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Contribution of Advanced Regeneration of Pinus radiata D. Don. to Transpiration by a Fragment of Native Forest in Central Chile Is out of Proportion with the Contribution to Sapwood Area

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Abstract: The transpiration of Nothofagus glauca (Phil.) Krasser and advanced Pinus radiata D. Don. regeneration was measured in a fragment of native N. glauca forest. Over the eight months of this study, P. radiata contributed approximately 60% of the total stand transpiration. This was out of proportion with the approximately 34% of the stand sapwood area contributed by P. radiata. This was due to the significantly greater sap flux density of the P. radiata compared to the N. glauca between May and October. Though the results are from a small study conducted as part of a larger experiment, it is argued that they suggest that invasion by P. radiata may substantially increase the risk from climate change to reserves of N. glauca forest in the Maule region of central Chile. In some reserves of N. glauca forest, Forestal Arauco S.A. manually removed P. radiata that regenerated after the wildfire of January 2017. This was a costly operation and there is a need for indices to assess competition. The ratio of sapwood area to leaf area is suggested as a potential index for assessing competition to identify stands at risk.

Keywords: Nothofagus glauca; sap flux density; competition; water-limited; invasive; weed; wildfire

1. Introduction

In the part of the coastal range of central Chile between the cities of Concepción and Santiago, the native forests are of type Roble-Hualo in which the deciduous Roble (Nothofagus obliqua (Mirb.) Oerst.) and Hualo (N. glauca (Phil.) Krasser) are the main species, especially on ridges and upper slopes of the range. This forest type has been described as vulnerable [1] due mainly to fragmentation. Existing reserves of this forest type have high conservation value.

There is a perception in Chile that the Pinus radiata D. Don. plantations were the primary cause of this fragmentation. Although some small areas of Roble-Hualo forest type were cleared to establish plantations of P. radiata, most of the forest was cleared for agriculture and the establishment of wheat
and pastures. The forests were also selectively logged until the late 1980s for wood and to produce charcoal [2]. On the shallow soils and steep slopes of the coastal range, agriculture was largely a failure and after decades of declining productivity and soil losses, much of this agricultural land, which was originally native forest, was planted to Pinus radiata [3,4].

Whatever the cause, the result is many small fragments of N. glauca and N. obliqua forests that are surrounded by P. radiata plantations. The authors of [5] concluded that invasion by the shade intolerant P. radiata occurred mostly at the edge of these reserves but advised ongoing monitoring of this situation, particularly after any major disturbance. In January of 2017, large wildfires burned more than 550,000 of mostly forested land in the coastal range in an area that overlaps almost entirely the natural range of Roble and Hualo. Of the total burned area, 223,605 hectares were plantations of P. radiata, Eucalyptus globulus Labill. or E. nitens Maiden (Deane and Maiden) and 60,995 ha were native forest, a lot of which was either N. obliqua or N. glauca [6].

The shallow soil, seasonally dry Mediterranean climate type and the inherent fertility of the soils combine to make water the most important limit to productivity in the Itata and Maule regions of the coastal range [7]. The recent fire, and the possibility of more serious invasion of N. glauca by a new generation of P. radiata seedlings, has elevated the existing need for an understanding of the nature of competition by P. radiata for water resources in mixtures with N. glauca. Post-fire invasion by P. radiata has the potential to change the water balance of these natural forests and increase pressure on these already vulnerable forests. Forestal Arauco S.A., the largest plantation grower in the region, manually removed all of the post-fire P. radiata regeneration from at least one reserve but this is a costly operation. It is therefore important to quantify competition of P. radiata for water when it occurs as a weed within the native Roble-Hualo forests to assist forest managers to quantify the net benefits of intervening to manage invasions.

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The aim of this research was to examine the relative consumption of water by naturally occurring and invasive exotic tree species in a region with a major plantation industry and subject to a Mediterranean climate. This paper reports concurrent measurements of transpiration in a mixed stand of N. glauca and advanced P. radiata regeneration. It tests the null hypothesis that water use per unit sapwood area is the same for N. glauca and P. radiata.

2. Materials and Methods

2.1. Site Description

The data reported in this study were measured within an N. glauca forest in which there were a number of 21- to 25-year old P. radiata trees. The area was not planted to P. radiata because it was too steep but is surrounded by a P. radiata plantation. The stand is on a South-East facing slope about 20 km East of the city of Constitución in the coastal range of central Chile. This study site is in the Mediterranean climate zone of central Chile and the rainfall is strongly winter dominant [8]; average annual rainfall from 2009 to 2019 was 950 mm [9].

The soil is very shallow with a clay loam texture and varies in depth from 0 cm to a maximum of 100 cm. Even in the surface, the soil is mixed with fragments of the local rocks. These and the rocks the soil overlies are of the Dollimo Complex of the western coastal range that was described in detail by [10]. The rocks of the region are a mix of albite schists, greenschist derived from metamorphism of oceanic tholeiitic basalts, iron and manganese rich metachaerts, serpentinites with occasional marble lenses.

In May of 2016, a circular plot with an area of 400 m$^2$ was established within this isolated fragment of N. glauca forest.

2.2. Rainfall Measurements

Measurements of rainfall were made at the township of Forel, about 5 km south-east of the site, using an automatic weather station (Weather Master 2000, Environdata—Warwick, Queensland, Australia) and using an RG12 tipping bucket rain gauge (Environdata—Warwick, Queensland,
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Australia) located in a clearing immediately adjacent to the top of the catchment. A correlation between rainfall measured with these gauges and with measurements made by the Chilean Dirección General de Aguas (DGA) at Forel was used to estimate rainfall at the site prior to the installation of the weather station and rain gauge.

2.3. Stand Characteristics

Prior to commencement of the measurements of transpiration, the diameter of all trees was measured together with the height of five individuals of each species. The basal area of each tree was calculated as well as the total basal area of each species. This study was part of a larger project in which a relationship between sapwood area and basal area was developed for both species [9]. This relationship was used to calculate the sapwood area of all trees and to estimate the sapwood area index for both species.

2.4. Selection of Trees for Transpiration

Each of the two species (N. glauca and P. radiata) was divided into three size classes, each contributing one-third of total stand basal area. The trees from each species were ranked in order of increasing size and the cumulative basal area was calculated starting with the smallest tree. The median tree from each of the resultant size classes was selected for measurement of transpiration.

2.5. Transpiration

In May of 2016, heat ratio type sapflow sensors were installed in three individuals each of P. radiata and N. glauca. These trees were selected as described above from three size classes that contributed one-third of the stand basal area of the species.

In each tree, a single heat ratio type sapflow sensor (Environmental Sensing Systems, Melbourne, Australia) was installed. Each sensor consisted of a logger with battery and solar panel and two thermocouple and one heater probes. The thermocouple and heater probes were inserted in 2.1 mm holes which were made using a cordless power drill and a 3 cm deep steel drill guide to assist in generating parallel holes. The centres of the holes were separated by 6 mm. A heater probe was installed in the central hole and a probe with a thermocouple was installed in each of the holes up and down the tree from the heater probe. The thickness of the bark was measured, and the probes were installed on the north facing side of the tree so that the thermocouples were situated 10 mm under the bark and in the sapwood.

A two second heat pulse was generated every thirty minutes and temperature was measured every second from just before the pulse to 120 s after the pulse. The change in temperature from before the pulse to after was measured between 60 and 120 s after the pulse and the mean change in temperature was recorded for the downstream ($\Delta T_1$) and upstream ($\Delta T_2$) probes. Heat pulse velocity ($v_h$) in cm h$^{-1}$ was calculated after [11] as

$$v_h = \frac{k}{x} \ln \left( \frac{\Delta T_1}{\Delta T_2} \right) 3600$$  \hspace{1cm} (1)

where $k$ was the thermal diffusivity of the sapwood and $x$ was the nominal distance of 0.6 cm between the heater and the thermocouples. Initially $k$ was given a default value of $2.5 \times 10^{-3}$ cm$^2$ s$^{-1}$.

The actual thermal diffusivity of sapwood ($k'$) was calculated using the method described in [11]. The sap velocity corrected for diffusivity was then calculated as:

$$v_{h, \text{diffusivity}} = \frac{k_{\text{actual}}}{k_{\text{default}}} v_h$$  \hspace{1cm} (2)

The actual separation between probes is rarely exactly 0.6 cm. To correct for probe misalignment, the average sap velocity between midnight and 4 am was calculated. At this time of day, it was
assumed that the real sap velocity was zero. The measured sap velocity in this time period \( (v_{h,\text{night}}) \) was then subtracted from all of the values already adjusted for diffusivity \( (v_{h,\text{diffusivity}}) \) to give a velocity corrected for probe misalignment \( (v_{h,\text{alignment}}) \).

\[
 v_{h,\text{alignment}} = v_{h,\text{diffusivity}} - v_{h,\text{night}}
\]  
(3)

After [11], the wound correction factor \( (\beta) \) was calculated as a function of the wound width \( (w) \) using the following polynomial. This linear correction factor was then multiplied by the velocity already corrected for diffusivity and alignment to give a velocity also corrected for the effect of wounding.

\[
 \beta = 7.06w^3 + 6.47w^2 + 0.54w + 1.53
\]

\[
 v_{h,\text{wounding}} = \beta v_{h,\text{alignment}}
\]  
(4)

Some correction must also be made for the fact that heat does not diffuse through wood and water at the same rate. The final sap velocity \( (v_s, \text{cm h}^{-1}) \) or sap flux density \( (\text{cm}^3 \text{ sap per cm}^2 \text{ of sapwood per hr}) \) of sap was calculated as:

\[
 v_s = \frac{v_{h,\text{wounding}} \rho_b (c_w + m_c c_s)}{\rho_s c_s}
\]  
(5)

where \( \rho_b \) was the basic density of the wood, \( c_w \) was the specific heat of water, \( m_c \) was the volumetric moisture content, \( c_s \) was the specific heat of sap and \( \rho_s \) was the density of sap.

These properties of the sapwood were estimated from samples collected in November of 2016 (before the fire) and in March of 2019 (after the fire). These were calculated as described in or using values provided in [11].

2.6. Stand Transpiration

Sapwood area was calculated for each tree using simple linear relationships between tree basal area and sapwood area. These models were developed and described in [9]. The slope of these models is 0.52 for the \( N. \text{ glauca} \) and 0.69 for the \( P. \text{ radiata} \). Stand sapwood area per species was calculated as the sum of the sapwood area of the individual trees and expressed on a per hectare basis \( A_s \). Stand transpiration \( (T) \) was calculated separately for the two species as the product of the average sap flux density for the three trees \( (v_s) \) and the stand sapwood area \( (A_s) \).

2.7. Data Analysis

For each month between May and December of 2016, the average hourly and daily sap flux density \( (v_s) \) for the month was calculated. The difference between species was analysed using a paired t-test. The data were analysed this way because there is a lot of variation within the species due to the low velocities in the smallest trees in each species because they are suppressed, and their crowns are less irradiated than either of the other trees.

3. Results

3.1. Weather Conditions

Rainfall at the site was 697 mm in 2016, 27% below the average from 2009 to 2018 of 951 mm. Rainfall from May to December in 2016 was 551 mm, 299 mm less than the average between 2009 and 2018 of 850 mm for this 8-month period (Figure 1). The measurement period was the driest 8-month period since 2009 but was preceded by a wetter than average year in 2015 (1106 mm).
Thus, these linear relationships between sapwood area (over bark) and basal area (under bark) were very similar for these two species in this mixed stand. The height and diameter distribution of both species were positively skewed (mean greater than median) due to the presence of a small number of large trees.

3.3. Basal Area and Sapwood Area

The slope of the relationship between sapwood area and basal area in this area was reported in [9] as 0.7 for *P. radiata* and 0.5 for *N. glauca*. This difference was statistically significant. Data from this mixed stand were included in that analysis and there was no evidence that the ratio of sapwood area to basal area was different for either species in this stand from that within pure stands of either species. Thus, these linear relationships between sapwood area (over bark) and basal area (under bark) were used to calculate the sapwood area of each *N. glauca* and *P. radiata* tree in the plot.

In both species, approximately 50% of the basal area and sapwood area in the stand was contributed by a small number of large trees (Figure 2). *Pinus radiata* contributed 34% (13) of the total of 38 trees in the plot. This translated to 27% of the total stand basal area of 37 m² ha⁻¹ and 34% of the total stand sapwood area of 19.9 m² ha⁻¹.
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3.4. Tree and Stand Sap Flux Density

Figure 3 shows the average daily sap flux density in volume (cm$^3$) of water per area of sapwood (cm$^2$) per day for each month between May and December of 2016 and for each of the three $P.\ radiata$ and $N.\ glauca$ trees measured. There was much larger variability between trees in the average daily sap flux density of $P.\ radiata$ than was evident in $N.\ glauca$. In winter and early spring, the smallest $P.\ radiata$ tree (which was suppressed) had a much lower daily flux than the two larger trees. Later in spring, the sap flux density of the largest $P.\ radiata$ tree decreased rapidly from 129 cm$^3$ cm$^{-2}$ day$^{-1}$ in September to 19 cm$^3$ cm$^{-2}$ day$^{-1}$ in December which was similar to the flux in the smallest tree. The sap flux density of all three $N.\ glauca$ trees was close to zero in winter and increased to maximum values of between 20 and 70 cm$^3$ cm$^{-2}$ day$^{-1}$ in November and December (Figure 3).

Although there was a lot of variation amongst the $P.\ radiata$ trees, the average sap flux density of $P.\ radiata$ was significantly greater between May and October than in $N.\ glauca$ (Figure 4). The difference was significant when the trees from the same size class of the two trees were treated as un-paired ($p < 0.05$) and highly significant when they were treated as paired ($p < 0.001$). In November and December, sap flux density did not differ significantly between the $P.\ radiata$ and $N.\ glauca$ (Figure 4).

Figure 2. Cumulative sapwood area as a function of tree number, where the trees were sorted from smallest to largest within species. This shows that $P.\ radiata$ contributed just over one-third of the total stand sapwood area and that in both species about half of the sapwood area was contributed by a small number of large trees.
The approximately one-third of the basal and sapwood area of the stand that was *P. radiata* contributed just under 60% of the total stand transpiration (Figure 5). The cumulative difference between the transpirations, expressed on a ground area basis, of *P. radiata* and *N. glauca* peaked by September of 2016. *P. radiata* competed very strongly for water in winter and early spring when the *N. glauca* was either without leaves or regrowing the canopy (Figure 6).

3.5. Summary of Stand Characteristics and Transpiration

The approximately one-third of the basal and sapwood area of the stand that was *P. radiata* contributed just under 60% of the total stand transpiration (Figure 5). The cumulative difference between the transpirations, expressed on a ground area basis, of *P. radiata* and *N. glauca* peaked by September of 2016. *P. radiata* competed very strongly for water in winter and early spring when the *N. glauca* was either without leaves or regrowing the canopy (Figure 6).
Figure 5. The proportion of the trees and stand basal area, sapwood area and transpiration contributed by *P. radiata* and *N. glauca* in this mixed stand.

Figure 6. Cumulative transpiration on a ground area basis of both *P. radiata* and *N. glauca* in a mixed stand in central Chile. The cumulative difference between the *P. radiata* and *N. glauca* is also shown.

4. Discussion

This study quantified the contribution of advanced *P. radiata* regeneration that was between 20 and 25 years-old to the total transpiration of an *N. glauca* forest. The *P. radiata* comprised about one-third of the trees in the stand and a similar proportion of the basal and sapwood area of that forest. Owing to much greater sap flux density, the *P. radiata* trees in this forest, while only contributing one-third of the basal area, contributed nearly 60% of the total stand transpiration of 201 mm. This is a very important result due to the vulnerability of fragments of the Roble-Hualo forests to invasion, especially after fire, from neighbouring *P. radiata* plantations [5]. It is therefore very important to consider the extent to which it can be argued that this behaviour will represent the effect of infestations more generally.

In this mixed forest, the *P. radiata* provided an evergreen presence in a mostly deciduous forest. The *N. glauca* in the plot were without leaves in June, July and August of 2016 [9]. The total cumulative difference between the transpiration of the *P. radiata* and *N. glauca* components of the forest was 49 mm at the end of August 2016 and 47 mm at the end of December (Figure 6). Thus, all of the difference...
The primary cause of the observed difference of 47 mm between the total transpiration of the *P. radiata* and the *N. glauca* in this stand was increased sap flux density of the *P. radiata* during winter and spring. Sapwood area index has emerged in recent times as a useful index of actual water use [25] and indeed, as a deficit, of stream flow in forested systems [26]. The effect of *P. radiata* on the total water use of this forest was out of proportion with the fraction of stand basal or sapwood area. When competing with more conservative species, the commercial plantation species *P. radiata* may have a large impact on local water balance and will therefore likely increase the vulnerability of this forest to water shortage.

The competitiveness of invasive plants in water limited situations can be quantified by measuring sap flux density. This study indicates that this will be a better indicator of competitiveness than sapwood area index. However, this variable is prohibitively difficult and costly to measure operationally. There is therefore a need for more easily measured indices of competitiveness to guide and allocate investment in management and control. In a nearby reserve to this study site, Forestal Arauco S.A. manually removed all of the *P. radiata* that regenerated after the recent fires. In natural ecosystems, functional convergence in hydraulic traits has been observed so that the ratio of one trait to another is often common amongst the species [27–29]. Invasive species disturb this general equilibrium and may be detected by looking at relationships amongst characteristics. For example, we might expect a lower Huber value, ratio of sapwood to leaf area, in invasives than in locally adapted plants. The Huber value has been shown to be a good indicator of temporary disequilibria with site resources [30,31].
Forest fire is forecast to increase in frequency and intensity in this region, associated with a warming and drying climate. This is known to affect the structure of the local Roble-Hualo forest in the absence of woody invasives [32]. If, as suggested by [33], fire promotes invasion by *P. radiata* in the native forests of central Chile then to avoid further fragmentation and loss of these vulnerable forests *P. radiata* must be actively managed and reduced, especially in small fragments of Roble-Hualo forest. Forestal Arauco S.A. did manage invasion by *P. radiata* in key reserves. This is an expensive operation and there is therefore a need to develop methods to identify areas at greatest risk in these water-limited forests.

5. Conclusions

In this paper, we have examined the relative contributions to total water balance of naturally occurring *Nothofagus* and invasive exotic *Pinus* species in a region of Central Chile subject to a Mediterranean climate. This issue is of concern in regions where exotic species may disturb the water balance of naturally forested catchments.

*P. radiata* contributed about one-third of both the basal area and the sapwood area index at the study site. Owing to much greater sap flux density than the local *N. glauca*, the *P. radiata* contributed just under 60% of total transpiration, an amount that was out of proportion to the contribution to the sapwood area index. The null hypothesis, that the contribution to transpiration would be in proportion to the sapwood area, was rejected.

We suggest that the Huber value, ratio of sapwood to leaf area, should be investigated to test the utility for quantifying the competitiveness of *P. radiata* and other plantation species as invasives in the coastal range of central Chile.

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