sobremaduros en ausencia de incendios (Gauthier et al., 2010), como es el caso de nuestra área de estudio, donde se comprueba debido al amplio rango de edad que presentan las plantas entre 12 y 40 años ubicadas en los claros existentes, este antecedente podría explicar, la relación de la regeneración con la formación y el desarrollo de diversos tamaños de claros en respuesta a perturbaciones de pequeña escala. Nuestros resultados indican que hasta el 30% de la transmisividad de la radiación solar difusa, la regeneración avanzada fue mayor (5 plantas m^{-2}) y bajo el 5%, la regeneración avanzada fue de solo 1 planta m^{-2}, con la excepción de una parcela con 8 plantas m^{-2} (Figure 2.4). Los mayores aumentos en AHG ocurrieron en el rango de transmisividad de radiación solar directa y global del 15 al 23% (Figure 2.6 y 2.7). Los factores que explican la relación de AHG con la transmisividad de radiación solar directa y global, también fueron informados por Lusk (2004), Ammer et al., (2008), y Promis et al., (2010), quienes observaron la transmisividad de la radiación solar directa y global ai como la edad como una explicación parcial del incremento en AHG (R^2 = 0.7; Figure 2.6 y 2.7), debido a que las plantas, también responden a otros recursos disponibles del sitio para el crecimiento. Por lo tanto, los aumentos máximos de crecimiento no se correlacionan con niveles de luz más alto ya que la competencia en la regeneración avanzada de *N. dombeyi* excluye a otras especies del sotobosque; por lo tanto, se podría argumentar que el ARG es mucho más sensible a la competencia intraespecífica que al crecimiento en altura (Ammer et al., 2005). Los patrones de AHG observados, sugieren que la regeneración avanzada de *N. dombeyi* compiten principalmente por luz, aumentando simultáneamente la biomasa en el área del tallo en términos de altura a expensas del crecimiento radial (Ammer et al., 2005). La regeneración en este estudio se desarrolló lentamente en el sotobosque, donde las plantas necesitaban de 20 a 40 años para alcanzar una altura de 5 m, sin formar un árbol en el estrato secundario, desde esta perspectiva, es necesario recomendar un sistema de silvicultura que asegure la regeneración natural en un bosque sobremaduro de *N. dombeyi*.

Las plantas de *N. dombeyi* crecen en condiciones ambientales cambiantes, de acuerdo a lo anterior, se establece la teoría que las plantas intolerantes, se condicionan para aplicar la asignación preferencial de biomasa a los órganos más eficientes, para la adquisición de luz (Givnish, 1984), agua, nutrientes (Grime et al., 1988) y plasticidad fenotípica, lo que les permite hacer frente a condiciones adversas (Messier et al., 1999; Sultan, 2000). En este segundo objetivo de estudio, no se encontraron pruebas con respecto al efecto de la luz en la asignación de biomasa para los componentes analizados (hojas, ramas, tallos y raíces) en plantas de *N. dombeyi*, tuvieron un impacto bajo en las hojas y los tallos, dado que la biomasa de hojas fue mayor en condiciones de sombra media en un 5% y un 5,9% en la biomasa de tallo (Table 3.4). Este hallazgo también fue informado por Curt et al., (2005), confirmando que la asignación es principalmente ontogenética y, por lo tanto, presenta variabilidad a lo largo de la vida de un árbol (Kitajima, 1994; Gedroc et al., 1996). En los rasgos morfológicos de la planta, las hojas juegan un papel fundamental en la adaptación a largo plazo al medio ambiente. Aunque comprenden básicamente epidermis, estomas y mesófilo, las hojas exhiben diferencias aparentes en el área, el grosor y la forma entre diferentes especies, como resultado de la adaptación a ambientes específicos (Xu et al., 2008). En este estudio los resultados actuales confirman que la luz afectó fuertemente el crecimiento y la morfología de las plantas. Encontramos que el tamaño de hoja fue un 18% mayor en condiciones de luz en comparación con las condiciones de sombra media, y que el número de hojas se duplicó en condiciones de luz (Table 3.6), lo que muestra una fuerte correlación con su área foliar (Table 3.2). En este sentido, estos resultados se basan en el hecho de que las hojas responden a diferentes hábitats con plasticidad fenotípica en la morfología de las hojas, lo que sugiere que este es un mecanismo importante para que las plantas se adapten a diferentes ambientes de luminosidad (Xu et al., 2008). Las implicancias silvícolas establecen que las plantas en sombra media pueden desarrollarse de igual forma que en condiciones de luz, considerando que este recurso solo afecta la densidad de las plantas (Encina et al., 2018) (Table 3.1). Por lo tanto, el manejo silvícola para la regeneración de *N. dombeyi* más adecuado, en un bosque sobremaduro sería el método de selección en grupo dirigido a la extracción de un solo árbol, lo que garantizaría una cobertura del dosel de acuerdo con los principios y la dinámica forestal como en los bosques naturales.

Al analizar los efectos de dos ambientes contrastante de luz en las variables morfológicas y de intercambio gaseoso de una planta, es necesario saber las competencias a las que se enfrentan, sea por: luz, humedad del suelo o nutrientes (Cannell y Grace, 1993; Nambiar y Sands, 1993), donde la evidencia de los bosques templados sugiere que la luz tiene una mayor influencia en el crecimiento y la supervivencia de las plantas (Pacala et al., 1994). En nuestro tercer objetivo, se observa que en condiciones de alta luminosidad el MAI en Dac presentó una correlación positiva y significativa con H / Dac y SLA (Table 4.3). La correlación de H / Dac se explica porque la altura y el Dac son componentes fundamentales para los procesos que van desde el comportamiento individual hasta la función de un ecosistema completo. La altura de la planta desempeña un papel importante en el soporte mecánico (Niklas, 1993; Lundqvist y Valinger, 1996) y refleja el intercambio entre crecimiento y supervivencia (King et al., 2006).

Las especies de regeneración avanzada en sombra, compiten especialmente por la luz, lo que reduce el aumento de la biomasa, aunque los carbohidratos disponibles se asignan al aumento de H, a expensas del crecimiento en Dac (Prévosto y Balandier, 2007; Einhorn et al., 2004; Ammer et al., 2005). En nuestro estudio las características morfológicas no resultaron ser determinantes en la variación interespecífica, a diferencia de las variables de intercambio de gases, en términos de crecimiento y supervivencia. Sin embargo, la supervivencia en condiciones de alta luminosidad, estuvo fuertemente correlacionada con una sola característica morfológica, el Dac, aunque en condiciones de baja luminosidad, se correlacionó con LSP (Table 4.3). Por lo tanto, nuestros datos sugieren una conexión metabólica íntima entre la fotosíntesis y el mantenimiento de las tasas respiratorias, lo que constituye una de las principales causas de la compensación. Esto se cita con frecuencia para privilegiar el crecimiento en condiciones de luz alta y la supervivencia con poca luz (Baraloto et al., 2005).

Entre las diferentes razones por las cuales el silvicultor favorece el proceso de regeneración natural de un bosque determinado, están las de optimizar la relación entre las demandas de la especie con el nivel de luminosidad que se ofrece a través del manejo del dosel en los estratos superiores. Esta tarea no es la misma para diferentes zonas climáticas. En el caso de nuestro estudio, existe una oferta de radiación solar muy alta sobre las copas de los árboles, debido a la ubicación geográfica del sitio de estudio localizado en un área de clima mediterráneo. Aunque la transmisividad del dosel de *N. dombeyi* con sus hojas siempre verdes y poco transparentes, absorbe la luz incidente en un 34% en los centros y en un 8% en los bordes de los claros, este efecto aún ofrece, en términos absolutos, una luminosidad a la regeneración avanzada de *N. dombeyi*, garantizando el establecimiento y a pesar de una alta mortalidad en los primeros años, una supervivencia aceptable de (18.000 árboles ha^{-1}). Sin embargo el bosque en estudio corresponde a un bosque sobremaduro, la característica de este tipo de bosques es que normalmente se encuentran en proceso de colapso, donde el avance del tiempo, se acentúa y la relación costo / beneficio del manejo forestal disminuye cada vez más. Además, al no avanzar en el rejuvenecimiento, su calidad como emisor de carbono neto se perpetúa, una característica muy importante a considerar.

Por lo tanto el establecimiento de plantaciones suplementarias con especies nativas, es una alternativa, para el rejuvenecimiento de los bosques sobremaduros. Por lo que en nuestro cuarto estudio, un primer aspecto fue analizar el efecto de los diferentes niveles de transmisividad de radiación solar en la supervivencia de plantas nativas. No se encontraron diferencias significativas en la supervivencia entre las especies en estudio *N. nervosa, L. philipiana* y *P. saligna* con los distintos rangos de transmisividad de radiación solar y la supervivencia. Nuestros resultados coinciden con lo reportado por Sandoval (2017), al comparar especies con distintos rangos de tolerancia a la sombra, tanto exóticas como nativas creciendo bajo dosel de *Eucalyptus globulus-Acacia melanoxylon*., estableciendo que en clima mediterráneo, la tolerancia a la sombra no afecta la supervivencia de plantas y para ello las especies adoptan diferentes estrategias funcionales, morfológicas y fisiológicas para sobrevivir (Givnish, 1988; Sack et al., 2003), lo que explica que la densidad de las especies se distribuya a lo largo de un eje de tolerancia de la sombra, lo cual solo es afectada por el tamaño de las plántulas (Baraloto et al., 2005; Kunstler et al., 2009).

N. Nervosa y *L. sempervirens* presentaron mayores incrementos en Dac que *P. saligna* en altos niveles de Dif, lo que revela que en niveles intermedios de Dif no existen diferencias significativas entre estas especies, con el incremento en Dac. Estos resultados coinciden con otros estudios en que Dac es mayor en condiciones de mayor luminosidad (Álvarez y Lara, 2008), debido a las características auteocológicas de *N. Nervosa* y *L. sempervirens*, como son la intolerancia a la sombra y su rápido crecimiento inicial. La especie tolerante *P. saligna* presentó las menores tasas de incremento en Dac, lo que se explica porque su estrategia de regeneración en claros con altos niveles de Dif es más bien episódica, asociada a un denso establecimiento inicial y una alta mortalidad posterior (Donoso y Utreras, 2006; Muñoz y González, 2009). El incremento en H fue significativamente mayor en *N. nervosa* con respecto a *L. sempervirens* y *P. saligna* en condiciones de altos niveles de Dif (Tabla 5.1), lo que concuerda con la relación entre incremento en altura de plantas jóvenes y el grado de tolerancia a la sombra, debido a que especies intolerantes crecen rápidamente en altura, asignando más crecimiento al tallo y ramas, y poseen copas con baja área foliar, como es el caso en este estudio de *N. nervosa* (Canham et al., 1994; Sheil et al., 2006; Hosseini et al., 2010). Sin embargo, en condiciones medias y bajas de Dif no se observaron diferencias significativas entre las tres especies. En este estudio se pudo confirmar que *N. nervosa*, tiene buen crecimiento bajo una condición de media a alta luminosidad. Las tasas de supervivencia y crecimiento de las tres especies presentaron una estrategia de claros, debido a la constante respuesta en las tasas de crecimiento al aumentar la luz. A la sombra, mostraron plasticidad para sacrificar tasas de crecimiento beneficiando la supervivencia (Petritan et al., 2008). Los resultados concuerdan con la visión del impacto de las compensaciones de crecimiento-supervivencia, en la dinámica forestal: las posiciones de las especies a lo largo del intercambio impulsan su capacidad para establecerse con alta o baja luz (Kobe, 1999). De acuerdo a lo anterior, las mayores tasas de crecimiento de Dac y H, en condiciones de alta y media radiación solar, se ordenaron de acuerdo al rango de tolerancia. *N. nervosa* presentó los mayores valores de A_{max}, seguida por la semitolerante *L. sempervirens* y la especie tolerante *P. saligna,* esto explicaría las altas tasas en incremento en Dac y H por sobre las otras especies. La conductancia estomatica, (g_s) no presentó diferencias significativas entre especies (Tabla 5.3), lo que puede explicar que a mayores valores de A_{max}, las especies intolerantes pueden sobrevivir y potencialmente crecer en claros de mayor tamaño que las especies semitolerantes y tolerantes (Peri et al., 2009). Los rasgos de intercambio de gases ilustran acerca de las diferencias entre especies que son capaces de adaptarse a condiciones de alta luminosidad respecto de plantas adaptadas a baja luminosidad (Poorter, 1999). Sin embargo, se conoce que un exceso de luz inhibe el crecimiento, debido a que cambia la morfología externa de la hoja y modifica la estructura del cloroplasto, que está involucrado en la saturación luminosa de la fotosíntesis en condiciones de alta luminosidad (Mache y Loiseaux, 1973). *P. saligna* presentó los valores más bajos de g_s en condiciones de alta luminosidad y positivamente correlacionado con Dac y el incremento en Dac (Figura 5.12; Figura 5.11), donde la fuerte correlación con g_s resulta en un incremento en Dac (Figura 5.11), siendo mayor en un 63% en alta luminosidad que en baja luminosidad (Tabla 5.2). Al respecto, se ha reportado que las relaciones entre la fotosíntesis y la conductancia estomática son casi lineales, por lo cual las diferencias en la reacción de la fotosíntesis a la conductancia estomática, se constituyen en un buen indicador de la adaptabilidad de las especies a la sequía estival (Anev et al., 2016), debido a que presenta el mayor valor en WUE en condiciones de alta luminosidad que todas las especies en estudio.

El desarrollo de bosques establecidos en mezclas con especies nativas representa una alternativa favorable desde el punto de vista ecológico, ambiental y económico. De acuerdo a los estudios realizados, se establece que en general las especies tolerantes, presentan buenas tasas de crecimiento, en tanto que algunas especies semitolerantes del bosque nativo, también presentaron buenas tasas de crecimiento como *L. sempervirens* y *P. saligna*. El uso de estas especies puede permitir una mayor productividad en los bosques mixtos con estructuras y especies que permitan un uso complementario de los recursos, en comparación con los bosques puros (Lusk y Ortega, 2003). En el proceso de la regeneración artificial de un bosque sobremaduro, se debe optimizar la relación entre la demanda de luz de la especie a tratar con el nivel de luminosidad que se pueda ofrecer a través de claros naturales o del manejo del dosel. En el caso de este estudio se cuenta con una oferta de alta radiación solar sobre las copas, dada la ubicación geográfica que lo sitúa en una zona de clima mediterráneo de montaña. De acuerdo a lo anterior es necesario ajustar las prácticas silvícolas, particularmente en el nivel de apertura del dosel, para mantener la mezcla de especies, como un indicador clave de sostenibilidad a escala de la unidad de manejo y que las especies elegidas no se vean afectadas (Sola et al., 2015).

CAPÍTULO VII

CONCLUSIONES GENERALES

En los bosques sobremaduros de *N. dombeyi*, ubicados en el centro-sur de la Cordillera de Los Andes en Chile, la transmisividad de la radiación solar difusa, no se correlaciona con las clases de altura, ARG y AHG de la regeneración avanzada *N. dombeyi*, estas variables solo mantienen correlación con la transmisividad directa y global. Los incrementos en el diámetro y la altura de las plantas de *N. dombeyi*, se explican mediante las variables de edad de las planta y la transmisividad de la radiación solar, donde las aperturas del dosel y los árboles circundantes desempeñan un papel fundamental en la regulación de la competencia en el crecimiento y la altura de la regeneración avanzada *N. dombeyi*.

La asignación de biomasa de las plantas *N. dombeyi* provenientes de la regeneración avanzada, en ambientes contrastante de luz, no se vio afectada por la transmisividad de la radiación solar en ninguno de los componentes de la planta como: hojas, ramas, tallos y raíces. La transmisividad tuvo un bajo impacto en la localización de biomasa en tallos y hojas. Sin embargo el tamaño de las hojas, el número de hojas y el largo de raíz, fue mayor en condiciones de alta luminosidad que en condiciones de baja luminosidad. Las plantas de *N. dombeyi* en condición de sombra asignan más biomasa sobre el suelo que bajo tierra, en respuesta a la baja luminosidad. Nuestros resultados coinciden con la hipótesis que especies intolerantes a la sombra presentan una mayor plasticidad morfológica de sus hojas, que la asignación de biomasa en respuesta a ambientes de luz contrastantes.

Las variables morfológicas de diámetro a la altura del cuello (Dac) y altuta (H) se correlacionaron con las variables de intercambio gaseoso en las plantas de la regeneración avanzada de *N. dombeyi*. El Dac depende de las condiciones de alta luminosidad y la H en menor medida. Las plantas de *N. dombeyi*, mostraron un mejor rendimiento fotosintético en condiciones de alta luminosidad, sin embargo el incremento medio anual IMA en H está limitado por los mecanismos de intercambio de gases, donde satura la fotosíntesis antes que se produzcan riesgos de fotoinhibición, esta condición permite que *N. dombeyi*, aumente el WUE, para mantener el rendimiento fotosintético. En condiciones de baja luminosidad esta especie desarrolla mecanismos de plasticidad morfológica asociado a L_{th} y la relación entre H/Dac, manteniendo valores de SLA relacionados con la absorción nutrientes.

El comportamiento de la mezcla de especies nativas: *N. nervosa*, *L. sempervirens* y *P. saligna* establecidas bajo el dosel del bosque sobremaduro de *N. dombeyi*, presentó la clásica teoría de intercambio en que la estrategia de las especies, es definida por su tasa de crecimiento en condiciones de alta luz y la capacidad por sobrevivir en condiciones de sombra se correlacionó negativamente con su tasa de crecimiento. Por consiguiente las especies sobreviven y crecen a lo largo de un eje de tolerancia de sombra. En relación a las variables de intercambio gaseoso, *N. nervosa* presentó los mayores valores de $A_{max,}$ seguido de *L. sempervirens* y *P. saligna*. Esto provocó que *N. nervosa*, presentara incrementos superiores en Dac y H con el aumento de la densidad de flujo de fotones PPDF, aunque puede presentar riesgos de fotoinhibición. Esta condición le permite desarrollar una economía de WUE, durante periodos de déficit hídrico. *P. saligna*, presentó los valores más bajos de g_s, en condiciones de alta luminosidad y una correlación positiva con el Dac y el incremento en Dac. Se sugiere la utilidad de plantaciones suplementarias con las especies estudiadas, para la provisión de servicios ecosistémicos y la productividad del bosque sobremaduro, interviniendo el bosque con métodos de selección en grupo, sobre 20% de transmisividad de radiación solar difusa.

CAPÍTULO VIII

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