Agricultural and Forest Meteorology

journal homepage: www.elsevier.com/locate/agrformet

The importance of seasonal temperature and moisture patterns on growth of Douglas-fir in western Oregon, USA

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ARTICLE INFO

ABSTRACT

Douglas-fir growth in the Pacific Northwest is thought to be water limited. However, discerning the relative influence of air temperature and plant available soil water (W) on growth is difficult because they interact with each other, with other climate factors and with the inherent seasonal timing of cambial activity. Douglas-fir growth response to air temperature and W patterns during the growing season was examined using time series regression analysis of dendrometer data collected at approximately four-week intervals from 1998 through 2009. Five study sites were located in mature forest stands along an elevation gradient from the Pacific coast to the west slope of the Cascade Mountains ($\sim$1200 m) in Oregon, USA. Maximum daily air temperature (T) and W were similar in relative importance to tree growth at four of the five sites. W was substantially more important at one site. Growth rate increased with T to an optimum (T_{opt}) and decreased with higher T. At the two drier sites T and W affected growth interactively in that T_{opt} decreased with decreasing W. We conclude that both T and W affect growth and that T consistently limits growth at three of the five sites and at all sites in years with above average summer temperature. Should climate change result in hotter summers in the region as predicted by climate models, we suggest that Douglas-fir will experience progressive temperature limitation.

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1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is an ecologically and economically important tree species in forests of the North American Pacific Northwest (PNW) (Waring and Franklin, 1979). The species is adapted to a wide range of climatic conditions from moderate winter temperatures and ample precipitation near the coast to cold winters and dry summers at higher elevations inland (Zhang and Hebda, 2004). It is the major timber species in the region constituting approximately 77% of the saw timber stumpage volume and 87% of sales in the states of Washington and Oregon in 2005 (Howard, 2007). Over 50% of the carbon in aboveground biomass in the state of Oregon is stored in Douglas-fir (Donnegan et al., 2008) making it a key species for the practice of carbon offset forestry (Ryan et al., 2010).

Annual summer drought, which typically lasts from July to October, plays a major role in the functioning of PNW forests (Waring and Franklin, 1979). Shoot elongation and most wood formation occur before the onset of summer drought and the depletion of soil moisture (Emmingham, 1977; Grotta et al., 2005;

Li and Adams, 1994). Global climate change (GCC) could alter the onset, magnitude and duration of the summer drought. Climate model simulations suggest that by mid-century the PNW will experience hotter, drier summers and warmer, wetter winters with substantial decreases in snowpack (Mote and Salathé, 2010). Such climate changes will affect growth and reproduction of Douglas-fir in the region both positively and negatively depending on elevation and site conditions (Littell et al., 2010). Changes in the timing and magnitude of summer drought will alter patterns of temperature and moisture within the growing season. Understanding the relative importance of temperature and soil moisture in the context of seasonal timing of Douglas-fir growth will improve assessments of GCC effects on forest productivity and carbon sequestration.

Soil moisture during summer is a primary factor limiting Douglas-fir growth in the PNW (Brubaker, 1980; Zhang and Hebda, 2004). Radial growth in Douglas-fir can be limited by low temperature at the highest, snowiest elevations, but growth is often limited by moisture in places that develop modest snowpack (Case and Peterson, 2005; Littell et al., 2008). At elevations below the seasonal snowpack, growth is negatively related to summer and annual temperature (Case and Peterson, 2005). The negative temperature effect is thought to result from increasing water deficit in trees as soil moisture is depleted during summer drought (Littell et al., 2008).

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The effects of soil moisture and temperature on tree growth are complex and interdependent. Tree water deficits develop when water uptake by roots is exceeded by transpirational loss from leaves, which is affected primarily by atmospheric Vapor Pressure Deficit (VPD) (Kramer, 1983). Water deficits reduce stomatal conductance, net CO_2 assimilation, cell division and cell enlargement (Hsiao and Acevedo, 1974) and develop under high or low soil moisture conditions (Lassoie, 1982). Temperature directly affects VPD as well as biochemical and enzymatic processes involved in cambial growth (Rossi et al., 2006; Savidge and Förster, 1998; Uggla et al., 1998). Further, the effects of temperature and soil moisture on annual growth can change during the growing season (Lee et al., 2009).

Tree rings effectively represent annual growth over long time periods, but the interactive effects of seasonal environmental factors on growth are difficult to discern. Periodic measurement of changes in stem radius or circumference using dendrometers allows the timing of growth to be dated and, hence, associated with seasonal climate factors (Bormann and Kozlowski, 1962). However, growth measured with dendrometers can be complicated by the shrink and swell caused by changes in tissue water content (Deslauriers et al., 2003b; Gall et al., 2002; Herzog et al., 1995; Lassoie, 1979; Zweifel and Häsler, 2001) and xylem water potential (Abe et al., 2003; Irvine and Grace, 1997). Despite issues of shrink–swell, dendrometer data taken at weekly to monthly intervals accurately represent both the timing and rate of growth (Deslauriers et al., 2007; Rossi et al., 2006; Tardif et al., 2001).

The objective of this study is to determine the relative importance of temperature and water to Douglas-fir growth. Dendrometer measurements were taken year-round at approximately four-week intervals from five Douglas-fir stands located along a gradient from the Pacific coast to ~1200 m elevation in the Cascade Mountains of western Oregon, USA. Dendrometer derived basal area increment data were compared with site specific meteorological and soil moisture data for the years 1998 through 2009. We hypothesized that the importance of those factors would vary across the region depending on elevation and site characteristics.

2. Materials and methods

2.1. Research sites

Five mature, closed-canopy forest stands dominated by Douglas-fir were located in western Oregon, USA (Fig. 1). The Coast site is in the Cascade Head Experimental Forest (US Forest Service) on the west slope of the Oregon Coast Range 8.5 km from the Pacific Ocean. The other four stands, collectively referred to as the Mountain sites, are located in the Willamette National Forest (US Forest Service) on the west slope of the Cascade Mountains. Two sites, Falls Creek and Moose Mt., were at mid-elevation and two sites, Toad Creek and Soapgrass were at high elevation (Table 1).

Paired meteorological stations at each site were located in the forest stand and in an adjacent open area (Beedlow et al., 2007a). Aboveground meteorological data from the open site were used to represent conditions at the top of the tree canopy. Data collected from duplicate sensors located in the top of each forest canopy throughout 2010 indicated that during the growing season, air temperature at the open sites was within a degree of the canopies. At the Mountain sites the open areas were recent clear cuts (~16 ha) within 500 m of the forest sites with similar elevation, slope and aspect. At the Coast site the open meteorological station was placed at an established weather monitoring station near the town of Otis, Oregon (~1 km from the Coast forest site, ~2 ha open area).

Data were collected automatically at 5-min intervals and averaged hourly year-round throughout the study with Campbell Scientific data loggers (Campbell Scientific, Logan, Utah). Sensors were placed at a height of 3 m at each site. Air temperature and relative humidity (RH) were measured using Campbell Scientific HMP45 temperature–humidity sensors. Vapor pressure deficit (VPD, MPa) was calculated from temperature and RH data. Photosynthetically Active Radiation (PAR) data were collected using LI-COR, LI-190SL sensors (Lincoln, NE, USA). Precipitation was measured hourly using Texas Electronics TES25I (Dallas, TX, USA) tipping bucket rain gages. Quality-assurance calibrations for the air temperature and RH sensors were completed by the manufacturer annually and every four years for dataloggers.

Volumetric soil moisture (Campbell Scientific CS-615 reflectometers) and soil temperature (Campbell Scientific 107 Thermistors) at 0.2 m increments to a depth of 0.6 m were automatically collected at each forest meteorological station at 5-min intervals and averaged hourly year-round throughout the study. Plant available soil water (W, mm) was calculated for the top 0.6 m of soil from moisture release curves developed for each site. Detailed soil characteristics and soil moisture calculations are provided in Lee et al. (2007) and Beedlow et al. (2007a).

Swiss Needle Cast (SNC) (*Phaeocryptopus gaeumannii*), a fungal disease of Douglas-fir needles common in near-coastal forests, was found at the Coast site. SNC affects both stomatal conductance and needle longevity with consequent reduction in tree growth while the inter-annual infection severity is affected by temperature and precipitation (Manter et al., 2005). Annual surveys of the areal extent of infection in coastal areas of the PNW conducted by the Swiss Needle Cast Cooperative at Oregon State University (Shaw and Woolley, 2009) were used as a proxy for infection severity at the Coast site.

2.2. Growing season

We defined the growing season as May 1 through October 31 at the Coast and mid-elevation sites, and June 1 through October 31 at the high elevation sites. Our cambial activity data supported this definition as did previous studies of Douglas-fir in western Oregon (Emmingham, 1977; Grotta et al., 2005; Lassoie, 1982). A soil temperature growth threshold of ~5 °C has been shown for Douglas-fir (Bailey and Harrington, 2006; Emmingham, 1977) and other northern hemisphere conifer species (Deslauriers et al., 2003b; Rossi et al., 2007; Shönenberger and Frey, 1988). Growth was assumed not to occur when the average soil temperature was <5 °C. Soil temperature typically reached 5 °C at the mid-elevation sites in May and at the high elevation sites in June. During years with cold springs, soil temperatures reached 5 °C later, which delayed the onset of growth. Soil temperature at the Coast site was consistently >5 °C throughout the year. While the cessation of wood production in the fall was more difficult to determine and can occur at higher temperatures than necessary for growth initiation (Denne, 1971), the growing season was considered to end when soil temperature dropped to 5 °C, or by 31 October at all sites.

2.3. Growth measurements

Stem growth is defined as increase in size over time (Vaganov et al., 2006) and is commonly determined by measuring positive changes in stem Basal Area (BA) (Avery, 1975). Increases in BA result from wood and bark formation or increased water content of the elastic tissues, or both, while decreases result from shrinkage of elastic tissues associated with water deficit (Zweifel et al., 2005). During shrinkage, growth is slowed or stopped as wood formation tends to cease when trees are under water stress for several days or more (Abe et al., 2003). In Douglas-fir, cambial growth abruptly ceases when pre-dawn xylem pressure potential falls below about
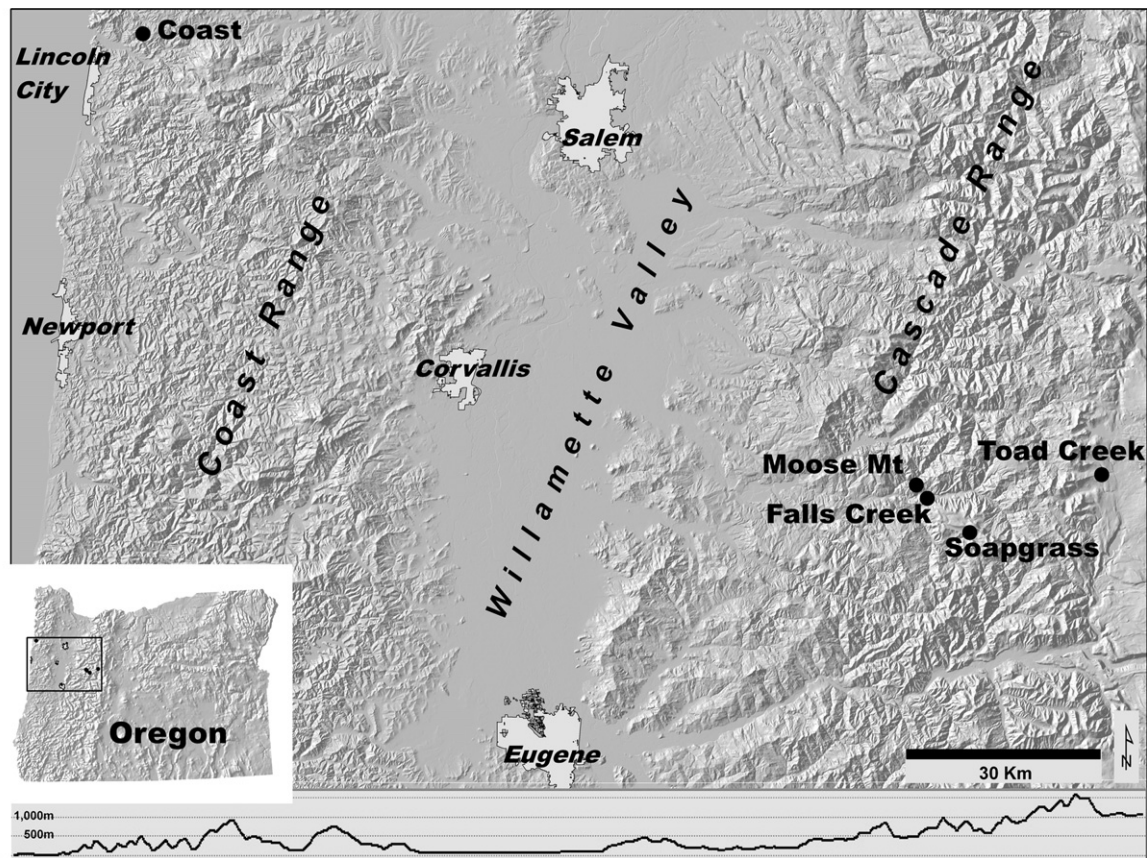
Fig. 1. Map showing the location of the study sites. An elevation profile from Lincoln City to the Cascade crest is shown at the bottom of the figure.

−0.5 MPa, which is common during summer drought (Lassoie, 1982).

We calculated changes in BA for each tree from repeated measurements of stem circumference using manually read band dendrometer (Series 5 manual band dendrometers, 0.1 mm accuracy, Agricultural Electronics Corp, Tucson AZ). The dendrometers were read at ∼4-week intervals, year-round throughout the study. Between the years 1998 and 2000, dendrometers were permanently mounted at ∼1.4 m on 16–26 Douglas-fir trees without visible signs of damage or disease at each site (Table 1). Trees were selected by stem diameter in proportion to their relative abundance and characterized by canopy class (following Avery,

1975). During installation the loose, outermost layers of bark were removed, which ensured that the dendrometer bands were seated firmly against bark. All sites were sampled within a week of each other, each month during the growing season. Damaged dendrometers and bands were replaced, but otherwise they remained on the trees year-round. To reduce error associated with diurnal water use, dendrometer readings were taken between 0900 and 1300 h Pacific Standard Time. Dendrometer data were corrected for thermal expansion (Beedlow et al., 2007b) and normalized to 10 °C for inter-site comparisons.

Basal Area Increment (BAI), the increase in BA over time, was determined from growth curves developed from each tree's

Table 1
Stand characteristics, mean temperature, precipitation and plant available soil water over the study period and characteristics of Douglas-fir trees with band dendrometers.

	Coast	Moose Mt	Falls Creek	Soapgrass	Toad Creek
Lat., Long. (deg, min)	45:02 N, 123:54 W	44:40 N, 122:37 W	44:25 N, 122:24 W	44:21 N, 122:17 W	44:26 N, 122:02 W
Elevation (m)	146	658	530	1190	1198
Stand Age (yr)	140–150	100–110	110–120	400–460	150–200
Stand Basal Area (m² ha⁻¹)[a]	82	61	60	148	85
Fine Root Biomass (g m⁻²)[a]	2.3	4.7	5.9	3.5	7.5
Number of trees sampled	17	26	26	16	21
Diameter range at 1.4 m (m)	1.0–1.5	0.6–0.9	0.6–1.1	1.0–1.8	0.8–1.3
Tree height range (m)	55–58	44–58	48–63	37–65	48–63
Jan mean daily air temperature (°C) [b]	5.4	4.3	3.5	1.7	1.3
Jul/Aug mean daily maximum air temperature (°C) [b]	20.0	24.0	24.8	23.8	25.7
Mean annual precipitation (mm) [b]	2041	1614	1708	2014	2062
Mean summer precipitation (mm) [c]	181	161	177	213	126
Mean daily VPD (MPa) [c]	0.22	0.66	0.52	0.62	0.72
Mean daily minimum plant available soil water (mm); 0–0.6 m depth, % of max in parentheses [b]	93.9 (39%)	13.2 (17%)	33.7 (23%)	36.0 (21%)	26.8 (32%)

[a] From Lee et al. (2007).
[b] Mean values for the study period.
[c] June–September for the study period.

$$ \text{Stand Basal Area} \quad (\text{m}^2 \, \text{ha}^{-1})^a $$
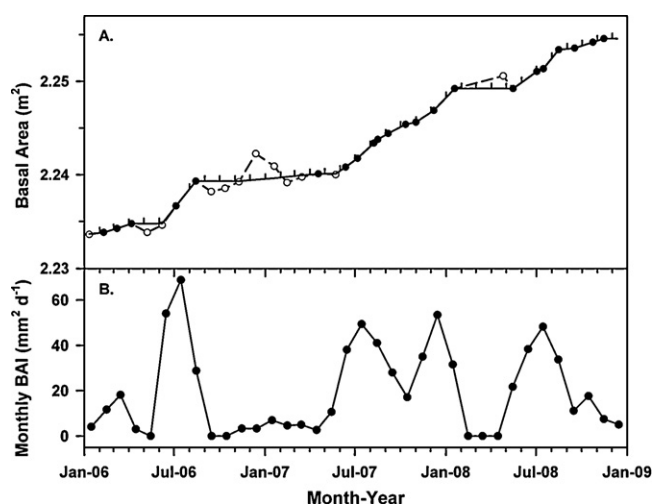
Fig. 2. Monthly Basal Area Increment (BAI). An example of how BAI was calculated from cumulative basal area (BA) data for the period from January 2006 to December 2009 using a 1.8 m (DBH) tree at the Soapgrass site. (A) Cumulative BA measurements (open circles). Monotonically non-decreasing growth curve (solid line) fit to the BA data (solid circles) from the start of each growing season to the start of the next. BA for the first of each month interpolated from the growth curve (vertical lines). (B) The daily BAI (mm² d⁻¹) linearly interpolated from annual growth curves and averaged for each month (solid circles). Tic marks on the *x*-axis represent the first day of each month. The high BAI values for November and December 2007 and January 2008 reflect a cold, wet period with relative high snow accumulation compared to low BAI values during the same period in the previous year, which was mild and dry.

Fig. 3. Tree-ring chronologies. The cross-dated time series tree-ring data were log-transformed and averaged across trees to produce a master tree-ring chronology for each site. Data were centered about zero by subtracting the mean value for the period 1950–2010.

cumulative BA data using a procedure derived from Zweifel et al. (2005) wherein growth was considered to be the monotonically non-decreasing (≥0) BA over time. This approach reduced the effects of summer shrinks and winter swells related to weather conditions. BAI was calculated for each tree over the study period as follows: (1) Cumulative BA measurements were plotted over the study period. (2) Growth curves from the start of each growing season to the start of the next were drawn through points in the BA data so that the resulting curve was monotonically non-decreasing. (3) BA for the first of each month was linearly interpolated from the growth curve. (4) The average daily BAI (mm² d⁻¹) was calculated for each tree each month over the study period. An example for a single tree over a portion of the study period is shown in Fig. 2.

Because changes in BA are affected by stem size, BAI was converted to Normalized Basal Area Increment (NBAI), a dimensionless unit, to allow comparisons (West, 1980). NBAI for each tree at each site was calculated as the average BAI for any given month divided by the average June BAI for the Coast and mid-elevation sites and July for high elevation sites. June and July are the months of highest BAI at the respective sites.

Tree cores were collected from each dendrometer tree over the period 2009–2011 using a 5 mm diameter increment borer (Suunto, Vantaa, Finland) to relate annual dendrometer growth data to wood formation. The cores were processed and optically scanned. The digital images were analyzed to measure annual growth increments to the nearest 0.01 mm using the WinDENDRO 2008 g tree-ring measuring system (Regent Instruments Inc., Quebec, Canada). The tree-ring width measurements were cross-dated using the COFECHA software (Tree-Ring Lab and Columbia University; Holmes, 1983) to ensure all annual radial growth increments were assigned the correct calendar year. Data were averaged across trees to produce a master tree-ring chronology for each site. The tree-ring width data displayed little to no non-climatic growth trend since 1950. Consequently, tree-ring width data after 1950 were not detrended, but were centered about zero by subtraction
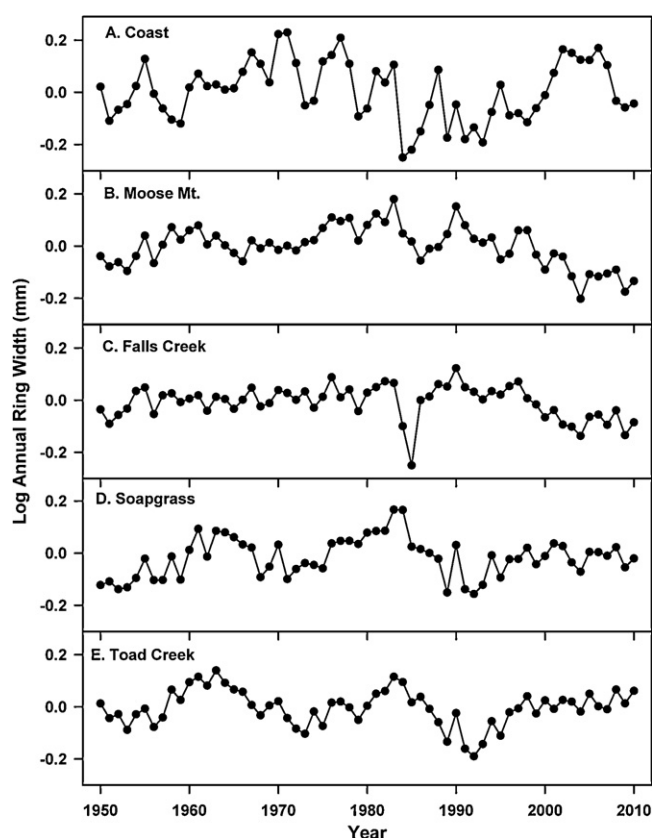
from the mean value for the period 1950–2010 so as not to remove any multi-decadal climatic trends (Fig. 3).

Shoot phenology, categorized as bud swell, bud break, shoot elongation, or bud formation, was observed at each dendrometer reading throughout the study. Cambial phenology, including cambial activation, early- and latewood production and dormancy was monitored from 2002 to 2004 at each dendrometer reading by removing 5 mm cores from representative trees followed by microscopic examination in the laboratory as described in Beedlow et al. (2007b).

2.4. Statistical analyses

To examine the relationship between NBAI, air temperature and *W*, we conducted a Structural Time Series (STS) analysis for each site. Traditionally used for economics and social data (Harvey, 1989), STS is an advanced regression technique that allows for simultaneously interacting variables. A key advantage of STS compared to multiple regression and correlation analyses is that it produces a seasonally adjusted and de-trended time series that removes these confounding factors allowing for a straightforward interpretation of the response to the factors of interest. More recently, STS has been applied to ecological data from controlled and observational studies of plant growth in response to climatic factors (Beedlow et al., 2007a; Lee et al., 2009; Tingey et al., 2007).

The STS approach assumes that the mean response function for NBAI can be attributed to seasonality, trend, and measured variables. In biological terms, seasonality is the inherent monthly pattern of stem growth, which includes unmeasured biological and climate-related factors. The mean NBAI changed from month to month throughout the growing season, consistent with the

Table 2

Components and measured variables in the structural time series regression model of Normalized Basal Area Increment (NBAI) shown in Eq. (1). The dependant variable, NBAI is the average monthly BAI (mm^2 day^{-1}) divided by the average June BAI over the study period (July for the high elevation sites) expressed as a dimensionless unit of rate. Model components are spelled out, variables are denoted with letters and parameters are denoted by Greek symbols in parentheses and correspond to the intercept for seasonality and slopes for the others in Eq. (1).

Component/Variable (Parameter)	Definition
Seasonality/NBAI (θ)	Average monthly pattern of NBAI for all years of the study.
Autoregression/NBAI (ρ_{12}, ρ_1)	Lagged values of NBAI in a given month from year to year (SAR(1)), and from month to month in a given year (AR (1)).
Trend/C (τ)	Calendar year (C); change in NBAI (τ) for specific months from year to year unaccounted for by the measured variables
T (β)	Mean daily maximum air temperature over a given month (°C).
W (β)	Mean daily plant available soil water (0–0.6 m depth) over a given month (mm).
VPD (α)	Mean daily vapor pressure deficit over a given month (MPa).
PAR (ω)	Mean total daily photosynthetically active solar radiation between 400 and 700 nm over the sample period (μE)
SNC (η)	Annual survey of Swiss needle cast fungal infection (Shaw and Woolly 2009) in acres.

seasonal growth pattern of the trees. Trend is a directional change in monthly NBAI over the study period not accounted for by the measured variables. The tendency for tree growth in a given month to affect growth in the next month or the next year was accounted for by stochastic components for regular and seasonal autoregression, AR(1) and SAR(1) respectively. The measured variables that significantly affected NBAI included: maximum daily air temperature (), W, VPD, and for the Coast site, PAR and SNC. The NBAI data for individual trees were treated as independent replications of a seasonal time series. Measured variable and components are shown in Table 2. The basic model follows:

$$NBAI_t^m - \mu_t^m = \rho_1(NBAI_{t-1}^{m-1} - \mu_{t-1}^{m-1}) + \rho_{12}(NBAI_{t-12}^m - \mu_{t-12}^m)$$
$$- \rho_1\rho_{12}(NBAI_{t-13^{m-1}} - \mu_{t-13^{m-1}}) + \varepsilon_t \qquad (1)$$

where, $\varepsilon_t \sim$ Normal Independent Distribution $(0, \sigma^2)$ for $t = 1, 2, \ldots, N$. and, $\mu_t^m = \theta^m + \tau^m C_t + \beta_2 T_t^2 + \beta_3 W_t + \beta_4 W_t^2 + \beta_5 T_t W_t + \beta_6 T_t^2 W + \beta_7 T_t W_t^2 + \alpha^m VPD_t + \omega PAR_t + \eta^m SNC_t$ for months m in the growing season, and $\mu_t^m = 0$ for months m outside the growing season.

$NBAI_t^m$ and C_t (calendar year) in time t for $t = 1, 2, \ldots, N$ month-years and month m. The unknown model coefficients are: θ^m = seasonality of month m, and $\beta_1, \beta_2, \ldots, \beta_7$ = response surface coefficients for T and W, τ^m = trend of month m, α^m = slope of VPD of month m, ω^m = slope of PAR of month m (Coast only), η^m: slope of SNC of month m (Coast only), ρ_1 and ρ_{12} = AR(1) and SAR(1) coefficients, respectively, and σ^2 are the error variance.

The month-years outside of the growing season and cool spring months with mean soil temperature <5 °C were excluded from the analysis. For the month-years included in the analysis, unseasonal weather events occasionally affected the timing or length of growing seasons, which affected the seasonal growth pattern. For example unseasonal cool, wet springs delayed the onset of growth but usually resulted in accelerated growth in summer. When all trees in a stand had a similar response to unseasonal weather and the weather event was recognized, adjustments to the seasonality component of the model were made using intervention analysis (Box and Tiao, 1975). This technique allowed NBAI to be adjusted for altered seasonal patterns due to extreme weather events and permitted a straightforward interpretation of response to climate variables.

Autocorrelation, the effect of NBAI in a given month on NBAI in the next month or year, was described by homogeneous first-order seasonal autoregressive and first-order regular autoregressive models, SAR(1) and AR(1) respectively. These were identified by using autocorrelation and partial autocorrelation functions (ACF and PACF, respectively) and optimization of the Akaike Information Criterion (AIC) and adjusted R^2 (Box and Jenkins, 1976; Chatfield, 2004), as well as the portmanteau test for zero autocorrelations (Ljung and Box, 1978). We used a heterogeneous AR(1)×SAR(1) model with a different ρ_1 and ρ_{12} for each month of the growing season based on fit to account for seasonal changes in autocorrelation.

The measured variables, W, VPD, PAR and SNC were compiled as daily means for each month of each year. To account for the effect of seasonality on NBAI, a different intercept for each month in the growing season (θ^m) was used (Fuller, 1976). We also considered modeling the seasonality component as a trigonometric function having periodicity of one year. The sinusoidal model for de-seasonalizing the time series gave similar results as the step function model, but it required more parameters and, so, was not used. Time series plots of NBAI versus year for a given month identified both positive and negative trends for the Mountain sites indicating that the monthly mean NBAI, θ^m, changed over the study period. These trends in monthly NBAI were confirmed by multi-decadal trends in the annual tree-ring width data that began around 1990 (Fig. 3). We included different month slopes for Trend in the STS model to account for non-stationarity in the monthly means for the Mountain sites. Similarly, inter-annual variations in NBAI for a given month were also found to be linearly related to VPD at all sites and to SNC and PAR at the Coast site. Consequently, different month slopes for VPD, SNC (Coast site), and PAR (Coast site) were used to account for the seasonal effects of these factors on NBAI.

The quadratic model for T was the simplest non-linear model that allowed for a daily maximum temperature optimum (T_{opt}) in NBAI (D'Arrigo et al., 2004). Given the response surface model in Eq. (1), a functional T_{opt} is consistent with a positive value for $\beta_1 + \beta_5 W_t + \beta_7 W_t^2$ and a negative value for $2\beta_2 + 2\beta_6 W_t$. Under these conditions, T_{opt} can be calculated by setting the partial derivative of Eq. (1) with respect to T to zero and solving for the T_{opt} as a function of W:

$$T_{opt} = -\frac{\beta_1 + \beta_5 W_t + \beta_7 W_t^2}{2\beta_2 + 2\beta_6 W_t} \qquad (2)$$

Maximum Likelihood Estimation (MLE) was used to fit the curvilinear relationship between NBAI and environmental data at each site assuming an AR(1) × SAR(1) autoregressive process for NBAI. MLE of the STS model parameters was performed using the PROC NLIN procedure in SAS/STAT® software, Version 9.2 of the SAS System, as described in Fuller (1976). The ACF and PACF calculations were performed using the R statistical package, Version 2.9.0 (R Development Core Team, 2009). Seasonal response surface models for each site were chosen based on fit and parsimony by optimizing the adjusted-R^2 and AIC. The monthly intercepts for seasonality and monthly coefficients for trend and VPD given in Eq. (1), and for SNC and PAR for the Coast site were included in the mean response function model with regard to parsimony. The relative contribution of seasonality, trend, autoregression,, W, VPD, PAR and SNC to NBAI was assessed using Kruskal's (1987) measure of relative importance.

Table 3
Kruskal values of importance for the Structural Time Series (STS) analysis. The Kruskal method (Kruskal, 1987) estimates the relative importance of each variable to the fit of the regression model (R^2). Each Kruskal value is the average of the squared partial correlation coefficients over all possible orderings of the predictor variables. Higher Kruskal values indicate greater relative importance within a site. Positive and negative effects are indicated in parentheses. Parameters are defined in Table 2.

Component/Variable	Coast	Moose Mt	Falls Creek	Soapgrass	Toad Creek
R^2	0.62	0.79	0.81	0.70	0.76
Seasonality	0.31	0.25	0.32	0.38	0.32
Autoregression	0.17	0.23	0.32	0.20	0.15
T (+/−)	0.06	0.14	0.08	0.09	0.11
W (+)	0.08	0.17	0.21	0.08	0.14
VPD (−)	0.12	0.17	0.26	0.17	0.24
SNC (−)	0.07	[a]	[a]	[a]	[a]
PAR (+)	0.05	[b]	[b]	[b]	[b]
Trend	[b]	0.23 (−)	0.04 (−)	0.09 (+)	0.17 (+)

[a] Not applicable at that site and was not included in the model.
[b] Omitted because of parsimony.

3. Results

The STS site-specific regression models fit the NBAI data very well. The models had a R^2 of 0.62 at the Coast, while they ranged from 0.70 to 0.81 at the Mountain sites (Table 3). The Kruskal method was used to indicate the relative importance of the components and measured variables on NBAI for each site (Table 3). Seasonality and autoregression of NBAI were important components of the STS model at all sites. Seasonality of NBAI, the inherent intra-annual growth pattern, was the dominant model component at all but Falls Creek where it was of equal importance with autoregression. Autoregression, the lagged effect of NBAI on subsequent months and years, was generally next most important at all but Toad Creek where VPD and trend had higher importance values. By accounting and adjusting the NBAI data for seasonality, autoregression and trend (see below) in the STS models, we were able to resolve the relative importance of the measured variables (Table 3).

3.1. Relative importance of T and W

Our results show that W is important to growth but must be considered in light of, both were of similar importance to NBAI except at Falls Creek where W was substantially more important (Table 3). To study the relation of T and W, NBAI data were plotted as a function of T and W (Fig. 4). The left-hand panels (A, C, E, G and I) show the adjusted NBAI averaged across all trees for each month, each year of the study period. The narrow temperature range at the Coast site is evident (Fig. 4A) compared to the relatively broad temperature range at Toad Creek (Fig. 4I). The Mountain sites experienced similar variations in W while the Coast was noticeably wetter (Fig. 4A).

To examine the complex non-linear effects of T and W we constructed response surfaces of predicted NBAI to varying levels of T and W for each site as shown in the right-hand panels of Fig. 4(B, D, F, H and J). Response surfaces were generated from the site-specific STS regression models to graphically show the relation between T and W. The response surfaces differed among sites, particularly with respect to temperature. Falls Creek (Fig. 4F) had a relatively flat NBAI response to T compared to the other sites, while at the Coast it was pronounced. The response surface at Toad Creek was unique showing both a positive and negative response over the same range of T depending on the level of W (Fig. 4J). Soapgrass had the steepest response to both T and W as reflected in shape of the response surface (Fig. 4H). The response of NBAI to W was flattest at the Coast (Fig. 4B).

Values for T_{opt} were calculated according to Eq. (2) and are shown as dashed lines in Fig. 5. T and W interacted at Moose Mt. and Toad Creek. The result of this interaction was that NBAI had temperature optima (T_{opt}) that decreased with decreasing W during earlywood production at Moose Mt., and throughout the growing season at Toad Creek (Fig. 5B and E). At Moose Mt. the T_{opt} dropped from 22.3 °C in May to 20.2 °C by July. The decrease at Toad Creek was more dramatic dropping from 30.7 °C in June to 12.7 °C in September. The trees at the Coast, Falls Creek and Soapgrass sites displayed no interaction between T and W and as a result, the T_{opt} was 19.5, 23.9 and 19.8 °C, respectively, at all levels of W.

Comparing the mean NBAI with mean T and W by month for the study period revealed that T substantially exceeded T_{opt} during the growing season at Moose Mt., Soapgrass and Toad Creek on average (Fig. 5B, D and E) and occurred every year of the study (data not shown). At the Coast and Falls Creek the monthly T was close to T_{opt} on average (Fig. 5A and C) and only in hot years was it substantially exceeded. In this figure values of, W and T_{opt} are scaled for ease of comparison. The highest NBAI occurred on average in June at all sites except Soapgrass, which was July. The highest rates of NBAI generally coincided with bud break, shoot elongation and earlywood formation except at Toad Creek where the phenology lagged somewhat. During July and August T exceeded T_{opt} maximally at Moose Mt., Soapgrass and Toad Creek. At this time W was rapidly being depleted. Summer temperatures at the Coast and Falls Creek were very close to T_{opt} on average. NBAI slowed markedly in August, which corresponded to latewood formation and the end of shoot elongation and T exceeded T_{opt}. During September, W reached minimum levels and T_{opt} was exceeded only at the Toad Creek site. NBAI increased in October at all sites. At that time T was below T_{opt} at all sites and W began to rise with fall rains.

3.2. Effects of VPD, PAR and SNC

The effect of VPD on NBAI was negative and roughly equal to the combined importance of T and W at all sites, except at Moose Mt. (Table 3). VPD had a negative effect on NBAI at all sites in all months, but was not statistically significant during all months of the growing season (Table 4). The effect tended to be stronger as reflected in the magnitude of the slope coefficient in the regression models, early in the growing season when NBAI was highest and W was greater than 50% of maximum (Fig. 5). At the Coast site VPD had the most effect in June and July, and although the effects in August–October were lower than June and July, they were higher than those at the other sites. The highest VPD effect at Moose Mt. occurred in June and at Falls Creek in May. In general, large VPD coefficients were associated with periods of rapid growth and ample W suggesting that stomatal conductance affected NBAI. The effect of VPD tended to be less at lower levels of W during the summer drought. The weakened VPD effect is likely related to the development of long-term water deficits and longer periods of stomatal closure during the day. With the onset of fall rains, usually in October, the effect of VPD increased at all sites, especially Toad Creek. This corresponded to high fall NBAI values which may be associated with tissue rehydration.
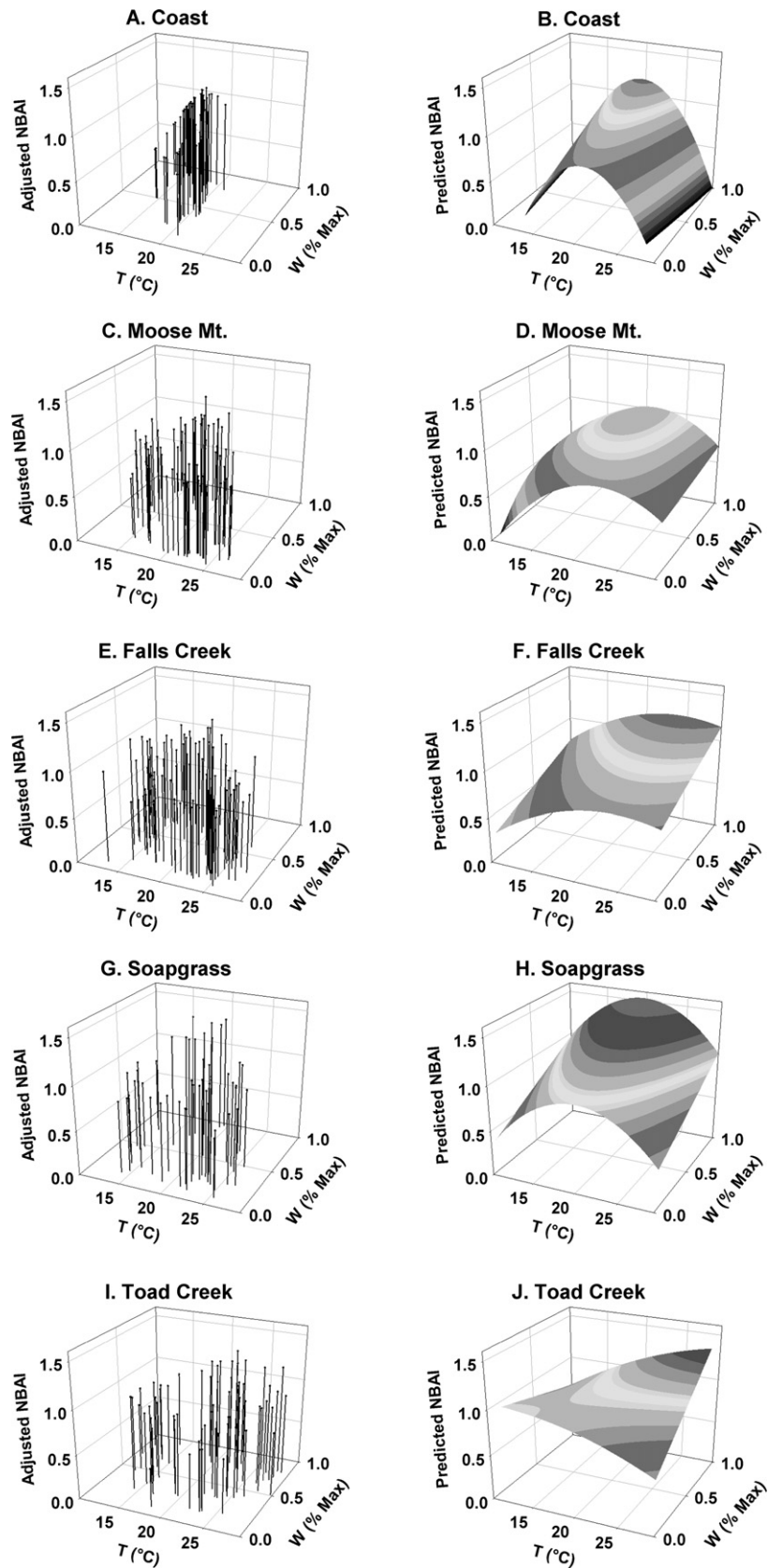
Fig. 4. The response of Normalized Basal Area Increment (NBAI) to maximum daily air temperature (T) and plant available soil water (W). Panels A, C, E, G and I show the adjusted NBAI averaged across all trees for each sample period, each year. The data were adjusted for the effects of seasonality, autoregression, and VPD at all sites and for trend, PAR and SNC at sites where significant. Following adjustment the data points were scaled to one based on July NBAI for the high elevation sites and June for the others. The response surfaces of predicted NBAI generated from the site-specific time series regression models are shown in panels B, D, F, H and J. The surfaces are scaled to one based on July NBAI for the high elevation sites and June for the others. Values greater than one occur when the NBAI in a given month exceeds the average value of the month used to standardize the data.
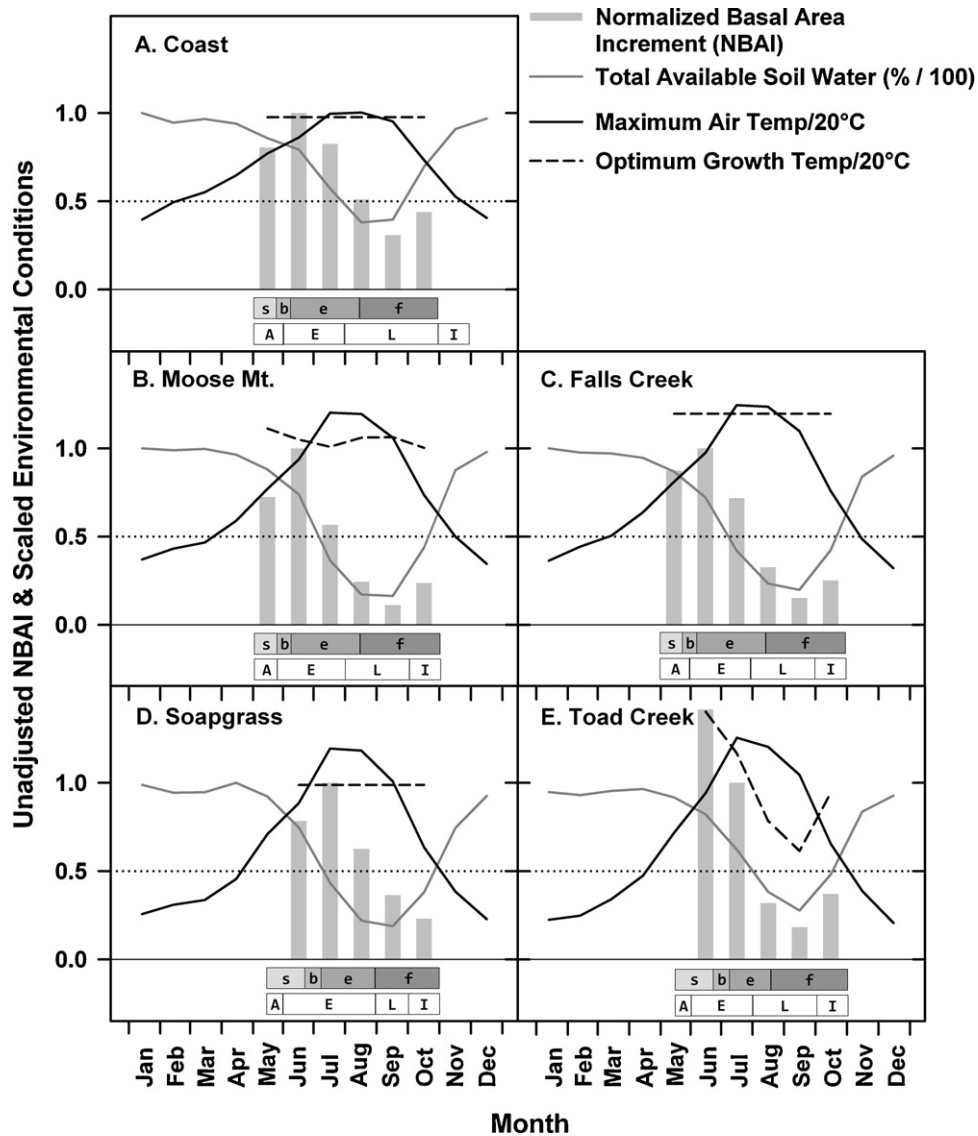
Fig. 5. Seasonal patterns in NBAI. Mean values of unadjusted NBAI for each month averaged over the study period and scaled to one based on July NBAI for the high elevation sites and June for the others. Climatic variables are daily averages for each month over the study period. Proportion of maximum plant available water soil water (W) is solid gray lines. Average daily maximum air temperature (T) is the solid black lines; values are scaled by dividing by 20 such that 1.0 on the y-axis represents 20 °C. Dashed black lines represent the calculated temperature optimum (T_{opt}) for each site. At the Coast (A), Falls Creek (C) and Soapgrass (D) sites, T and W did not interact; consequently the T_{opt} was the same at all levels of W, 19.5, 23.9 and 19.8 °C, respectively. Moose Mt. (B) and Toad Creek (E) both showed declining T_{opt} with decreasing W. Shoot phenology is shown in the gray shaded boxes: Bud swell (s), Bud break (b), Shoot elongation (e), Bud formation (f). Cambial phenology is shown in the un-shaded boxes: Activation (A), Earlywood formation (E), Latewood formation (L), Inactive (I). Tic marks on the x-axis represent the first day of each month.

Only at the Coast site did SNC and PAR contributed significantly to variation in NBAI at a level comparable to T and W (Table 3). SNC was significant and negatively related in the months of August and September. During these months NBAI may have been affected by stomatal impairment and early abscission of the older needle classes from the growth of the fungal hyphae during high infestation years. PAR was significant and positively related during June and July. During these months coastal fog can be very common. Compared to the Mountain sites during June and July, the Coast receives about 20% less total radiation and about 20% fewer hours where radiation exceeds 600 μmol m^{-2} s^{-1}, the light saturation point of Douglas-fir (Lassoie, 1982).

Table 4
Vapor pressure deficit (VPD) importance during the growing season. The slope coefficients represent the importance of the VPD variable on NBAI each month during the growing season. Values are regression slopes with standard errors in parentheses and are significantly different than zero with $p < 0.01$ (Likelihood Ratio Test).

Month	Coast	Moose Mt	Falls Creek	Soapgrass	Toad Creek
May			−0.99 (0.11)		
June	−3.69 (0.70)	−0.80 (0.09)		−1.76 (0.26)	−0.80 (0.20)
July	−5.30 (0.87)		−0.43 (0.11)		
August	−1.81 (0.67)	−0.31 (0.08)	−1.00 (0.10)	−0.06 (0.11)	−0.31 (0.14)
September	−0.43 (0.65)	−0.15 (0.07)	−0.46 (0.08)	−0.14 (0.11)	−0.38 (0.11)
October	−1.31 (0.84)	−0.33 (0.14)	−0.59 (0.13)	−0.52 (0.24)	−3.49 (0.40)

3.3. Trends in NBAI

Trend represents a shift in the seasonality of NBAI though the study period, which was unaccounted for by the measured variables, and it was more important at the drier sites, Moose Mt. and Toad Creek, although it was notable at Falls Creek and Soapgrass (Table 3). The Coast site had no significant trend. Both mid-elevation sites had negative trends for July–August and for June at Moose Mt. (Table 5). Moose Mt. shifted NBAI earlier as indicated by a positive trend in May. At the high elevation sites, Toad Creek showed a positive trend in June, which reflected a shift in peak NBAI from July to June. Soapgrass, the other high elevation site, showed a positive NBAI trend in July and August though of less relative importance (Table 3).

Correlation analyses were done to determine the relation between annual BAI and tree-ring widths over the years with dendrometer data. Tree-ring data taken from the trees with dendrometers were compared with annual BAI calculated from the same trees. Correlation coefficients were positive at all sites: Coast = 0.78, Moose Mt. = 0.84, Falls Creek = 0.71, Soapgrass = 0.67 and Toad Creek = 0.68. The close correlation between BAI and tree-ring widths provided a means to examine trends in NBAI within a longer time-frame. The negative summer NBAI trend at Moose Mt. and Falls Creek was a continuation of declining growth since ~1990 as seen in decreasing tree ring widths (Fig. 3). At the cooler, high elevation sites, the positive NBAI trend corresponded with increased tree ring widths since the early 1990s.

4. Discussion

Growth limitation in PNW Douglas-fir has been generally ascribed to water stress during annual summer drought while high productivity is associated with cool, wet summers and mild winters (Brubaker, 1980; Littell et al., 2008; Peterson and Heath, 1990; Waring and Franklin, 1979; Zhang and Hebda, 2004). We found that both T and W affected Douglas-fir growth in similar proportions on the west slope of the Oregon Cascade Mountains. Summer temperatures exceed the growth optimum (T_{opt}), and soil drying exacerbated this by lowering the T_{opt} at drier sites.

At the biochemical level increasing temperature above an optimum reduces the CO_2 specificity of Rubisco resulting in increased photorespiration (Brooks and Farquhar, 1985). Approximately 20 °C is optimal for Douglas-fir photosynthetic rates with sharp declines above 25 °C during rapid growth in western Oregon, USA (Lewis et al., 2001), which supports our finding of roughly 20 °C as T_{opt} for NBAI at sites where it does not shift with soil drying. Further, increasing respiration with temperature has been shown to increase the light compensation point in Douglas-fir resulting in reduced net photosynthesis (Lewis et al., 1999). Stomatal conductance for CO_2 in Douglas-fir is optimal at about 20 °C (Lassoie, 1982) although a temperature optimum range of 10–15 °C has been reported during late winter and spring (Doehlert and Walker, 1981). Under experimentally elevated air temperature of ~4 °C, relative growth rates of Douglas-fir were higher in early spring but lower during summer than controls (Olszyk et al., 1998) suggesting that summer temperatures exceeded optimum.

Variation in annual wood production is largely dependent on the rate of cell division and size of the tracheids, which are affected by temperature and available water, respectively (Mäkinen et al., 2003; Rossi et al., 2009). The rate of cell division has a stronger effect on annual ring width than the duration of cell division (Emmingham, 1977; Deslauriers et al., 2003a). In *Pinus densiflora* tracheid diameter shows temperature optima of 16–18 °C for earlywood and 23–25 °C for latewood (Vaganov et al., 2006). In *Pinus sylvestris* mean daytime temperature of 21 °C is optimal for radial

cell growth (Antonova & Stasova, 1993). Our dendrometer data support a ~20 °C temperature optimum as seen in physiology studies. Similar to our findings with Douglas-fir, dendrometer measurements of growth in boreal conifers demonstrate temperature optima by responding positively to April and May air temperature but negatively to June and July temperature (Tardif et al., 2001).

The strong correlations between our dendrometer and tree ring data confirm that NBAI is reflective of wood formation. Dendrochronology data support an optimum temperature response by recognizing a positive correlation of tree-ring width in PNW Douglas-fir to spring temperature and a negative correlation to summer temperature (Littell et al., 2008; Yeh and Wensel, 2000; Zhang and Hebda, 2004). Further evidence of temperature optimum is that ring width is positively correlated with growing season length and summer temperature at higher elevations and negatively correlated with summer temperature at mid-elevations (Case and Peterson, 2005; Peterson and Heath, 1990). Dendrochronology studies (Griesbauer and Green, 2010; Littell et al., 2008) emphasize the importance of temperature and precipitation in prior years to growth in the current year. The hypothesis is that carbon assimilation and growth in prior years affects growth in the current year. The high relative importance of the autoregressive component to NBAI at our sites supports this hypothesis.

While we were not able to precisely determine the level of W at which T_{opt} began to decrease at Moose Mt. and Toad Creek, Granier et al. (1999) suggests that water stress begins when 40% of plant available water remains in the soil. In Douglas-fir sap flux begins to fall rapidly once approximately 50% of available water in upper 0.6 m of soil is used (Warren et al., 2005). At our sites W typically fell below 50% in July and T typically exceeded T_{opt} before W fell below 50% (Fig. 5).

Different patterns of T and W interactions with NBAI were found for the five study sites (Fig. 4). Differences in environmental conditions between the sites are responsible for the varying response of NBAI to T and W. Although increasing regional temperature since 1990 likely influenced increased growth trends at the high elevations sites and decreased growth trends the mid-elevation sites (Fig. 3), local conditions influenced the relative importance of T and W. As was suggested by Griesbauer and Green (2010), local spatial and temporal complexities make applying general species-level predictions to climate difficult. For example it might be expected that water limitation would decrease with increasing elevation. Yet, W was substantially more important at one high elevation site (Toad Creek) than at the other and was comparable to the mid-elevation sites (Table 3). This difference was influenced by both the lower water hold capacity of the soil and the fact that Toad Creek receives about 60% of the summer precipitation received at Soapgrass due to orographic influences.

Similarly, the relative importance of T and W to NBAI at the mid-elevation sites was affected by site-specific conditions. At Falls Creek, W was substantially more important than T even though W was depleted to a lesser extent than at Moose Mt. during the summer. At Moose Mt. W and T were nearly equal in their relative importance to NBAI. Again site conditions can explain these differences. Falls Creek has a northern aspect and sits on a toe slope. Moose Mt. has a southern aspect and sits atop a ridge. As a result temperatures at Falls Creek rarely exceed T_{opt} during the growing season; at Moose Mt. it is commonplace. Moreover, the water holding capacity of the soils at Falls Creek is almost twice that at Moose Mt.

The exposure and comparatively low water holding capacity of the Moose Mt. and Toad Creek sites contribute to their hot and dry nature (Table 1). As a result both T and W are more often limiting and exhibit an interactive effect—T_{opt} decreased with decreasing W. There was no interaction between T and W at the more mesic sites,

Table 5
Trends in NBAI during the growing season. The slope and standard errors in parentheses of the significant trend components of the STS regression models by month during the growing season for the study period. The Coast site had no significant trend. The slope represents the importance of the trend component on NBAI. Values are regression slopes with standard errors in parentheses and are significantly different than zero with $p < 0.01$ (Likelihood Ratio Test).

	Moose Mt	Falls Creek	Soapgrass	Toad Creek
May	0.024 (0.009)			
June	−0.048 (0.005)			0.068 (0.009)
July	−0.017 (0.006)	−0.022 (0.005)	0.034 (0.011)	
August	−0.013 (0.004)	−0.013 (0.004)	0.027 (0.008)	

Soapgrass, Falls Creek and the Coast. At Soapgrass, T and W were similarly important even though W in the top 0.6 m became fairly depleted during summer (Table 1) and T exceeded T_{opt} from late June to late September on average (Fig. 5). However, because the Soapgrass site has a shallow water table, the trees are able to access water below the measured 0.6 m throughout the growing season. At Falls Creek growing season T was near T_{opt} on average and was less extreme than Soapgrass (Fig. 3), which may have resulted in the low importance of T compared to W at this site.

Over the course of the study at the Coast site, T exceeded the T_{opt} of 19.5 °C during summer by less then 1.5 °C (Fig. 5). Average daily maximum temperature for the months of July and August, the warmest months, did not exceeded 21 °C. Proximity to the ocean and frequent fog kept this site relatively cool throughout the summer. The strong response to T shown in Fig. 4 reflects the strong influence of VPD in NBAI (Table 4) more than limitation by exceeding T_{opt}. PAR had a positive effect on NBAI, which was likely due to prevalence of summer fog and cloud cover. The areal infection of SNC was negatively related to NBAI. The fungal hyphae, which visibly protrude from the stomata, impede gas exchange and regulation of transpiration, and impair photosynthetic activity (Johnson et al., 2003, Manter et al., 2000). Most prevalent in coastal Douglas-fir plantations, SNC is endemic to naturally regenerated Douglas-fir forests and is favored by warm winter and cool spring air temperature and needle wetness (Black et al., 2010).

VPD can influence dendrometer measurements by affecting wood formation and shrink–swell of elastic tissues through changes in stomatal conductance, water balance, air temperature and direct wetting of the bark (Gall et al., 2002; Zweifel et al., 2005). The importance of VPD at all sites resulted from these factors to varying degrees throughout the growing season. The relation between VPD and NBAI from May to July is inconsistent across the sites (Table 4). The reason for these inconsistencies is unclear but may reflect the micro-climate differences between sites. For example, Falls Creek had higher T and soil temperature compared to the other mountains sites in both May and July, which may increase the importance of VPD in those months. High VPD under well-watered conditions, such as spring and early summer, could cause tissue shrinkage associated with internal water deficits and reduced assimilation due to stomatal closure. The VPD effect on NBAI was diminished during the dry, late summer and fall (Table 4) likely the result of long-term water deficits and stomatal closure during greater portions of the day (Lassoie, 1982), but the effect on extensible tissues of the cortex and phloem could have resulted in shrink–swell.

The relative contribution of tissue swell and wood formation to NBAI during the fall is uncertain. All sites displayed increases in NBAI after September, which was most pronounced at Toad Creek (Fig. 5) and the coefficient for VPD was greatest in October (Table 4). Our phenology data showed that the cambium was inactive by early October at the high elevation sites and by the end of October at the rest. This suggests that increases in NBAI at that time are the result of tissue rehydration or continued expansion of immature tracheids. Cambial division has been reported to end in western Oregon Douglas-fir between mid-September and mid-October (Emmingham, 1977; Grotta et al., 2005) although

Emmingham (1977) noted that cambial activity can occur in the fall under favorable conditions. Further, growth can resume in the fall with replenishment of soil water (Abe et al., 2003; Mäkinen et al., 2003). Consequently, the extent to which the increased NBAI in late summer and fall was a resumption of growth or tissue rehydration, or a combination of both, is unclear.

The response of Douglas-fir growth to T and W demonstrated in this study provides a basis for hypothesizing effects of GCC on forests of the PNW, particularly the heavily forested areas dominated by Douglas-fir west of the Cascade crest. The rate of global warming has been consistent over the past 30 years with the first decade of the 21st century the hottest on record (Foster and Rahmstorf, 2011). Regional climate models predict progressively hotter summers in the PNW through the 21st century with little change in summer precipitation and substantial loss of snowpack (Mote and Salathé, 2010). The negative trends in NBAI over the study period and declining tree ring widths since 1990 at the mid-elevation sites suggest these forests are already being negatively affected by changing climate (Fig. 3). Conversely, higher elevation forests are experiencing positive growth trends, both in NBAI and tree ring width over the same timeframe, though this trend will likely be reversed in the future as warming progresses and snow pack declines. The T_{opt} decreased with W at our drier sites suggesting that temperature could become progressively more limiting to Douglas-fir productivity with climate warming during the summer growing season.

5. Conclusions

The objective of this study was to evaluate the relative importance of air temperature and soil moisture by relating seasonal growth of Douglas-fir to intra-annual temperature and moisture conditions during the growing season. We hypothesized that their relative importance would vary across the region depending on elevation and site conditions. We found that both T and W affect NBAI more or less equally at four of our five sites. NBAI exhibited a temperature optimum, T_{opt}, above which NBAI declined, and T and W affected NBAI interactively at drier sites resulting in decreasing T_{opt} with decreasing W. T is affecting growth consistently each year at three of the five sites, at both mid- and high elevation. In years with above average summer temperature, all sites are affected. We conclude that both temperature and water are currently limiting growth in western Oregon, and that shifting T_{opt} is exacerbating temperature limitation at drier sites. Our results suggest that Douglas-fir, the dominant species in these forests, is vulnerable to hotter summers predicted by climate change models, particularly on drier sites.

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