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Short communication

Factors affecting diurnal stem contraction in young Douglas-fir

Warren D. Devine*, Constance A. Harrington

USDA Forest Service Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Avenue SW, Olympia, WA 98512, USA

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ABSTRACT

Diurnal fluctuation in a tree's stem diameter is a function of daily growth and of the tree's water balance, as water is temporarily stored in the relatively elastic outer cambial and phloem tissues. On a very productive site in southwestern Washington, U.S.A., we used recording dendrometers to monitor stem diameter fluctuations of Douglas-fir at plantation ages 7 and 8 and related the fluctuations to environmental variables measured on-site. Growing-season diurnal stem contraction (DSC) averaged 0.21% of stem diameter, while dormant-season DSC averaged 0.03% of stem diameter. Maximum daily stem diameter generally occurred between 7:00 and 9:00 Pacific Standard Time (PST) and minimum stem diameter occurred between 17:00 and 20:00 PST. Diurnal stem contraction during the growing season was predicted by a model that included vapor pressure deficit and solar radiation (adjusted $R^2 = 0.84$). A similar model predicted DSC during the dormant season with an adjusted $R^2 = 0.26$. Soil water availability was high, and soil water content was not correlated with DSC. On four of the coldest winter days (mean daytime air temperature <0 °C), large decreases in stem diameter were observed. Recording dendrometers, used for continuous diameter measurements throughout the growing season, have the potential to provide important information not only on tree growth but also on a tree's water balance.

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1. Introduction

The diurnal fluctuation in diameter of woody plant stems has been studied for over a century and is documented across a variety of tree species from boreal to tropical climates (Downes et al., 1999; Deslauriers et al., 2003; Sheil, 2003). During the growing season, stem diameter continually changes as a function of a tree's cambial growth and as a result of diurnal patterns associated with water movement within the stem (Dobbs and Scott, 1971; Lassoie, 1979; McLaughlin et al., 2003; Deslauriers et al., 2007). A tree's xylem and phloem expand and contract according to the amount of stored water that they contain. However, the majority of diurnal stem diameter fluctuation is a result of fluctuation in the thickness of the relatively elastic cambial and phloem tissues rather than fluctuations in xylem diameter or radial growth (Dobbs and Scott, 1971; Molz and Klepper, 1973; Hinckley and Bruckerhoff, 1975; Jarvis, 1975; Brough et al., 1986). Xylem is relatively rigid while phloem thickness varies significantly with water content as a result of daily exchange of water between phloem and xylem (Zweifel et al., 2001). This exchange is affected by transpiration of water stored in the stem and by the rate of soil water uptake via the tree's roots.

The amount of water in the phloem makes up only a small fraction of the total daily volume of water transpired by a tree (Zweifel and Häsler, 2001), but the movement of water to and from the phloem occurs in a cyclical pattern. For several species, the magnitude of this pattern is correlated with the amount of moisture stress that the tree experiences (Zaerr, 1971; Lassoie, 1979; Zweifel et al., 2001). On a typical day, both stem diameter and phloem water content reach a maximum in the morning and then decline to a minimum by late afternoon. On overcast or rainy days, the decrease in stem diameter following the daily maximum is usually much smaller than on clear, warm days (Holmes and Shim, 1968; Lövdahl and Odin, 1992). On some hot, dry days when transpiration is substantial, stem contraction may be great enough to produce maximum or minimum diameters that are smaller than the previous day's respective values; this indicates that soil water uptake was insufficient to fully recharge the tree's stem tissues (Lassoie, 1979).

Diurnal fluctuation in stem size has been related to several environmental variables including air temperature, humidity, precipitation, and soil water content (Downes et al., 1999; Deslauriers et al., 2003). These variables influence a tree's water balance and are reflected in diurnal diameter fluctuation as well as in the duration of the daily stem expansion and contraction phases (Deslauriers et al., 2007). The focus of this study is diurnal stem contraction (DSC), defined here as the difference between the daily maximum and minimum stem diameter. Diurnal stem contraction is an indication of the fraction of the water taken up at night that is lost from elastic stem tissues during the day, as a result of transpiration, and not yet

* Corresponding author. Tel.: +1 360 456 8520; fax: +1 360 753 7737.
E-mail addresses: wdevine27@yahoo.com (W.D. Devine), charrington@fs.fed.us (C.A. Harrington).

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replaced. Previous studies have shown for a variety of tree species that DSC follows predictable patterns in response to stem water potential and to environmental factors such as soil water availability (Zaerr, 1971; Cohen et al., 2001; Offenthaler et al., 2001; Zweifel et al., 2006). However, few studies have examined DSC patterns in Douglas-fir; prior studies have focused on large trees (Dobbs and Scott, 1971; Lassoie, 1979) or only a small number of days, usually late in the growing season when moisture stress peaks (Zaerr, 1971; Lassoie, 1973). Our objective was to use environmental variables to explain growing-season and dormant-season DSC in a 7- and 8-year-old Douglas-fir plantation.

2. Methods

2.1. Study site

This two-year study took place at the Fall River Long Term Site Productivity study site; a full description of the site and treatments is given in Ares et al. (2007). The study site was located in the Coast Range of southwestern Washington (46°43′N; 123°24′W) at an elevation of 300 m. The site has a 10% slope and a westerly aspect. The climate is mild with a mean January minimum air temperature of 2.4 °C and a mean August maximum air temperature of 22.8 °C (data from on-site weather station). Mean annual precipitation at the study site is 1711 mm, but an average of only 188 mm precipitation occurs annually between 1 June and 30 September. For the same period during study years 1 and 2 (2006 and 2007), precipitation was 57 and 11 mm below the long-term average in nearby Centralia, WA (WRCC, 2007). Mean air temperatures from 1 June through 30 September in study years 1 and 2 were 1.1 and 0.1 °C above the long-term average, respectively (WRCC, 2007). Soils are of the Boistfort series, a medial over clayey, ferrihydritic over parasesquic, mesic Typic Fulvudand that was formed in basalt residuum and volcanic ash (Soil Survey Staff, 1999; Ares et al., 2007). The site is very productive with age-50 site index for Douglas-fir between 41 and 43 m (King, 1966).

2.2. Experiment procedure

The study site was planted in March 2000 with 1 + 1 Douglas-fir seedlings on a 2.5 m × 2.5 m grid. In April 2006 (plantation age 7), five typical trees with no apparent defects, located at least 25 m apart, were selected for this two-year study. At that time, the five study trees ranged from 4.0 to 5.4 m in height and from 4.7 to 8.7 cm in diameter at breast height (130 cm). For two of these five trees, competing vegetation was controlled chemically during the first five years after planting as a study treatment. Our analysis showed that diurnal stem diameter fluctuation was not affected by this earlier vegetation control treatment; thus, vegetation control was not used as a treatment variable and all trees were analyzed together in this study.

Stem diameter data were collected from five study trees during year 7 and from one tree in year 8. Recording diameter dendrometers Type DD (Ecomatik, Dachau, Germany) were installed at 30 cm above groundline (approximate height of live-crown base) on 4 trees (numbered 1 through 4) on 8 June of year 7 and on the fifth tree (Tree 5) on 19 July of that year. Trees 1 through 4 were measured throughout the remainder of the year-7 growing season and the subsequent dormant season. Tree 5 was measured until the end of the year-8 growing season. Because logistical constraints delayed instrument installation until day 160 of year 7, we defined the beginning of the growing season as day of year (DOY) 160 for both years of this study. The end of the growing season was defined as DOY 290 because, based on our data, that was the approximate date when stem diameter growth became negligible. The dormant season was defined as day 291 of year 7 through day 90 of year 8, the date when diameter growth resumed. Data from days 90 through 160 of the year-8 growing season are presented here but were not included in our growing-season model because we did not have data from year 7 for that interval. Tree diameters were measured every 5 s, and the average diameter of each tree was recorded every 15 min by CR10X dataloggers (Campbell Scientific, Inc., Logan, UT). Instrument resolution was ±1 μm; accuracy was ±5 μm.

A centrally located, on-site weather station was used to record hourly air temperature (type-T thermocouple), relative humidity, solar radiation (MJ m^{-2} day^{-1}) (LI-200 SZ pyranometer; LI-COR, Lincoln, NE), soil temperature at 10- and 20-cm depths, and cumulative precipitation at 2 m above ground level. Weather station data were recorded by a CR10X data logger with a reference thermistor at the panel (Campbell Scientific, Inc.). Soil water content was measured at 10- and 50-cm depths near each of the 5 trees as described in Devine and Harrington (2009).

2.3. Data analysis

Diurnal stem contraction was calculated as the difference between the daily maximum and minimum stem diameters (given that the former preceded the latter), expressed as a percentage of total stem diameter. As the first step in the analysis, Proc REG, Proc CORR, and Proc GPLOT (The SAS system for Windows, 9.2, SAS Institute Inc., Cary, NC, USA) were used to examine the growing-season and the dormant-season relationships between DSC and the following environmental variables: mean, minimum, and maximum daily air temperatures, mean vapor pressure deficit during daylight hours (VPD; calculated from air temperature and relative humidity at a height of 2.0 m), daily solar radiation, mean soil water content at 10- and 50-cm depths, daily precipitation total, and day-of-year (to account for potential seasonal trends). Daylight hours were based on the time of sunrise and sunset. The relationship between DSC and potential evapotranspiration (PET), calculated by the Hargeraves Model (Hargreaves and Samani, 1985) using air temperature and insolation (Wu, 1997), also was examined.

Next, a model was constructed to predict DSC during the growing and dormant seasons. All of the aforementioned environmental variables plus PET and day-of-year were tested as predictors of DSC. Linear, quadratic, and logarithmic forms of the predictor variables were evaluated by examining the results of variable selection methods (stepwise, backward, and *R*-squared) to identify the best consensus model (Proc REG and Proc MIXED, SAS). Mean square error, coefficient of determination, and visual interpretation of residuals were compared among candidate models to confirm model selection. Because daily stem diameter growth had an unquantified effect on DSC values during the growing season but not during the dormant season, all relationships between DSC and environmental variables were tested separately for the growing season and dormant season. For the dormant-season model, which spanned two years, we used day-of-study instead of day-of-year; day-of-study was defined as the number of days since the first day of year 7.

Differences in DSC among individual trees were accounted for with a random effect variable in a mixed model (Proc MIXED, SAS). An analysis incorporating data from both years (Tree 5 only), was used to test whether DSC was significantly affected by year. Models were tested with and without autocorrelation structure, and it was determined that models without autocorrelation structure were more meaningful, because reducing autocorrelative effects diminished the effects of multi-day weather patterns which were of primary interest in this research. Therefore, we accept that data recorded on sequential days are somewhat correlated owing to the duration of the weather patterns.

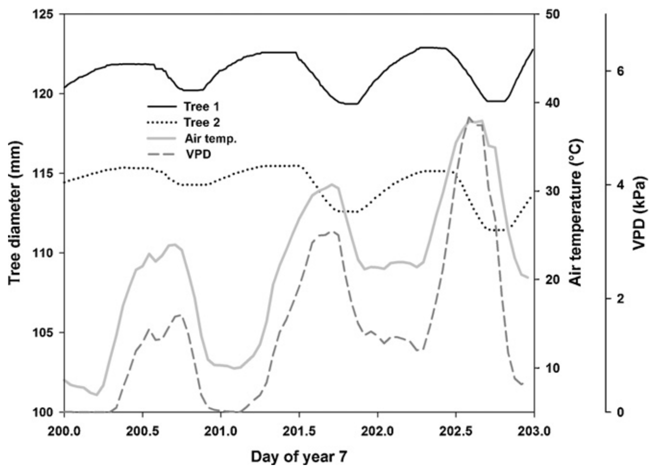

Fig. 1. Typical growing-season diurnal diameter fluctuation for two Douglas-fir trees, with air temperature and VPD, during year 7. During the time period shown in this graph, volumetric soil water content averaged 38 and 39% at soil depths of 10 and 50 cm, respectively.

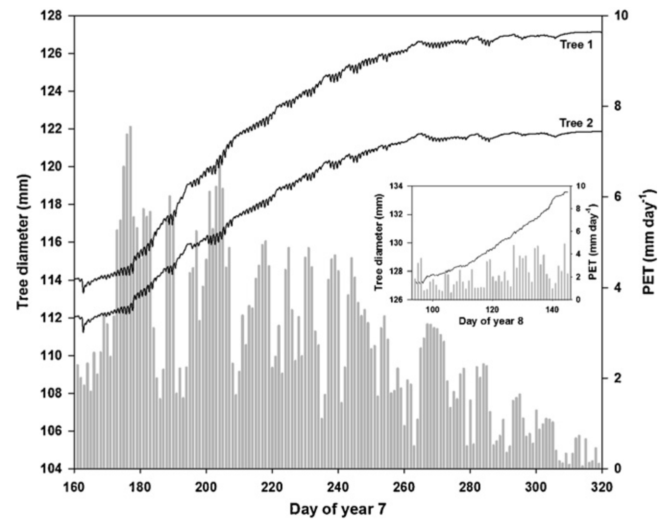

Fig. 2. Diameter of two Douglas-fir trees from day 160 through the end of the year-7 growing season and diameter of one Douglas-fir tree during the early part of the year-8 growing season (inset). Daily potential evapotranspiration (PET) is represented by the gray bars.

3. Results and discussion

3.1. Overview of DSC observations

Diurnal stem contractions ranged from 0 to 0.90% of stem diameter (0–667 μm) during the year-7 growing season, with a mean of $0.21 \pm 0.18\%$ (standard deviation) of stem diameter (187 ± 147 μm). During the dormant season, DSC ranged from 0 to 0.55% of stem diameter (0–410 μm), with a mean of $0.03 \pm 0.05\%$ of stem diameter (28 ± 44 μm). The typical diurnal pattern of stem fluctuation is shown in Fig. 1. The diurnal maximum stem diameter usually occurred between 7:00 and 9:00 Pacific Standard Time (PST), with the minimum between 17:00 and 20:00 PST. The maximum diameter in this age-7 plantation occurred approximately 2 h earlier than that of 22-year-old Douglas-fir trees (Lassoie, 1973). In a related trial, 3-year-old potted Douglas-fir seedlings reached their maximum stem diameter between 5:00 and 7:00 PST (data on file); this trend suggests that tree size is inversely correlated with the time until daily maximum diameter is reached.

The seasonal pattern of DSC differed from that of mature western Washington Douglas-fir trees (Lassoie, 1979), as relatively large DSC values occurred throughout the period of rapid diameter growth in our study (see days 160–260 in year 7) as well as throughout the rest of the growing season (Fig. 2). In contrast, Lassoie (1979) found that DSC values for Douglas-fir trees reached a maximum in late summer; at that time, diameter growth had stopped, trees were still relatively well-hydrated, but water stress had increased as a result of seasonal drought. This difference in DSC pattern between Lassoie's (1979) trees and our trees may have been related to differences in drought stress between sites or differences in seasonal growth patterns. For example, trees in Lassoie's study completed their seasonal diameter growth around DOY 200, while ours completed their growth between DOY 260 and 290. Although we do not have data to compare drought stress between the studies, soil water content remained relatively high throughout the growing-season at our site (Devine and Harrington, 2009), suggesting that drought stress was low.

3.2. Growing-season DSC prediction

Of the environmental variables measured, mean daytime air temperature, mean daytime VPD, and PET had the strongest correlations with growing-season DSC ($r = 0.90$, 0.89, and 0.86, respectively; Fig. 3). The relationship between DSC and VPD was steep at low kPa values, but became less steep at higher kPa values. This relationship between DSC and VPD followed the same pattern as the response of stomatal conductance to VPD (Oren et al., 1999), although it is not clear whether the leveling off of DSC at high VPD values is a result of stomatal closure or simply a limit to the degree to which the elastic tissues of the outer stem contract.

Variable selection techniques provided a consensus model of growing season DSC using two environmental variables: mean daytime VPD and daily solar radiation (model adj. $R^2 = 0.84$; Table 1). In this model, VPD had a quadratic relationship with DSC, while the relationship between daily solar radiation and DSC was linear. Daytime mean air temperature was nearly as strong a predictor of DSC as VPD but was not included in the final model because VPD was calculated from air temperature and relative humidity, and thus VPD and air temperature were not independent of one another. Modeled and observed DSC values for the growing season of year 7 are shown in Fig. 4.

A model with the same predictors, mean daytime VPD and daily solar radiation, was then applied to data collected from Tree 5, for which DSC was recorded over both year-7 and year-8 growing seasons. The adjusted R^2 of the two-year model was 0.90. The greatest difference between years 7 and 8 was that observed DSC values were lower in year 8. During the year-8 growing season, DSC averaged $0.06 \pm 0.06\%$ of stem diameter (77 ± 73 μm); during the year-7 growing season, DSC averaged $0.18 \pm 12\%$ of stem diameter (177 ± 135 μm). The smaller DSC values in year 8 may have been associated with interannual differences in climate, including differences in VPD and solar radiation. Growing-season VPD averaged 0.78 and 0.49 kPa in years 7 and 8, respectively, while mean daily solar radiation was 17.8 and 15.2 MJ m^{-2} in years 7 and 8, respectively. It is unlikely that a larger tree diameter in year 8 was related to the smaller DSC values; it has been shown that, when environmental conditions are similar, DSC generally increases with tree diameter (Intrigliolo and Castel, 2006).

It is not surprising that, during the growing season, the correlation between DSC and PET was no stronger than the correlations between DSC and VPD and DSC and solar radiation. Potential evapotranspiration is the predicted maximum amount of surface evaporation plus transpiration from plants, given no soil water limitation. Precise prediction of PET requires knowledge of surface heat flux, vegetation roughness, humidity, and wind (Lu et al., 2005). Daily PET estimates in this study were based only on solar radi-

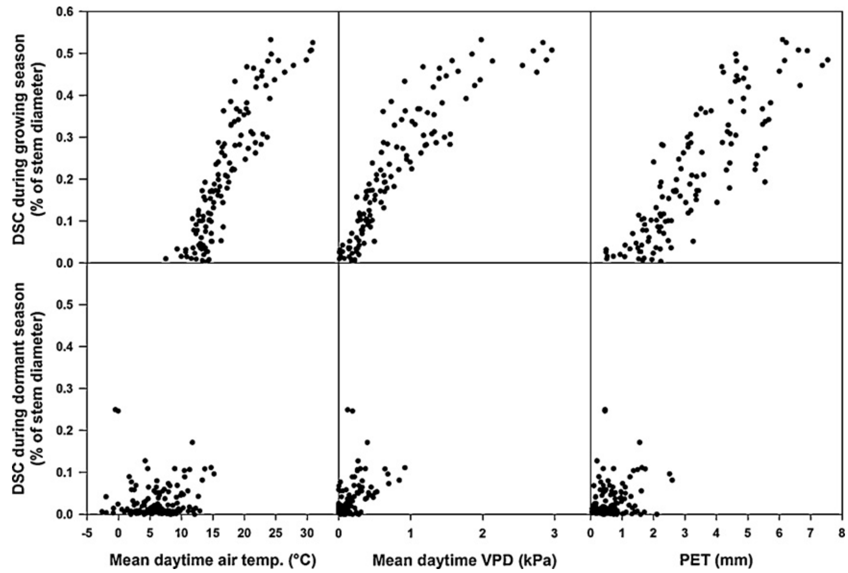

Fig. 3. Growing- and dormant-season relationships between diurnal stem contraction (DSC) and air temperature, vapor pressure deficit (VPD), and potential evapotranspiration (PET) for Douglas-fir at plantation age 7.

ation and temperature measurements, and thus may have lacked the necessary precision to accurately predict water flux. Compared to solar radiation and temperature, VPD, which strongly influences water transfer at the leaf surface, is more closely linked to transpirative water loss (Oren et al., 1999). Water loss from trees occurs primarily as a result of transpiration and is driven by the difference in water vapor concentration between the leaf air spaces in and around the stomatal pore and the external air (Taiz and Zeiger, 2010). Water movement from the soil to the leaves occurs as a liquid, but it evaporates from the cell walls of the mesophyll into the air spaces of the leaf. Transport of the vapor phase is by diffusion so it is regulated by the concentration gradient of water vapor from the leaf to the atmosphere outside the leaf.

3.3. Dormant-season DSC prediction

Relationships between dormant-season DSC and environmental variables were weaker than those of the growing season (Fig. 3). Correlation coefficients for mean daytime air temperature, mean daytime VPD, and PET were 0.07, 0.54, and 0.27, respectively. The cyclical diurnal pattern of stem diameter evident through most of the growing season was diminished and sometimes altogether absent during the dormant season (e.g., days 290–320, Fig. 2). The transition from the growing-season to the dormant-season DSC pattern occurred around day 290 of year 7 (mid-October), approximately the same time that stem growth became negligible. Stem growth resumed in early April of year 8, around the time growing-season DSC patterns resumed (Fig. 2 inset). During the dormant season, the majority of days exhibited very little DSC; these days were generally rainy with extremely low VPD. Dormant-season days with no rainfall and relatively high VPD were associated with somewhat larger DSC values.

The dormant-season DSC model included VPD and day-of-study (Table 1). The model had a relatively low adjusted R^2 of 0.26; however, there were four dormant-season days with unusually large DSC values. When these four days were removed from the dataset, the model fit was improved, with an adjusted R^2 of 0.40. The four atypical days (28 and 29 November and 14 and 15 January) on which the largest dormant-season DSC values occurred were among the 10 days in the study when daytime air temperature averaged less than 0 °C. Nighttime temperatures on the four days reached a minimum between −6 and −9 °C, while daytime temperatures briefly attained a maximum between 2 and 4 °C (Fig. 5). All environmental variables other than temperature were normal for the season on these days. On all four of these days, the large stem contractions occurred over a period of 6 h or less.

Rapid stem contractions under freezing conditions have been reported previously (Zweifel and Häsler, 2000; Améglio et al., 2001; Gall et al., 2002). One hypothesis explaining this diameter shrinkage describes the movement of freezing water to extracellular space within the living, outer tissues of the tree; the freezing water dis-

Table 1
Models developed for predicting growing- and dormant-season DSC in a 7- and 8-year-old Douglas-fir plantation in western Washington, U.S.A.

Model	Variable	Estimate	Std. err.	*F*-value	Pr > F	Model adj. R^2
Year-7 growing season	Intercept	−0.0917	0.0405	–	–	0.84
	VPD	0.2085	0.0195	114.8	<0.0001	
	VPD^2	−0.0283	0.0064	19.7	<0.0001	
	Solar radiation	0.0098	0.0007	194.5	<0.0001	
Both growing seasons	Intercept	−0.0251	0.0082	–	–	0.90
	VPD	0.1966	0.0174	128.0	<0.0001	
	VPD^2	−0.0340	0.0058	34.0	<0.0001	
	Solar radiation	0.0050	0.0006	65.0	<0.0001	
	Year	−0.0393	0.0071	30.5	<0.0001	
Dormant season	Intercept	0.0580	0.0167	–	–	0.26
	VPD	0.1317	0.0122	116.5	<0.0001	
	Day of study	−0.0001	0.00004	7.4	0.0067	

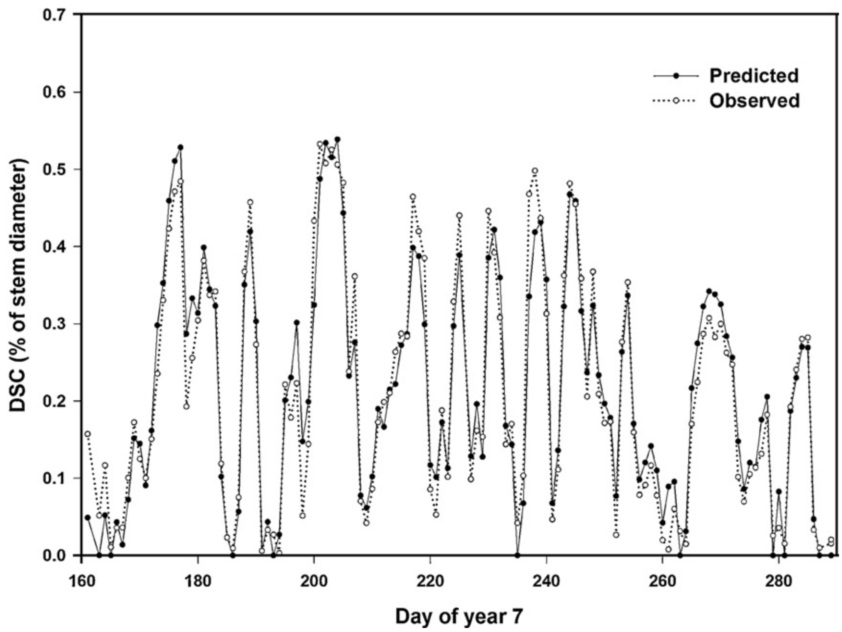

Fig. 4. Predicted and observed growing-season diurnal stem contraction (DSC) for Douglas-fir at plantation age 7.

places air, while cells that lose water shrink (Améglio et al., 2001). Elsewhere, it has been hypothesized that the stem shrinkage is caused by the rapid transfer of water under freezing temperatures from the living tissues of the bark (cambium, phloem, and parenchyma) inward to the frozen xylem in response to a water potential gradient (Zweifel and Häsler, 2000). As with extracellular freezing of water, this process would result in protection of outer, living cells from frost damage. While it remains unclear what mechanism caused the abnormally large winter DSC values in our study, these values were clearly associated with the coldest days of the year. Because DSC values on these cold days were outliers according to the dormant-season model created in this study, the mechanism causing these large winter values is clearly a different one than that contained in the model.

3.4. DSC and soil water content

This study and others across a range of species have found that diurnal stem fluctuation is a function of the specific environmental variables that most strongly influence trees' daily water balance (Zaerr, 1971; Lassoie, 1979; Cohen et al., 2001; Offenthaler et al., 2001; Zweifel et al., 2005; Deslauriers et al., 2003). Uptake of water from the soil and transpirative water loss are of primary importance in determining this water balance. In the present study, soil water content was never strongly correlated with DSC, likely because soil water availability remained relatively high throughout the growing season (Devine and Harrington, 2009). If we had found periods when maximum daily stem size decreased notably over successive days, we might have inferred that there was insufficient soil water to recharge the stem overnight (Lassoie, 1979). On sites where soil water availability declines to low levels during the summer, diurnal stem diameter fluctuation is a function of the interaction between soil water availability, atmospheric evaporative demand, and rate of water transport (Hinckley et al., 1978; Zweifel et al., 2005). However, under conditions of no soil water limitation, transpiration rate is closely related to aboveground environmental variables (Oren et al., 1999). In this study, DSC was well-explained by VPD, which determines the maximum rate of vapor loss from the stomates.

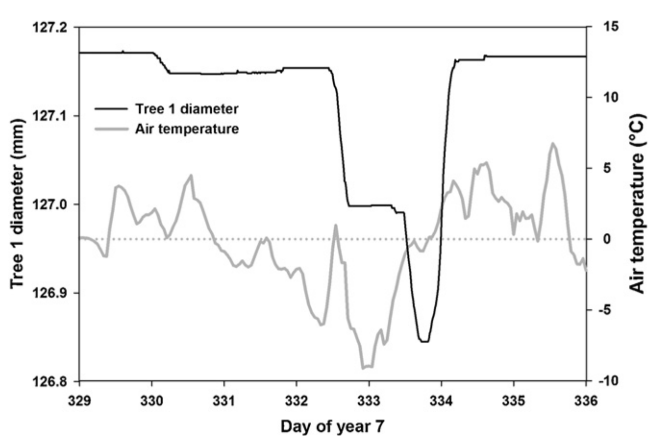

Fig. 5. Tree 1 diameter and air temperature during one of the two cold winter periods when unusually large diurnal stem contraction occurred. The dotted line represents freezing.

3.5. Conclusions

Using DSC as an index of depletion of the water stored in the elastic, living tissues of young Douglas-fir, we found that this estimate of stored water was highly predictable from environmental factors that influence transpiration but was apparently not influenced by soil water limitation at our study site. Although a variety of techniques can be used for assessing soil water limitation in trees, our data support the idea that continuous diameter measurements throughout a growing season have the potential to provide important information not only on tree growth but also on a tree's water balance.

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