



Use of water stress integral to evaluate relationships between soil moisture, plant water stress and stand productivity in young Douglas-fir trees

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Abstract

Water stress integral (WSI) is a method of assessing cumulative plant water stress over a chosen period of time. While the technique has been used in other tree species, it has not been applied for reforestation projects. In this study we used the WSI approach for newly planted Douglas-fir in the Pacific Northwest (USA), where the Mediterranean climate, plant community development, and competition for water all play key roles in the success of establishment efforts. In this study, previously reported seedling growth, xylem water potential, and soil moisture data were utilized to provide direct correlations between Douglas-fir productivity, soil water availability and WSI. For each growing season, a strong relationship between WSI and volume growth as well as a strong linear relationship between WSI and soil moisture measured during mid-August was found. On average, for each reduction of $0.01 \text{ cm}^3 \text{ cm}^{-3}$ in soil moisture measured during mid-August, Douglas-fir seedling volume growth decreased by 5.6 and 7.7% in the first and second growing seasons, respectively. Preserving soil moisture until early-August through the judicious application of vegetation management regimes was critical for maximizing stand productivity. Based on these results, a single evaluation of soil volumetric water content during early-August can be used as a predictor of stand productivity during the initial two seasons of forest establishment.

Keywords Forest vegetation management · Herbicide · Reforestation · Intensive silviculture · Plant water stress · Soil water availability

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Introduction

Competition between newly planted seedlings and the surrounding vegetation community (native or invasive) is a major process limiting seedling growth and survival (Balandier et al. 2006; Wagner and Robinson 2006). Vegetation management treatments create a temporal reduction in the amount of competing vegetation that increases water, nutrient, and light availability (Balandier et al. 2006; Eyles et al. 2012) allowing crop seedlings to better capture site resources. This reduction in competition has been shown to increase the survival and growth of various tree species (Adams et al. 2003; Albaugh et al. 2004; Wagner et al. 2006; Little et al. 2007; Jokela et al. 2010) including Douglas-fir (Newton and Preest 1988; Rose et al. 2006; Dinger and Rose 2009). Chemical forest vegetation management (FVM) treatments are a key tool used by managers to successfully establish plantations. Common chemical vegetation control treatments include an herbicide application during fall prior to planting (fall site preparation) followed by one or more years of post-planting herbicide application during spring (spring release) (Balandier et al. 2006; Wagner and Robinson 2006). The magnitude of responses to FVM treatments depends on crop tree species, vegetation composition, site characteristics (soil and climate) and type of vegetation control treatment applied (Balandier et al. 2006).

There have been several FVM studies in plantations that have reported data from ecophysiological measurements (Sands and Nambiar 1984; Nambiar and Sands 1993; Albaugh et al. 2004, 2015; Watt et al. 2003, 2007; Eyles et al. 2012). In the Pacific Northwest United States (PNW), there are also examples of such studies on conifer reforestation (Newton and Preest 1988; Powers and Reynolds 1999; Mason et al. 2007; Dinger and Rose 2009, 2010; Maguire et al. 2009; Pinto et al. 2012). These studies concluded that competition for water plays a crucial role in crop seedling growth and survival. While this body of literature has described treatment effects on gas exchange, soil moisture and xylem water potential, ecophysiological methods need to couple tree growth and survival with these measurements of plant water relations. The combination of tree ecophysiological traits with growth would provide a more mechanistic understanding of treatment efficacy and improve applicability of predictive models.

Even though xylem water potential has been widely used as an index of water stress (Waring and Cleary 1967; Sands and Nambiar 1984), it only represents a snap shot of plant water stress at the time of measurement and no clear relationships have been developed between whole-season seedling productivity and single measurements of xylem water potential. One of the few examples of direct relationships between xylem water potential and seedling growth was reported by Watt et al. (2003). In that study, the authors reported a strong relationship between two monthly average needle water potential and biomass growth for *Pinus radiata* seedlings. One index of cumulated plant water stress throughout the growing season is the Water Stress Integral (WSI), which corresponds to the summation of pre-dawn xylem water potential measurements over a chosen period of time (Myers 1988). WSI has been shown to be well-correlated with productivity (Hanson et al. 2001; Fernandez et al. 2010; De la Rosa et al. 2016), mortality (Hanson et al. 2001; Nepstad et al. 2007) and has been used for irrigation management and modeling in agricultural crops (Ballester et al. 2013; Brillante et al. 2016). While WSI has been used to describe water relations in some tree species (Myers 1988; Myers and Landsberg 1989; Nepstad et al. 2007), the concept has not been applied to growth and survival of newly established forest plantations. In this study, we utilize the WSI approach to quantify the links between cumulative water stress and growth in a newly established Douglas-fir plantation in the PNW.

The Vegetation Management Research Cooperative (VMRC) at Oregon State University (OSU) developed a study that quantified the impact of six herbaceous vegetation control regimes on Douglas-fir seedling growth, xylem water potential and soil moisture availability during the first two growing seasons (Dinger and Rose 2009, 2010). Results indicated that the initial fall-spring vegetation management regimes which reduced competitive plant cover below 20%, improved soil moisture conditions and plant water relations, increasing Douglas-fir seedling growth. There is an opportunity to further analyze these datasets within the context of WSI in order to provide direct correlations between Douglas-fir productivity, xylem water potential, and soil water availability.

The overall objective of this study was to utilize WSI as a tool to quantitatively link Douglas-fir seedling water status and growth. The specific objectives of this study were to: (1) quantify seasonal dynamics in WSI on Douglas-fir seedlings growing under contrasting vegetation management regimes applied during stand establishment, (2) correlate WSI with seedling growth during the first two growing seasons after planting, and (3) determine if pre-dawn water potential and soil moisture measured at some point during the dry season can be used as a surrogate for seasonal WSI and volume growth.

Materials and methods

Experimental design, treatments and site characteristics

The Evaluating Common Regimes study contains six vegetation management treatments (Table 1) arranged in a randomized complete block design with four replications on 24.4×24.4 m treatment plots. Douglas-fir seedlings (bareroot 1 + 1) were planted on February 25, 2006 at a spacing of 3.05×3.05 m. Measurements of seedling height and diameter at ground-line were taken one month after planting (March 2006) and at the end of the first two growing seasons (October 2006 and October 2007) in the central 18.3×18.3 m measurement plots allowing for a one tree buffer on all sides. The study area was surrounded by a perimeter fence prior to planting in order to protect seedlings from ungulate browse damage. The average precipitation is 1450 mm, with only 110 mm occurring between July and September. Soils are fine-loamy, mixed, mesic xeric Palehumults with an argillic horizon at 50–70 cm depth

Table 1 Description of treatment regimes tested

Treatment	Year 1 (2006)	Year 2 (2007)
1	No control	No control
2	Fall site preparation	No control
3	Fall site preparation	Spring release
4	Fall site preparation, spring release	Spring release
5	Fall site preparation, spring release, glyphosate release	Spring release
6	Fall site preparation, spring release, glyphosate release	Spring release, glyphosate release

Fall site preparation is pre-planting herbicide application during previous fall. Spring release is post-planting herbicide application during early in the growing season (spring). Further details about the treatment regimes can be found in Dinger and Rose (2009)

(Dinger and Rose 2009). A more detailed description of the full suite of measurements taken at this study site can be found in Dinger and Rose (2009, 2010).

Seedling growth and vegetation cover

Stem volume (dm^3) was computed from measurements of ground-line diameter and height, using the formula for a cone. After summing the stem volume of all living seedlings, volume per hectare ($\text{dm}^3 \text{ ha}^{-1}$) was determined on each measurement plot. Volume growth per growing season ($\text{dm}^3 \text{ ha}^{-1} \text{ year}^{-1}$) was calculated as the difference between volume per hectare at the beginning and at the end of each growing season. Percent cover by species was visually determined using seven 1-m radius vegetation survey sub-plots ($n = 168$) on 19 July 2006 and 16 August 2007. Vegetative growth habit according to six categories was then assigned to each species found during these surveys (i.e. forb, fern, graminoid, shrub, vine/shrub, and tree).

Xylem water potential and soil moisture

Xylem water potential (Ψ , MPa) was measured using a portable pressure chamber (PMS 600; PMS Instruments Co., Oregon, USA) biweekly from May to October in 2006 and 2007. Two seedlings per plot were measured at pre-dawn (4:00–6:00) and midday (12:00–14:00). For the purposes of this analysis, only the pre-dawn xylem water potential (Ψ_{PD}) measurements were used. On each selected seedling, one branch tip of 8 cm length was cut from the middle third of a randomly selected seedling's crown. Seedlings were only sampled on one date to avoid excessive loss of foliage.

On the same dates when xylem water potential was measured, soil volumetric water content (θ_v , $\text{cm}^3 \text{ cm}^{-3}$) was assessed on seven random points associated with the vegetation survey sub-plots occurring in each treatment plot. A time domain reflectometry (TDR) soil moisture probe (Hydrosense CS620, Spectrum Technologies, Illinois, USA) with 20 cm prongs was used to vertically measure θ_v in the upper soil profile. Soil moisture estimates using the TDR probe were calibrated for the study site using soil cores taken on all treatment plots during the 2006 growing season. The developed calibration curve was reported by Dinger and Rose (2009). An automatic weather station (HOBO H21-002; Onset Computer Corporation, Massachusetts, USA) was used to collect weather data, including air temperature, relative humidity, wind speed, solar radiation and rainfall.

Following Myers (1988), water stress integral (WSI, MPa day) was computed as the summation of Ψ_{PD} on each day during the period of interest (May to October). WSI was calculated using 12 Ψ_{PD} measurements in 2006 and 9 Ψ_{PD} measurements in 2007 at intervals of n days as follows:

$$\text{WSI} = \sum (\Psi_{i,i+1} - c) \cdot n$$

where $\Psi_{i,i+1}$ is the mean Ψ_{PD} for any interval $i,i+1$, c is the datum value or maximum (less negative) Ψ_{PD} measured, and n is the number of days in each interval.

Data analysis

Analysis of variance including Fisher's protected least significant difference t test was used to test the effects of treatments on plot means of seasonal stand volume growth, vegetation cover percent, volumetric water content and xylem water potential (PROC GLM; SAS Institute Inc., Cary, NC, USA).

In order to develop equations that could be evaluated in the field and applied operationally, the relationship between WSI and Ψ_{PD} was tested at different dates between May and October of each growing season. Furthermore, Ψ_{PD} is difficult to measure so further analysis was conducted to develop a practical tool that synthesizes the relationship between WSI, θ_v and Ψ_{PD} . As during the night, especially at pre-dawn in small plants, stomata are closed and soil and plant water potential are near equilibrium (Kramer and Boyer 1995). Measurements of Ψ_{PD} can then be used as a surrogate of soil matric potential. Using independent data of θ_v and Ψ_{PD} , a relationship between θ_v and Ψ_{PD} was fitted. This relationship resembled a soil water release curve (Sellin 1999).

Correlation analysis and non-linear model regression were used to test the relationships between: WSI and Douglas-fir stand growth for the whole season, WSI and Ψ_{PD} evaluated at different dates between May and October of each growing season, and Ψ_{PD} and θ_v (PROC GLM, PROC REG and PROC NLIN). Model assumptions of normality, linearity and constant variance were examined on the residuals of each variable (PROC UNIVARIATE). When non-linear model fitting was carried out, several models were tested and the BIC criteria was using for final model selection.

Results

Figures 1 and 2 (previously reported in Dinger and Rose 2009, 2010) were included to reinforce the linkage between plant community growth, seasonal precipitation, soil moisture and plant water stress dynamics as influenced by the vegetation management regimes included in this study. Vegetation management treatments had a large impact on competing plant cover ($P < 0.05$), creating a gradient that decreased as treatment intensity increased (Fig. 1). The control treatment (T1) represents unrestrained plant community growth

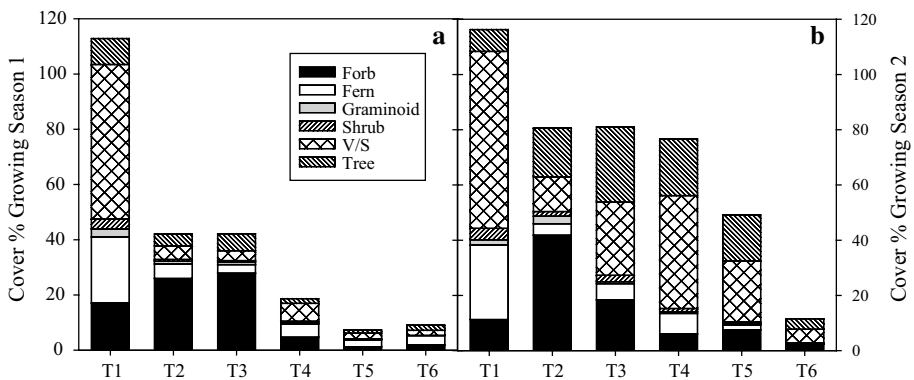


Fig. 1 Mean vegetation cover by treatment and growth form on July 2006 (a) and August 2007 (b). Each bar is the mean of 4 plots. Treatment legend is described in Table 1

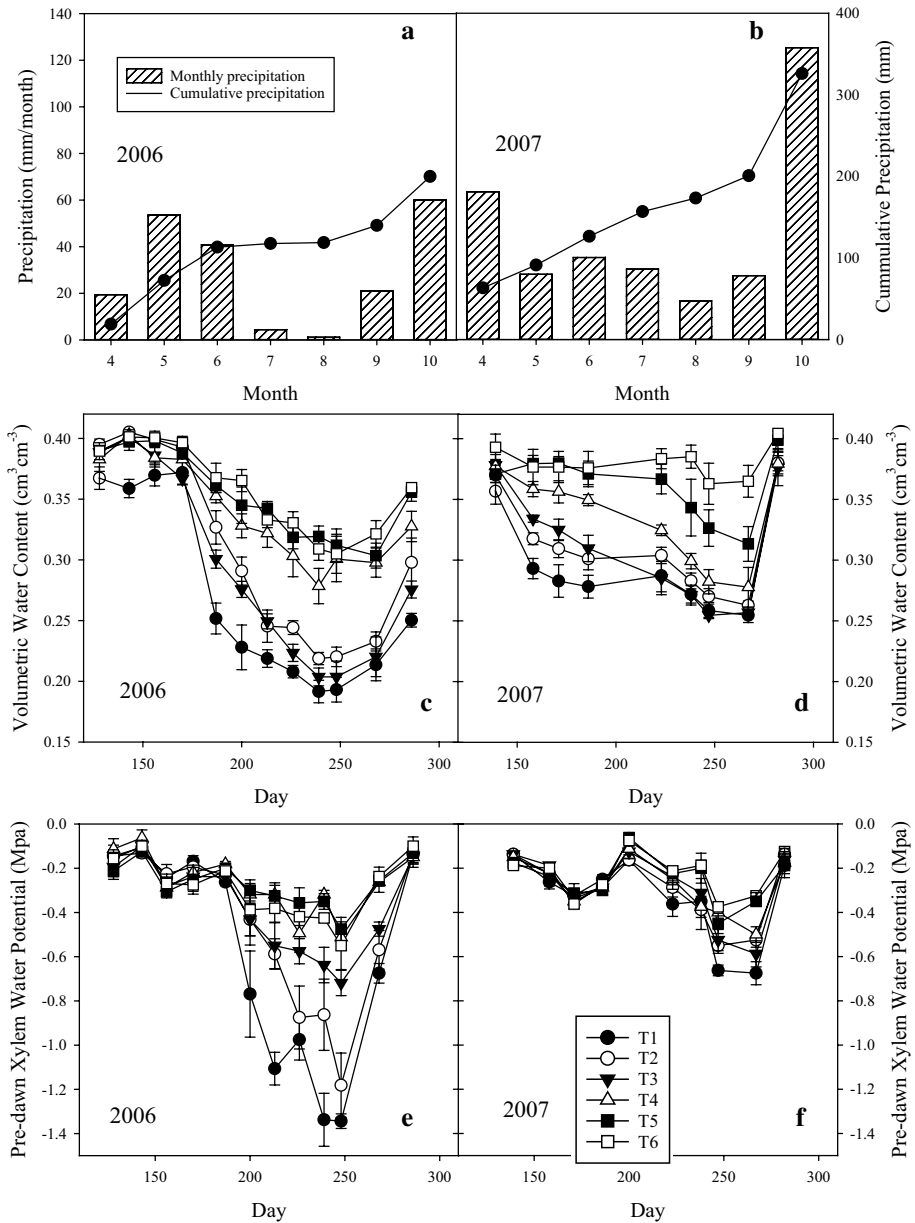


Fig. 2 Monthly (dashed bar) and cumulative (solid line) precipitation between April and October of 2006 (a) and 2007 (a, b), and treatment effects on volumetric water content (c, d) and pre-dawn xylem water potential (e, f) for Douglas-fir seedlings growing under different vegetation control regimes. For panels c to f, each point is the mean of 4 plots. Standard errors are calculated by treatment over replication. Treatment legend is described in Table 1. (Data from Dinger and Rose 2009)

increasing to over 90% during both years of forest establishment. In year-1, a fall site preparation initially limited community growth to 40% (T2 and T3) but the spring release treatment was necessary to decrease competitive cover below 20% (T4, T5, and T6). In year-2, the spring release had less impact as demonstrated by the plants growing in T2, T3, and T4 which increased to > 50% by August 2007. Without the directed application of glyphosate in 2007, T5 increased to nearly 40%. Only the most intense treatment (T6) was able to limit plant community growth below 20% for the second growing season.

The 2006 growing season was dryer than that of 2007 and the total accumulated precipitation from March 1st to October 31st was 203 and 478 mm, respectively. During the driest portion of the 2006 summer (June–August), the total precipitation was 46.4 mm, while during the summer of 2007, total precipitation was 82.0 mm (Fig. 2a, b). Vegetation management treatments created a large gradient in soil moisture and xylem water potential during the droughty conditions in 2006 (Fig. 2c–f). By comparison, the vegetation management treatments in 2007 had a less pronounced impact on soil moisture availability due to the additional precipitation received in the summer months. For example, in 2006 (Fig. 2c, e), treatments that did not include a spring release (T1, T2 and T3) had lower θ_v and Ψ_{PD} than in 2007 ($P < 0.001$). Treatments showed different θ_v and Ψ_{PD} across both growing seasons. During 2007 (Fig. 1d, f), plots that received a directed application of glyphosate during the first growing season (T5) and during the summer of the first and second growing seasons (T6) had higher θ_v and Ψ_{PD} than the treatments that did not receive glyphosate during the summer ($P < 0.001$). During 2007, the control treatment (T1) continued to have lower θ_v and Ψ_{PD} than any other treatment ($P < 0.044$), even though rainfall was higher than that observed in the prior summer.

The average maximum Ψ_{PD} (c in the WSI calculation) was -0.15 MPa (Fig. 2e, f). In 2006, the cumulative WSI for the whole season for T1 was -98 MPa day. Treatments that received a fall site preparation and spring release had a 54% reduction in WSI, averaging about -45 MPa day by the end of the same growing season (Fig. 3a, b). WSI in 2006 began to separate among the treatments by July 7th (day 188), and reached a difference of about -20 MPa day 15 days later. Similar to θ_v and Ψ_{PD} , this effect was more accentuated in 2006 due to lower precipitation. While the study site received increased precipitation in 2007, T1 retained the lowest cumulative WSI for the whole-season, reaching -55 MPa day, while T5 and T6 reached at the end of the growing season a WSI of -37 MPa day.

Seedling stress patterns were similar for both growing seasons, however, the magnitude of the changes were different due to the increased precipitation in 2007. For example, (Fig. 3c) treatments that did not include a spring release during the first growing season (T1, T2 and T3) had lower volume growth than plots that received the herbicide application (T4, T5 and T6) ($P < 0.001$). In both growing seasons, treatments that received more intensive vegetation management responded with greater volume growth when compared to control plots (T1) (Fig. 3c, d). The control treatment (T1) in 2007 continued to have lower volume growth ($P < 0.046$). There were no differences in volume growth between plots that received fall site preparation and spring release during second growing season (T3) and those plots that received fall site preparation and spring release during first and second growing seasons (T4) ($P = 0.373$).

Table 2 shows the parameter estimates and fitting statistics of the relationships between WSI and volume growth, Ψ_{PD} and WSI, and θ_v and Ψ_{PD} . There was a strong relationship between WSI and volume growth during 2006 ($P < 0.01$; $R^2 = 0.77$) and 2007 ($P < 0.01$; $R^2 = 0.69$). During the droughty 2006 growing season, 1 year-old stands with less than 20% plant cover that reached a WSI of approximately -40 MPa day had a volume growth of about $22 \text{ dm}^3 \text{ ha}^{-1} \text{ year}^{-1}$. On the other hand, stands with over 90% competitive plant cover

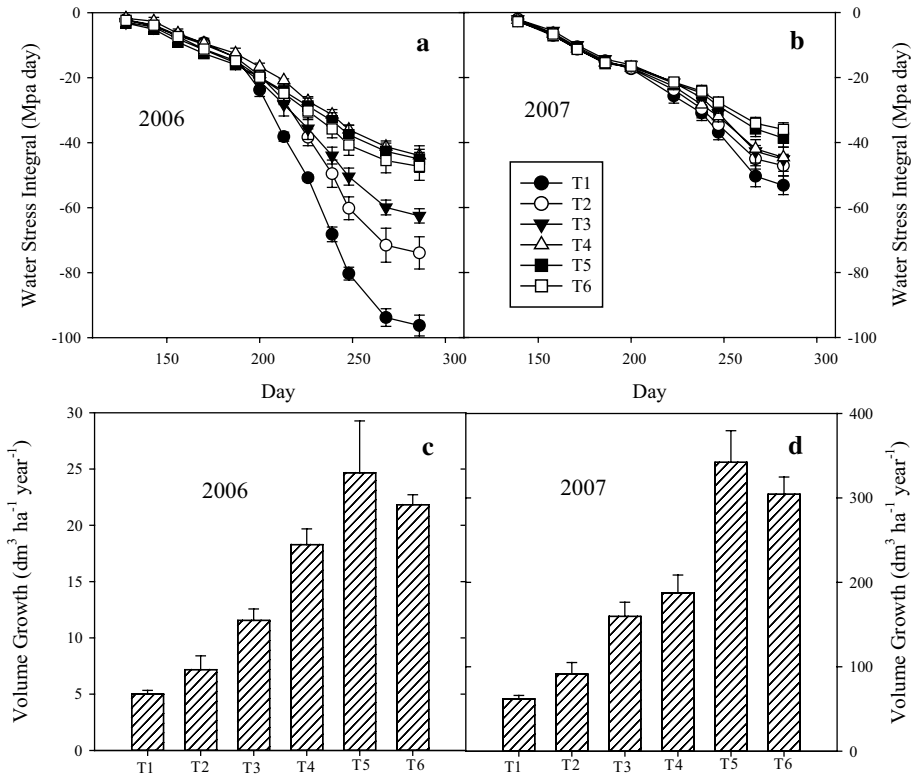


Fig. 3 Treatment effects on Douglas-fir seedling water stress integral (WSI) (**a** and **b**) and volume growth per ha (**c** and **d**) during the 2006 and 2007 growing seasons. For panels **a** and **b**, each point is the mean of 4 plots. For panels **c** and **d**, each bar is the mean of 4 plots. Standard errors were calculated by treatment over replication. The treatment legend is described in Table 1

reached a WSI of about -100 MPa day and had a volume growth 4.4 times lower, averaging $5 \text{ dm}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (Fig. 4a). The increased precipitation in 2007 enabled seedlings with $<20\%$ competitive plant cover to achieve a WSI of about -30 MPa day and a volume growth of nearly $400 \text{ dm}^3 \text{ ha}^{-1} \text{ year}^{-1}$. Seedlings that reached a WSI of about -60 MPa day during the same year had a volume growth 8 times lower, averaging $50 \text{ dm}^3 \text{ ha}^{-1} \text{ year}^{-1}$ (Fig. 4b).

WSI was correlated with Ψ_{PD} evaluated at different dates between May and October of each growing season (Fig. 5). The best correlation was found between Ψ_{PD} measured during the first half of August ($\Psi_{\text{PD-8}}$; Aug 3 in 2006, Fig. 5a; Aug 13 in 2007; Fig. 5b). Even though θ_v remained constant until the return of rainfall in September, no further gain in model fitting was observed when using the measurements of late-August or early-September (analysis not shown). There was not a significant relationship for Ψ_{PD} measured at any other time before August (i.e. July 2006: $P=0.63$; July 2007: $P=0.32$). This lack of relationship is demonstrated for measurements taken on 7 July 2006 (Fig. 5a) and 6 July 2007 (Fig. 5b). When data from both years were pooled, a unique relationship was found ($P<0.001$; $R^2=0.82$; Fig. 5c) and the slopes from the individual years were not different from one another ($P=0.25$). Parameter estimates and fit statistics are shown in Table 2

Table 2 Parameter estimates and fit statistics of the relationships between WSI and volume growth (VG), Ψ_{PD} and WSI, θ_v and Ψ_{PD} , and θ_{v-8} and WSI and whole-season volume growth of Douglas-fir seedlings during the first two seasons of establishment

Year	Equation	Model	Parameter	Parameter estimate	SE	R ²	RMSE
2006	Eq. 1	VG = $a \cdot e^{b \cdot WSI}$	<i>a</i>	64.0523	5.9402	0.77	1.89
			<i>b</i>	0.0267	0.00481		
2007	Eq. 2	VG = $a \cdot e^{b \cdot WSI}$	<i>a</i>	274.9982	42.3482	0.69	7.73
			<i>b</i>	0.0641	0.0080		
2006–2007	Eq. 3	WSI = $a + b \cdot \Psi_{PD-8}$	<i>a</i>	−19.7436	4.7711	0.82	216.76
			<i>b</i>	60.3392	6.1599		
2006–2007	Eq. 4	$\Psi_{PD} = a \cdot e^{b \cdot \theta_v}$	<i>a</i>	−5.1784	0.6350	0.57	0.20
			<i>b</i>	−8.4159	0.4691		
2006–2007	Eq. 5	WSI = $a + b \cdot \theta_{v-8}$	<i>a</i>	341.7453	24.1036	0.83	262.48
			<i>b</i>	−147.1724	6.6967		
2006	Eq. 6	VG = $a \cdot e^{b \cdot \theta_{v-8}}$	<i>a</i>	1.5429	0.8307	0.58	51.05
			<i>b</i>	8.3609	1.8637		
2007	Eq. 7	VG = $a \cdot e^{b \cdot \theta_{v-8}}$	<i>a</i>	1.6679	2.3392	0.42	455.75
			<i>b</i>	15.2422	4.3887		

VG: stem volume growth (dm³ ha^{−1} year^{−1}); WSI: water stress integral at the end of the growing season (MPa day); Ψ_{PD} : pre-dawn xylem water potential (MPa); Ψ_{PD-8} : pre-dawn xylem water potential measured in August (MPa); θ_v : soil volumetric water content (cm³ cm^{−3}); θ_{v-8} : soil volumetric water content measured in August (cm³ cm^{−3}); SE: standard error of the parameter estimate; R²: coefficient of determination; RMSE: root mean square error of the model. For all parameter estimates: $P < 0.001$

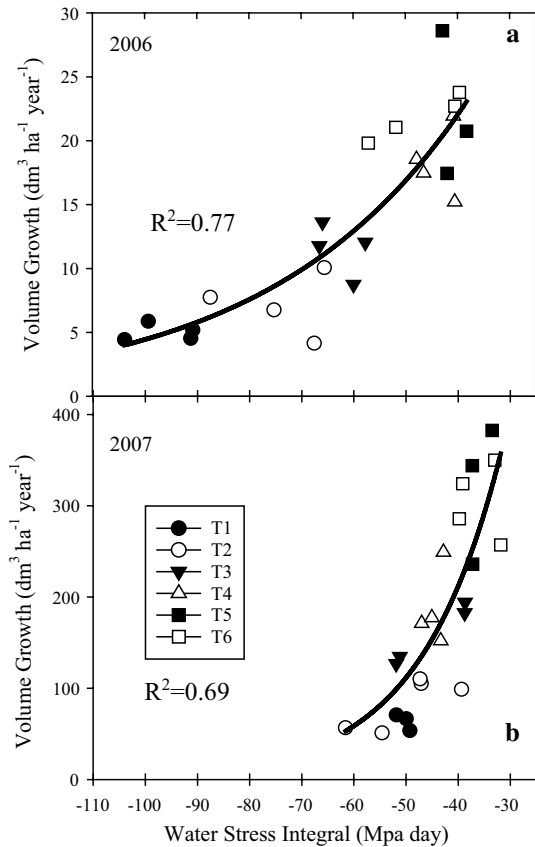
(Eq. 3). On average, seedlings that had a Ψ_{PD-8} of −0.5 MPa have a WSI of −50 MPa day, while seedlings that show Ψ_{PD-8} of −1.5 MPa have a WSI of −110 MPa day.

Using the data for both growing seasons presented in Fig. 1, a relationship between θ_v and Ψ_{PD} was developed (Fig. 6a; $P < 0.001$; $R^2 = 0.65$). Parameter estimates and fitting statistics are shown in Table 2 (Eq. 4). On average, when θ_v is greater than 0.35 cm³ cm^{−3}, Ψ_{PD} will have values between −0.2 and −0.3 MPa, and when θ_v is about 0.15 cm³ cm^{−3}, Ψ_{PD} will be −1.25 MPa. There was a strong relationship between θ_v measured during the first half of August (θ_{v-8}) and WSI (Fig. 6b; $P < 0.001$; $R^2 = 0.83$). Parameter estimates and fitting statistics are shown in Table 2 (Eq. 5). On average, when θ_{v-8} was approximately 0.3 cm³ cm^{−3}, the stand had a whole-season WSI of nearly −44.5 MPa day. For a reduction of 0.1 cm³ cm^{−3} in θ_{v-8} , WSI decreased by 1.47 MPa day.

There was a significant relationship between θ_{v-8} and whole-season stand volume growth. Parameter estimates and fitting statistics are shown in Table 2 (Eqs. 6 and 7). On average, if the stand had a θ_v of 0.3 cm³ cm^{−3} in August of the initial growing season, the predicted whole-season volume growth will be 19 dm³ ha^{−1} year^{−1}. By comparison, when θ_v was measured at the same time, the dry 0.15 cm³ cm^{−3} conditions reduce predicted volume growth to 5 dm³ ha^{−1} year^{−1} for the initial growing season. During the second growing season, if a stand had a θ_{v-8} of 0.3, the predicted volume growth would be 161 dm³ ha^{−1} year^{−1}. On average, for each reduction of 0.01 cm³ cm^{−3} in θ_{v-8} , volume growth will decrease by 5.6 and 7.7%, for the first and second growing seasons, respectively.

The relationships between WSI and whole-season volume growth (Table 2; Fig. 4b) included different size seedlings at the beginning of the second year. This seedling size difference was a product of the response to the vegetation management treatments already

Fig. 4 Relationship between Douglas-fir seedling water stress integral and volume growth for **a** the first (2006) and **b** the second (2007) growing seasons. The treatment legend is described in Table 1



applied. In order to separate the confounding effects of water availability and initial seedling size, the average seedling volume (v_i , dm^3) at the end of growing season 1 was used as the covariate in a multiple linear model that also included WSI. In order to ensure normality and homoscedasticity, all variables were log-transformed (for WSI, the absolute value was used).

Both, initial seedling size and WSI had a significant effect on whole-season volume growth during the second growing season. For a given WSI, plots with larger seedlings at the beginning of the growing season had larger stem volume growth during second growing season (Table 3). The model explained 85.6% of VG variability and VG was controlled mainly by WSI (partial $R^2=0.698$), followed by v_i (partial $R^2=0.158$). Scatter plots of residuals showed no evidence of bias for any of the multivariate model.

Discussion

Xylem water potential has been widely used as an index of water stress for forest trees (Waring and Cleary 1967; Nambiar and Sands 1993; Eyles et al. 2012). It represents a snap shot of plant water stress at the time of measurement (Kramer and Boyer 1995). Even though multiple measurements during the growing season can describe the

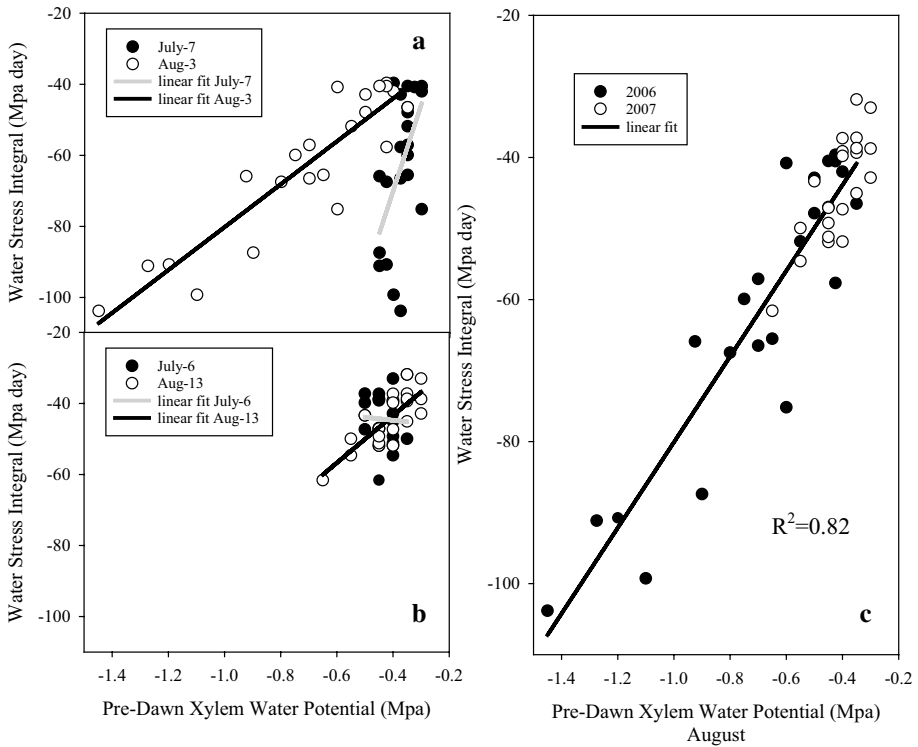


Fig. 5 Relationship between Douglas-fir water stress integral and pre-dawn xylem water potential measured in July and August of the first (2006, **a**) and second (2007, **b**) growing seasons. Panel c shows the relationship between pre-dawn xylem water potential measured in first half of August and the water stress integral of the whole growing season using the pooled data from both years

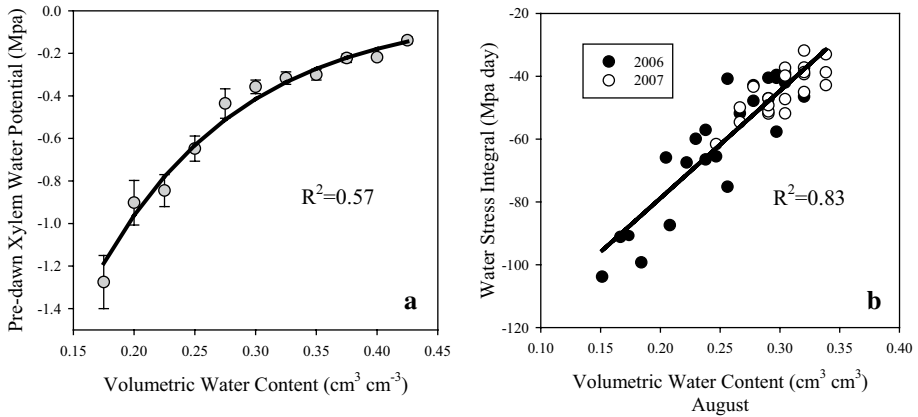


Fig. 6 Relationship between volumetric water content and pre-dawn xylem water potential (**a**) and volumetric water content measured during the first half of August and water stress integral (**b**) for Douglas-fir seedlings growing for the first and second 2006 and 2007 growing seasons

Table 3 Parameter estimates and fit statistics of the models to estimate whole-season volume growth during second season of Douglas-fir seedlings growing under varying soil water availability

Model	Parameter	Parameter estimate	SE	R ²	Partial-R ²	RMSE	CV%
VG = exp ^{(a+b*ln(WSI)+c*ln(v_i))}	a	11.32194	1.63619	0.856		0.254	5.06
	b	-2.11389	0.37475		0.698		
	c	0.82832	0.17619		0.158		

VG: stem volume growth during second growing season (dm³ ha⁻¹ year⁻¹); WSI: water stress integral (MPa day); v_i: mean volume at end of growing season 1 (dm³); SE: standard error, R²: coefficient of determination, RMSE: root mean square error, CV%: coefficient of variation as percent (100 RMSE/mean). For all parameter estimates: $P < 0.001$. WSI is expressed as absolute value

seasonal dynamics in xylem water potential, no clear relationships have been developed between seedling productivity and single measurements of xylem water potential. Watt et al. (2003) reported a strong relationship between two monthly average needle water potential and biomass growth for *Pinus radiata* seedlings. Jacobs et al. (2004) reported a strong relationship between early summer root-volume growth and xylem water potential of Douglas-fir seedlings during the first growing season. The short-term responses of growth to xylem water potential reported on those studies does not warrant extrapolations to whole-season productivity. This is the first study to utilize the water stress integral approach to quantify the link between whole-season cumulative water availability and stand productivity in a newly established plantation. These results are unique among the literature but supported by research in other species. For example, De la Rosa et al. (2016) showed a linear relationship between diameter growth and WSI on *Prunus persica* trees. Myers (1988) reported a strong relationship between basal area growth and WSI in *Pinus radiata*. Myers and Landsberg (1989) reported a correlation between leaf expansion and WSI for seedlings of two Eucalyptus species.

The magnitude of the effect of competing vegetation control on seasonal WSI was proportional to the productivity of the stand. Reducing competing vegetation cover below 20% had a 5- and 4-fold increase in early stem volume growth when compared to unhindered vegetation community growth. Douglas-fir seedlings growing on plots that maintained competitive plant cover below 20% retained adequate θ_v and had higher xylem water potential when compared to plots that did not limit growth below this level (Dinger and Rose (2009). A similar result was found by Nambiar (1980) for *Pinus radiata* seedlings, where increased competing vegetation cover caused a decrease in water potential and growth, concluding that specific composition of weeds and percent cover could be used to assess the intensity of drought likely to be experienced by newly planted radiata pine seedlings.

In this study, when WSI was > -40 MPa day, there was little effect on volume growth. For a three-month period in the summer with little precipitation, that value corresponds to having average Ψ_{PD} of about -0.44 MPa (or $\theta_v \sim 0.3$ cm³ cm⁻³) across the growing season. This represents high soil water availability only reached in conditions with little competing vegetation despite lower amounts of rainfall during the summer months (Newton and Preest 1988). The second growing season had higher precipitation that reduced seedling water stress when compared to the prior year. The magnitude of the volume growth response to the vegetation control regimes (in absolute and relative terms) was larger than in the first growing season. This result is attributed to

the gradation of soil water created in the initial season of establishment as well as the inverse relationship between seedling root system development and stresses received (Dinger and Rose 2010).

Ψ_{PD} is the physiological trait that was used to determine WSI as well as the correlation between water stress and volume growth. However, measurements of Ψ_{PD} can be difficult to carry out. The relationships shown in Figs. 5 and 6 demonstrate the strong correlation between soil moisture, plant water stress and stand productivity confirming that θ_v can be utilized in lieu of or in concert with Ψ_{PD} . These results support the conclusions of Newton and Preest (1988) who proposed that the relationship between θ_v and Ψ_{PD} is non-linear. Small reductions in θ_v below $0.25 \text{ cm}^3 \text{ cm}^{-3}$ caused large declines on Ψ_{PD} , which translated into large decreases in Douglas-fir seedling growth when integrated over the growing season. Assessments of θ_v can be more efficient to take in field settings and, as reported here, an evaluation can be conducted at a single point in the growing season to understand the efficacy of vegetation management regimes.

The strong relationship between WSI and Ψ_{PD} measured in early-August corresponds with the time when θ_v and Ψ_{PD} initially reached the minimum values for each growing season. This earlier detection of growing season productivity could be used to plan future treatments or target high priority areas. Preserving soil moisture until early-August was critical for maximizing stand productivity during first two growing seasons. If forest managers can use tailored vegetation management prescriptions to preserve adequate soil water until early-August, a newly planted stand has an increased potential for a successful growth year, even in the presence of significant drought.

WSI also has the potential to be used for predicting seedling mortality. Hanson et al. (2001) found that, for hardwoods growing under contrasting water availability treatments, mortality was larger in years with higher (more negative) WSI, where water-limited plots reached values $< -110 \text{ MPa day}$. Working with radiata pine seedlings in Chile, Gonzalez-Benecke (unpublished) observed that on dry sites, mortality started when WSI reached values $< -120 \text{ MPa day}$, following an exponential increase as WSI increased (more negative). Control plots in this study reached WSI of about -100 to -110 MPa day at the end of the first growing season. Even though water stress significantly reduced Douglas-fir seedling growth, the levels of water stress observed were not high enough to induce mortality, as demonstrated by seedlings growing in the control plots during the evaluation period. Species-specific relationships between WSI and seedling mortality need to be determined, as xylem vulnerability to cavitation depends on xylem structure traits unique to a species (Tyree and Sperry 1989; McCulloh et al. 2014).

During season 2 (2007) volume growth was larger than in season 1 (2006) mainly because seedlings were larger at the beginning. Larger initial leaf area and root volume allowed seedlings to intercept more radiation and absorb more water and nutrients. When the effects of initial seedling size and whole-season water stress were separated, WSI explained most of the volume production during the second growing season.

Conclusions and management implications

Continued analysis of these datasets has developed necessary correlations between observed data allowing for further estimations of productivity and plant-soil-water relations. In this study, an alternative methodology to correlate soil water availability, plant water stress and stand growth is presented. The results from this study reinforce the

importance of competing vegetation management on soil water availability, plant water stress and stand growth for young seedlings. We demonstrated that determining whole-season water stress through the WSI approach is a useful tool for assessing the effects of soil water availability on seedling growth. The methodology reported in this study can be applied to other species and to larger trees growing under water-limited conditions. Furthermore, the equations reported here are a helpful tool for managers and researchers working on Douglas-fir reforestation. Using these results, determination of WSI or a single evaluation of soil volumetric water content during early-August in the PNW can be used as a predictor of stand productivity during a growing season.

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References

- Adams PR, Beadle CL, Mendham NJ, Smethurst PJ (2003) The impact of timing and duration of grass control on the growth of a young *Eucalyptus globulus* Labill. plantation. *N For* 26:147–165
- Albaugh TJ, Allen HL, Dougherty P, Johnsen KH (2004) Long term growth responses of loblolly pine to optimal nutrient and water resource availability, nutrient and water resource availability. *For Ecol Manage* 192:3–19
- Albaugh TJ, Alvarez J, Rubilar RA, Fox TR, Allen HL, Stape JL, Mardones O (2015) Long-Term *Pinus radiata* productivity gains from tillage, vegetation control, and fertilization. *For Sci* 61:800–808
- Balandier P, Collet C, Miller JH, Reynolds PE, Zedaker SM (2006) Designing forest vegetation management strategies based on the mechanisms and dynamics of crop tree competition by neighboring vegetation. *Forestry* 79:3–27
- Ballester C, Castel J, Intrigliolo DS, Castel JR (2013) Response of Navel Lane Late citrus trees to regulated deficit irrigation: yield components and fruit composition. *Irrig Sci* 31:333–341
- Brillante L, Mathieu O, Lévêque J, Bois B (2016) Ecophysiological modeling of grapevine water stress in burgundy terroirs by a machine-learning approach. *Front Plant Sci* 7:796. <https://doi.org/10.3389/fpls.2016.00796>
- De la Rosa JM, Conesa MR, Domingo R, Aguayo E, Falagán N, Pérez-Pastor A (2016) Combined effects of deficit irrigation and crop level on early nectarine trees. *Agric Water Manage* 170:120–132
- Dinger EJ, Rose R (2009) The integration of soil moisture, xylem water potential, and fall-spring herbicide treatments to achieve the maximum growth response in newly planted Douglas-fir seedlings. *Can J For Res* 39:1401–1414
- Dinger EJ, Rose R (2010) Initial autumn-spring vegetation management regimes improve moisture conditions and maximize third-year Douglas-fir seedling growth in a Pacific Northwest plantation. *N Z J For Sci* 40:93–108
- Eyles A, Worledge D, Sands P, Ottenschlaege ML, Paterson SC, Mendham D, O'Grady AP (2012) Ecophysiological responses of a young blue gum (*Eucalyptus globulus*) plantation to weed control. *Tree Physiol* 32:1008–1020
- Fernandez MD, Hueso JJ, Cuevas J (2010) Water stress integral for successful modification of flowering dates in 'Algerie' loquat. *Irrig Sci* 28:127–134
- Hanson PH, Todd DE, Amthor JS (2001) A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. *Tree Physiol* 21:345–358
- Jacobs DF, Rose R, Haase DL, Alzugaray PO (2004) Fertilization at planting impairs root system development and drought avoidance of Douglas-fir (*Pseudotsuga menziesii*) seedlings. *Ann For Sci* 64:643–651
- Jokela EJ, Martin TA, Vogel JG (2010) Twenty-five years of intensive forest management with southern pines: important lessons learned. *J For* 108:338–347
- Kramer PJ, Boyer J (1995) Water relations of plants and soil. Academic Press, San Diego
- Little K, Rolando C, Morris C (2007) An integrated analysis of 33 Eucalyptus trials linking the onset of competition-induced tree growth suppression with management, physiographic and climatic factors. *Ann For Sci* 64:585–591

- Maguire DA, Mainwaring DB, Rose R, Garber SM, Dinger EJ (2009) Response of coastal Douglas-fir and competing vegetation to repeated and delayed weed control treatments during early plantation development. *Can J For Res* 39:1208–1219
- Mason EG, Rose R, Rosner LS (2007) Time vs. light: a potentially useable light sum hybrid model to represent the juvenile growth of Douglas-fir subject to varying levels of competition. *Can J For Res* 37:795–805
- McCulloh KA, Johnson DM, Meinzer FC, Woodruff DR (2014) The dynamic pipeline: hydraulic capacitance and xylem hydraulic safety in four tall conifer species. *Plant Cell Environ* 37:1171–1183
- Myers BJ (1988) Water stress integral. A link between short-term stress and long-term growth. *Tree Physiol* 4:315–323
- Myers BJ, Landsberg JJ (1989) Water stress and seedling growth of two eucalypt species from contrasting habitats. *Tree Physiol* 2:207–218
- Nambiar EKS (1980) Influence of weeds on the water potential, nutrient content and growth of young radiata pine. *Aust For Res* 10:279–288
- Nambiar EKS, Sands P (1993) Competition for water and nutrients in forests. *Can J For Res* 23:1955–1968
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an amazon forest. *Ecology* 88:2259–2269
- Newton M, Prest DS (1988) Growth and water relations of Douglas fir (*Pseudotsuga menziesii*) seedlings under different weed control regimes. *Weed Sci* 36:653–662
- Pinto JR, Marshall JD, Dumroese RK, Davis AS, Cobos DR (2012) Photosynthetic response, carbon isotopic composition, survival, and growth of three stock types under water stress enhanced by vegetative competition. *Can J For Res* 42:333–344
- Powers R, Reynolds PE (1999) Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. *Can J For Res* 29:1027–1038
- Rose R, Rosner LS, Ketchum JS (2006) Twelfth-year response of Douglas-fir to area of weed control and herbaceous versus woody weed control treatments. *Can J For Res* 36:2464–2473
- Sands R, Nambiar EKS (1984) Water relations of *Pinus radiata* in competition with weeds. *Can J For Res* 14:233–237
- Sellin A (1999) Does pre-dawn water potential reflect conditions of equilibrium in plant and soil water status? *Acta Oecol* 20:51–59
- Tyree MT, Sperry JS (1989) Vulnerability of xylem to Cavitation and embolism. *Ann Rev Plant Phys Mol Biol* 40:19–38
- Wagner RG, Robinson AP (2006) Critical period of interspecific competition for four northern conifers: 10-year growth response and associated vegetation dynamics. *Can J For Res* 36:2474–2485
- Wagner RG, Little KM, Richardson B, McNabb K (2006) The role of vegetation management for enhancing productivity of the world's forests. *Forestry* 79:57–79
- Waring RH, Cleary BD (1967) Plant moisture stress: evaluation by pressure bomb. *Science* 155:1248–1254
- Watt MS, Whitehead D, Mason EG, Richardson B, Kimberley MO (2003) The influence of weed competition for light and water on growth and dry matter partitioning of young *Pinus radiata* at a dryland site. *For Ecol Manage* 183:363–376
- Watt MS, Kimberley MO, Coker GWR, Richardson B, Estcourt G (2007) Modelling the influence of weed competition on growth of *Pinus radiata*. Development and parameterisation of a hybrid model across an environmental gradient. *Can J For Res* 37:607–616