Summary  Purportedly, large Douglas-fir trees in the American Pacific Northwest use water stored in bole tissues to ameliorate the effects of seasonal summer drought, the water content of bole tissues being drawn down over the summer months and replenished during the winter. Continuous monitoring of bole relative water content (RWC) in two 110–120-year-old Douglas-fir trees with ThetaProbe impedance devices provided an integrated measure of phloem–sapwood water content over 4 years. Seasonal changes in RWC closely tracked cambial activity and wood formation, but lagged changes in soil water content by 2–3 months. The RWC in the combined phloem and sapwood markedly increased during earlywood production in the late spring and early summer to maximum values of 64–77% as plant available soil water (ASW) decreased by ~60%. With transition and latewood formation, RWC decreased to minimum values of 59–72%, even as ASW increased in the fall. The difference between minimum RWC in the fall and maximum RWC in midsummer was only ~5%. Seasonal changes in bole RWC corresponded to cambial phenology, although decreasing AWS appeared to trigger the shift from earlywood to latewood formation.

Keywords: basal area increment, bole water storage, cambial phenology, relative water content, soil water, summer drought, ThetaProbe, wood formation.

Introduction

Summer drought and wet mild winters are defining features of low- to mid-elevation forests in the American Pacific Northwest. Summer drought typically starts in July and continues into October, but the timing and duration can vary substantially from year to year depending on precipitation patterns. The onset of fall rains ushers in higher precipitation during winter months, which usually decreases in the spring and summer. In the mountains of the Oregon Coast Range and at elevations below 1000 m on the western slope of the Cascade Mountains, the period of wood production, generally considered the growing season, can last from May to November—spanning the annual summer drought (Emmingham 1977, Waring and Franklin 1979, Grotta et al. 2005). The ability to fix carbon during the winter, and to offset transpirational demands by using water stored in bole sapwood during the dry summer are considered to be major factors responsible for the dominance of coniferous forests in this region (Waring and Franklin 1979).

Water stored in the boles of large Pacific Northwest trees is thought to provide a buffer against seasonal summer drought, allowing increased annual carbon assimilation (Waring and Running 1978, 1998, Waring and Franklin 1979). This paradigm holds that, with decreasing soil water content, stored water is progressively drawn down—by as much as 50% in sapwood relative water content (RWC)—starting in the spring and continuing until soil water begins to recharge in the fall. Bole water then increases as soil water content reaches maximum values in the winter.

In addition to old-growth Douglas-fir (Waring and Running 1978), a progressive, summer draw-down in bole water content corresponding to drought conditions has been seen in sapwood of mature ponderosa pine (Pinus ponderosa Dougl.), although the decrease was substantially less than in Douglas-fir (Domec et al. 2005). Waring et al. (1979) reported a 27% draw-down in RWC over a 2-week period in Scots pine sapwood. Domec and Gartner (2001, 2002a) found decreases in sapwood RWC of up to 20% in stems of both mature and sapling Douglas-fir from winter to late summer.

In these studies as well as that of Waring and Running (1978), the tissue water data were collected by using increment cores, which can be affected by rapid water migration (Constantz and Murphy 1990). Moreover, repeated sampling on a single tree requires that cores be taken from different locations around the bole, increasing the variability in measured water content.

Time domain reflectometry (TDR) has been used to measure the water content of various materials, including tree boles (Constantz and Murphy 1990). After the initial probe placement, data can be collected repeatedly from a single position on the bole with minimal disturbance to tissues. The TDR technique measures the dielectric constant of a medium, such as wood or soil, and depends on the fact that the dielectric con-
stant of water is about 80 compared with about 4, 2 and 1 for soil, wood and air, respectively (Gaskin and Miller 1996). Measurements obtained with TDR probes permanently placed in trees indicate that the tissue water content of hardwood species and Scots pine (Pinus sylvestris L.) displays little variability throughout the year and actually increases during the growing season (Wullschleger et al. 1996, Irvine and Grace 1997). In Scots pine, even experimentally induced drought produced no significant decreases in sapwood water content in a Scottish forest (Irvine et al. 1998).

Here, we report observations of tissue water content measured continuously from fixed locations on two mature Douglas-fir trees over 4 years. Measurements were made with commercially available impedance devices (ThetaProbe) that estimate water content based on changes in the dielectric constant similar to other TDR technologies. We hypothesized that bole water content would change directly with, and in proportion to, soil water content—decreasing in the spring and continuing to decrease through the summer drought, and then increasing following the onset of fall rains, rising to a maximum in the winter.

Materials and methods

Study site

Two study trees were selected within an established 0.85-ha site located at 530 m on the west slope of the Oregon Cascade Mountains (122.3721° W, 44.3962° N). The stand, dominated by 110–120-year-old Douglas-fir, was naturally regenerated following fires that burned large areas of the western Oregon Cascades in the latter part of the 19th century (Burke 1979). Stand density was 238 trees ha⁻¹ (> 0.20 m DBH)—predominantly Douglas-fir. Additional characteristics of the vegetation and soils on the site are reported elsewhere (Tingey et al. 2005, identified as “High resource site”). Precipitation was continuously measured at a clear-cut ~300 m away, which was similar in elevation, slope, and aspect; soil temperature and plant available soil water (ASW) were measured at a central location on the forest site (Tingey et al. 2005).

Table 1. Comparison of the study trees with Douglas-fir trees at the field site.

<table>
<thead>
<tr>
<th></th>
<th>Tree 545</th>
<th>Tree 544</th>
<th>Stand</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>117</td>
<td>110</td>
<td>110–20</td>
</tr>
<tr>
<td>Basal area in 2004 (m²)</td>
<td>0.60</td>
<td>0.34</td>
<td>0.43 (0.01)¹</td>
</tr>
<tr>
<td>Basal area increment (% year⁻¹)²</td>
<td>1.60 (0.10)</td>
<td>0.75 (0.09)</td>
<td>1.14 (0.04)</td>
</tr>
<tr>
<td>Height (m)</td>
<td>56</td>
<td>54</td>
<td>55 (1)³</td>
</tr>
<tr>
<td>Sapwood area (m²)</td>
<td>0.11</td>
<td>0.07</td>
<td>0.09⁴</td>
</tr>
</tbody>
</table>

¹ Mean basal area of Douglas-fir > 0.20 m measured at breast height (1.37 m), n = 146 trees, standard error in parenthesis.
² Mean annual basal area increment was determined with band dendrometers on 28 trees for the period 2001–2004. Data are shown as the mean and associated standard error in parenthesis; the data for the individual trees are from their own dendrometer measurements.
³ Mean and standard error for 52 trees > 0.20 m.
⁴ Based on a stand average sapwood area to basal area ratio of 0.21 (0.01) for trees > 0.20 m (dbh), n = 52 trees, standard error in parenthesis.

Tissue water measurement

Tissue water was continuously measured with ThetaProbe moisture sensors (Delta-T Devices Ltd, Cambridge, U.K.). The device measures water content (± 1% v/v, from 0–40° C) by the well-established method of measuring changes in the apparent dielectric constant, but it uses a capacitance rather than a time-domain approach as in traditional TDR technology (Gaskin and Miller 1996). Changes in the apparent dielectric constant are directly proportional to water content.

The two study trees, about 5 m apart, were chosen to represent the range of trees found in the stand (Table 1). The larger tree, Tree 545 (0.85 m DBH), exceeded the stand mean in basal area and height, and the smaller tree, Tree 544 (0.65 m DBH), was below average. The study trees showed no signs of physical damage or disease.

The probes were installed on the boles at a height of 1.4 m. There was one probe on the north and one on the south side of each tree installed in December 1999 and hereafter identified as Probe 544N and 544S, respectively. The boles were prepared by removing bark with a Forstner bit to within 5 mm of the phloem. Guide holes were drilled into the boles for the 60-mm probe rods using a jig to keep the holes aligned. The diameter of the guide holes was slightly smaller than that of the probe rods to maximize rod–wood contact. Probe 545N was lost within a year of installation. Air temperature next to the bole was measured (Campbell Scientific, Logan UT, Model 107B) on the north side of Tree 545 at the same height as the moisture probes. Water and temperature readings were collected every 30 minutes and stored as hourly means on a Cambell Scientific CR10X data logger. Here we report data from October 2001 through December 2005.

Probe calibration

The ThetaProbe was calibrated to measure percent relative water content (RWC, %) of the bole tissues following the procedure suggested by the manufacturer, and discussed by Gaskin and Miller (1996). The probes measure water content within a cylinder of ~20 mm in radius along the 60-mm length of the probe rods. The RWC is the amount of water in the sample divided by the potential maximum amount of water in the...
sample assuming a cell wall density of 1530 kg m\(^{-3}\) (Waring and Running 1978, Domec and Gartner 2002\(\alpha\)) and is calculated as:

$$\text{RWC} = \frac{(W_f - W_d)}{(V_f - V_i)} D100$$  \hspace{1cm} (1)

where \(W_f\) is fresh mass of wood (kg), \(W_d\) is dry mass of wood (kg), \(V_f\) is fresh volume of wood (m\(^3\)), \(V_i\) is volume of solid material in wood (m\(^3\) = \(W_d/1530\) kg m\(^{-3}\)), and \(D\) is density of water (1000 kg m\(^{-3}\)).

The relationship between the apparent dielectric constant and the RWC is:

$$\sqrt{\varepsilon} = \alpha_0 + \alpha_1 \text{RWC}$$  \hspace{1cm} (2)

where \(\varepsilon\) is apparent dielectric constant, and \(\alpha_0\) and \(\alpha_1\) are coefficients determined experimentally during the calibration process.

The coefficient \(\alpha_0 = \sqrt{\varepsilon}\) when RWC = 0, and

$$\alpha_1 = \frac{(\sqrt{\varepsilon_{\text{fresh}}} - \sqrt{\varepsilon_{\text{dry}}})}{\text{RWC}_{\text{fresh}}}$$  \hspace{1cm} (3)

where subscript fresh is fresh wood, and subscript dry is dry wood.

On April 21, 2004, increment cores were taken from the study trees in proximity to the ThetaProbes. Because the probes provide an integrated measure of water content along the entire length of the 60-mm rods, measurements of density (\(W_d/V_i\)) and depth for each tissue along the length of the probe rods were used to weight the readings by tissue type. Samples of the outer bark (OB), phloem (PH), sapwood (SW) and heartwood (HW) intersected by the probe rods were extracted directly above and to each side of the probes—but not from below the probes in order to minimize cavitation effects. An increment borer (5-mm inside diameter, Suunto, Finland) was used to collect sample cores from within 20 mm of the guide holes in the boles. The holes were plugged with wooden dowel rods immediately after the cores were removed. The RWC was determined gravimetrically as described below.

Fresh bole samples were collected from two felled trees in an adjacent stand. Three bole sections were cut from each tree starting at a position corresponding to about 1 m above ground. Each sample was a cross section of the bole 0.3–0.5 m in diameter and 0.3–0.4 m in height. Samples were wrapped in plastic and placed in plastic bags that were sealed for transport to the laboratory where they were refrigerated. Guide holes were drilled in each sample for ThetaProbe insertion as was done in the study trees.

The value of the coefficient \(\alpha_0\) was determined from the bole samples after they had been dried to constant mass at 60 °C (~2 months). The RWC was assumed to be zero at this time. Readings were taken on each bole sample with the ThetaProbe. A mean of 1.313 (standard error = 0.011) was calculated for \(\alpha_0\).

The value of the coefficient \(\alpha_1\) was determined from the RWC of the fresh bole samples (before drying). ThetaProbe readings were taken on each fresh bole sample. Cores were collected as for the study trees, within 20 mm of the probe guide holes, and RWC of each tissue was determined gravimetrically as described below. The tree core samples were combined with the bole samples in determining \(\alpha_1\). A mean of 0.047 (standard error = 0.014) was calculated for \(\alpha_1\) by Equation 3.

**Temperature sensitivity**

Above freezing, increasing temperature decreases \(\varepsilon\) of materials, and consequently, the apparent water content also decreases (Pepin et al. 1995). The manufacturer has minimized the influence of temperature on the output of the ThetaProbe by a compensating technique (Gaskin and Miller 1996). We tested the actual sensitivity of the probes over the range of temperatures expected in the field. Readings were taken at 5, 20 and 30 °C. The laboratory test indicated that the ThetaProbe was stable (no significant difference in \(\varepsilon\), \(P < 0.001\)) as the temperature increased from 5 to 20 °C. A further temperature increase to 30 °C resulted in a decreased \(\varepsilon\) equivalent to an apparent decrease of 0.36% RWC in the study trees.

Based on Pepin et al. (1995), a theoretical decrease in \(\varepsilon\) equivalent to 0.7–0.8% RWC in the study trees was calculated for a temperature increase from 5 to 30 °C. The temperature sensitivity of the probes was an order of magnitude less than the seasonal changes in bole RWC. Because temperature and \(\varepsilon\) are inversely related, any temperature effect decreases the measured difference between summer and winter RWC. Therefore, temperature sensitivity of the ThetaProbes was not considered in the analysis of results.

**Gravimetric tissue measurements**

The RWC of each tissue type was measured gravimetrically in cores taken from the study trees and from the bole samples used to calibrate the ThetaProbes. In addition, the study trees were cored monthly from February 2003 through July 2004 at a height of 1.3–1.4 m to compare gravimetric measures of RWC with those obtained with the ThetaProbes. Each successive monthly core was taken a minimum of 0.15 m from the previous core and the holes were immediately plugged with wooden dowel rods.

All cores were separated into OB, PH, SW and HW. The lengths of each tissue were measured with a digital caliper (Mititoyo, Inc., Japan) accurate to ± 0.02 mm. After measuring the length of each sample, the samples were immediately placed in pre-weighed vials and sealed with air-tight lids. The fresh mass of each sample was measured and the samples were oven dried at 60 °C for 5–7 days and reweighed. The RWC content of each tissue was then determined by Equation 1.

**Cambial activity and shoot phenology**

To relate changes in bole water content with physiological processes within the trees, phenological observations of the cam-
bium and shoots were made. Cambial activity was qualita-
tively determined from the tissue cores taken for gravimetric
analysis each month during 2004 and from additional cores
during 2005. The presence of earlywood (EW), transition
wood (T) or latewood (LW) was determined with the aid of a
dissecting microscope by comparing the relative sizes of the
lumina and walls of xylem cells closest to the cambium
(Creber and Chaloner 1984). Inactivity was defined as the for-
mation of a distinct border between the cambium and the xyl-
lem (Rensing and Owens 1994).

Shoot phenology was visually determined during each site
visit—about every 4 weeks—by examining the tree canopies
with binoculars. Enlarging buds and color change from dark
reddish brown to golden identified bud swell. Bud break was
marked by the appearance of new needles, which were light
green and tightly clustered at the branch tips. Light-green nee-
dles and drooping young branch tips characterized shoot elon-
gation. New bud formation was the period when the cur-
rent-year needles matured and darkened in color, and ended
when hardened dark brown buds formed at the shoot tips. Nee-
dle fall occurred after bud formation, typically during dry peri-
ods in the fall.

Basal area increment—the change in basal area through
time—was used to infer phenological patterns relative to
changes in bole RWC. Phenological data were unavailable for
2002 and 2003 for direct comparisons with RWC. However,
broad dendrometers were installed with the ThetaProbes in
1999; data collection was initiated then and continued through
December 2005 at ~4-week intervals. Series 5 manual band
dendrometers (Agricultural Electronics Corp., Tucson, AZ)
were mounted at breast height (1.37 m) on each study tree.
During installation, the loose outermost layers and decaying
portions of bark were removed with a rasp. The preparation in-
sured that the dendrometer bands were seated against firm
healthy bark. The dendrometers were accurate to within a
0.1 mm change in circumference—corresponding to a basal
area change of 0.004 m² on a tree 0.8 m in diameter. The
dendrometers were read when gravimetric water samples were
collected from February 2003 through July 2004. To constrain
the effect of diurnal water use on measures of basal area incre-
ment, readings and samples were taken between 1000 and
1300 h Pacific Standard Time. The data were adjusted for the
effect of temperature on the bands by adding to the field read-
ings, the mean air temperature for the study period, the band length and
mean air temperature for the day of the reading less the

\[
\text{BAI}_t = \frac{\text{BA}_{\text{rel}} - \text{BA}_t}{d_{\text{rel}} - d_t} \times 100\% 
\]

where BAI, is relative basal area increment, BA is measured
basal area, \(d\) is day of the year, and \(t\) is sample date.

Results

Seasonal water patterns

Over the 4 years, RWC (measured by the ThetaProbes) ranged
from 60 to 65% in the larger tree, Tree 545, and from 50 to
55% in the smaller, Tree 544, with the south side of Tree 544
having slightly higher values than the north side (Figure 1a).
Values of RWC increased each year from May to early August
and declined in the fall. During the winter months, RWC gen-
erally held constant or slightly increased.

In 2004, the peak in RWC did not occur until September
perhaps the result of coring on April 21, 2004 close to the
ThetaProbe to measure tissue density and depth (dashed verti-
cal line in Figure 1a). The effect of coring can be seen most
clearly in the readings from both probes in Tree 544, which
showed a pronounced decrease in RWC (Figure 1a). Both
trees showed a delay in the timing of peak RWC until October
2004 compared with August in previous and subsequent years.
Although the holes were plugged with dry dowel rods immedi-
ately after coring, these plugs likely affected the readings. By
the following year the normal seasonal pattern of RWC—peak
in early August—resumed, although the difference in RWC
between Probes 544N and 544S disappeared and the RWC in
Probe 545S appeared higher.

The soil water pattern in the upper 0.6 m of the soil was not
synchronous with the pattern of RWC. A rapid draw-down in
ASW began in May or June, and ASW reached a minimum in
September (Figure 1b). The pattern in ASW reflected the sea-
sonal precipitation. The peak RWC corresponded to an ASW
content of ~60 mm in all years except 2004 when the RWC ap-
pears to have been affected by coring (Figures 1a and 1b).

Freezing was associated with dramatic drops in apparent tis-
sue water in both trees (indicated by circles in Figures 1a and
1c). There was no indication of water loss following the freez-
ing events in 2002, 2003 or 2005. The RWC was similar before
and after the freezing events, and the patterns were similar to
that in 2004 when freezing did not occur.

In contrast to the pattern obtained with the ThetaProbes,
gravimetric RWC data revealed no seasonal patterns in any tis-
sue type (Figure 2). The variability in RWC, estimated gravimetrically, for all tissues exceeded the seasonal range in
RWC measured by the ThetaProbes. In both trees, RWC of OB and PH ranged from 5 to 50% and from 55 to 90%, respectively. The RWC of SW ranged from 45 to 70% in Tree 544, and from 60 to 80% in Tree 545. The RWC of HW ranged from 19 to 27% in Tree 544, and from 23 to 32% in Tree 545. Variability within individual trees was likely caused by differences in aspect and changes in wood density \((W_d/V_f)\) around the bole.

Density of SW and HW ranged from 460 to 600 kg m\(^{-3}\) in Tree 544, and from 520 to 590 kg m\(^{-3}\) in Tree 545. Error associated with sample handling was not estimated, however, weather differences between sampling sessions may have affected the estimates. Notably, no indication of decreasing RWC during the summer was observed in the gravimetric data.

Sapwood + phloem water content

Changes in RWC of the living tissue (PH and SW) were estimated to better evaluate the effects associated with growth processes. The ThetaProbe integrates water content across all tissues contacted by the probe. Because the 60-mm probes penetrated all four tissue types, they integrated the RWC over a small portion of the OB, the entire PH and SW, and a small portion of the HW in each tree (Table 2). The probe rods crossed ~15 annual rings in Tree 545 and ~50 annual rings in Tree 544. Consequently, the RWC of the whole sample was less than that of the PH and SW because of the influence of the drier HW and OB on the probe readings.

The RWC readings were adjusted to reflect the RWC of the combined PH and SW by considering the amount of tissue contacted by the probe rod along its length. The monthly tissue cores showed that the RWC of PH (hereafter PH RWC) and the RWC of SW (hereafter SW RWC) were similar with that of PH, being 5–10% higher and also more variable (Figures 2b and 2c), and there was no consistent relationship between PH and...
RWC and SW RWC. Consequently, PH and SW were lumped together in the calculation to determine the RWC of the living tissues (PH + SW). The RWC of PH + SW was calculated from the daily average ThetaProbe readings as:

$$RWC_{\text{total}} = RWC_{\text{HW}}d_{\text{HW}} + RWC_{\text{OB}}d_{\text{OB}} + RWC_{\text{PH+SW}}d_{\text{PH+SW}}$$

(5)

where $RWC_{\text{total}}$ is relative water content over the probe length, and $d$ is relative length along the 60-mm probe rod. Subscript HW is heartwood; the long-term monthly mean for each tree was assumed as it was relatively stable (Figure 2d), 23.3 and 28.5% for Tree 544 and 545, respectively. Subscript OB is outer bark; monthly values were highly variable (Figure 2a), but the amount of OB intersected by the probe rods was small (1.3–4.2 mm); the OB RWC obtained during the April 21, 2004 coring of the study trees was used for the constant value of the OB—35% for both probes on Tree 544 and 29% for Tree 545. Subscript PH + SW indicates combined phloem and sapwood tissues.

Rearranging Equation 5 to solve for $RWC_{\text{PH+SW}}$ gives:

$$RWC_{\text{PH+SW}} = \frac{(RWC_{\text{total}} - RWC_{\text{HW}}d_{\text{HW}} - RWC_{\text{OB}}d_{\text{OB}})}{d_{\text{PH+SW}}}$$

(6)

The calculated PH + SW RWC (Figure 3) showed that both trees had similar RWC on the south sides. The RWC on the north side of Tree 544 was approximately 15% lower throughout the study period. The adjusted PH + SW RWC showed the same overall pattern as the integrated readings for all tissues, except that the values were 10–20% higher (cf. Figure 1a). The main difference was that values indicated by Probe 544S were higher relative to those of the other two probes, being more similar to Probe 545S in PH + SW RWC than to
Probe 544N. This was because SW and PH accounted for a smaller portion of the probe length in Probe 544S compared with the other two probes (Table 2).

The annual change in tissue RWC was small. The difference between the mean annual maximum and minimum RWC of the combined PH + SW tissue was 4.3–5.5% (Table 3). Minimum values occurred after wood formation ended and maximum values occurred during earlywood formation (Figure 4). Using measures of bole diameter at 2-m intervals from the base to the top of nearby similar-sized trees in combination with measures of tissue area and density at 10-m intervals, the annual change in bole water content was calculated based on Waring and Running (1978). The difference between the mean annual maximum and minimum bole water content on the wetter, south-side, of the trees was estimated to be 0.07 m$^3$ for Tree 544 and 0.12 m$^3$ for the larger Tree 545 (Table 3).

**Phenology and growth**

The seasonal change in bole RWC generally corresponded with the May–September growing season (Figure 3). To evaluate how growth processes were associated with bole RWC, the phenological stages of wood formation and shoot growth were examined with respect to seasonal changes in PH + SW RWC. Because phenological data were unavailable for the entire length of this study, we inferred the phenological phases in 2002 and 2003 from the dendrometer data.

Cambium and shoot phenology were compared to BAI, during 2004 and 2005 (Figure 4). The pattern of BAI, was similar for both trees, corresponding to their cambial phenology. An increase in BAI, accompanied bud swell in April. In Tree 545, a marked increase in BAI, corresponded to the period of bud break and earlywood formation; this increase was less pronounced in the smaller Tree 544 in 2004. Maximum BAI, occurred during bud break and earlywood formation. Before the

![Figure 4. Relative basal area increment (BAI) and phenology. The BAI values were normalized as the daily % increase in basal area from the previous measurement. Cambial phenology is indicated for each sampling date during the growing season (○ represents periods when the cambium was inactive) as determined in increment cores from the study trees. Abbreviations: EW = earlywood; T = transition; and LW = latewood. The coded boxes at the top of the graph indicate the shoot phenology: BS = bud swell; BB = bud break; SE = shoot elongation; NB = new bud formation; and NF = needle fall.](http://www.heronpublishing.com/)

**Table 3.** Mean annual maximum and minimum water content of the combined phloem and sapwood tissues (PH + SW) of the study trees. Tissue volume and density of the PH + SW (Columns 2 and 3) were combined with the maximum and minimum RWC calculated from the ThetaProbe data (Columns 4 and 5) to estimate the maximum and minimum exchangeable water volume for each tree (Columns 6 and 7). Relative water content (RWC) is given as the mean annual maximum and minimum (± standard error) over the study period.

<table>
<thead>
<tr>
<th>Tree</th>
<th>Tissue volume (m$^3$)</th>
<th>Density (kg m$^{-3}$)</th>
<th>Maximum PH + SW RWC (%)</th>
<th>Minimum PH + SW RWC (%)</th>
<th>Maximum PH + SW water (m$^3$)</th>
<th>Minimum PH + SW water (m$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>544N</td>
<td>2.57</td>
<td>548</td>
<td>63.5 ± 0.4</td>
<td>59.2 ± 0.5</td>
<td>0.84</td>
<td>0.78</td>
</tr>
<tr>
<td>544S</td>
<td>2.57</td>
<td>548</td>
<td>77.2 ± 0.3</td>
<td>71.7 ± 1.3</td>
<td>1.02</td>
<td>0.95</td>
</tr>
<tr>
<td>545S</td>
<td>4.70</td>
<td>544</td>
<td>76.5 ± 0.7</td>
<td>71.8 ± 0.7</td>
<td>1.86</td>
<td>1.74</td>
</tr>
</tbody>
</table>

1. Bole volume is based on allometric data from similar sized trees in an adjacent stand. Tissue proportions are based on samples from the study trees.
2. Density ($W_d/V_t$) of combined phloem and sapwood tissues weighted by their relative volume. Mean density (kg m$^{-3}$) for individual tissues: Tree 544—phloem 509 ± 8, sapwood 553 ± 12; Tree 545—phloem 495 ± 7, sapwood 549 ± 4; ± standard error, $n = 19$.
3. Amount of water available for exchange; calculated as in Waring and Running (1978) assuming fiber saturation of 0.2.
end of earlywood formation, BAIr began to decrease and the decrease continued through transition and lateward formation. The decrease in BAIr, began to slow with shoot elongation and continued to slow until the formation of new buds in mid-August marked the end of shoot elongation. A slight increase in BAIr during the fall corresponded with the end of the summer drought and the onset of fall rains (Figure 1b). Formation of latewood ended in late September to early October and was associated with bud hardening and needle fall. By November, the cambium was inactive in both trees and BAIr had returned to the values of the previous March and April.

The seasonal pattern of BAIr was similar to that of tissue water content—increasing from late spring to midsummer and declining in the fall and winter (Figure 3). Peak RWC corresponded with, or closely followed, maximum BAIr, in 2002, 2003 and 2005. Peak tissue water content occurred several months later than peak BAIr in 2004, but as noted earlier, this was likely a result of the coring in April 2004. Periods of shrinkage—negative BAIr—were visible during rainless periods with relatively warm days and cool soil in late winter of 2002, 2004 and 2005 (Figure 3). No decrease in tissue water content was observed during periods of bole shrinkage.

Discussion

Increased water content in summer

Observations of two vigorously growing, mature Douglas-fir indicated that bole RWC increased markedly with the onset of growth in the late spring even though ASW was rapidly decreasing. In midsummer as ASW approached 60 mm in the upper 0.6 m of the soil, RWC peaked and began to decrease. Bole RWC reached minimum values in the fall. Although slight increases in RWC were seen during winter, substantial and consistent increases did not occur until growth resumed the following year (Figure 1). This is in contrast to the pattern of bole RWC reported in old-growth Douglas-fir by Waring and Running (1978). They showed that RWC began to decrease with the onset of growth in the spring, reached minimum values in the fall and gained maximum values in the winter. The magnitude of change in bole RWC also differed in our study from that of Waring and Running (1978). We found that ASW decreased > 60% each year from winter to summer, whereas bole RWC showed a consistent increase of ~5% over the same time period. Waring and Running (1978) reported decreases of up to 50% in sapwood RWC from winter to summer with comparable decreases in soil water content. Our observations suggest that bole RWC changes with the growth and phenology of the tree and is not directly coupled to ASW.

The apparent discrepancy between our study and that of Waring and Running (1978) may be, at least in part, the result of tree age and condition. Other than differences in method, the major difference between the studies was in stand age. Site and soil characteristics are similar in both studies—concave pediment footslopes, similar silt loam soils with comparable N concentrations, located near small streams and at similar elevations on the west slope of the Oregon Cascade Mountains. Our study was conducted on a younger stand dominated solely by Douglas-fir, whereas Waring and Running (1978) sampled old-growth trees (400+ years) in a stand dominated by Douglas-fir and western hemlock (Tsuga heterophylla (Raf.) Sarg.). Tree size and age can affect wood characteristics and, consequently, water storage capacity (Domec and Gartner 2001, 2002a, Phillips et al. 2003).

Constantz and Murphy (1990) suggested that increment borers affect sample water content. Using a 12-mm inside diameter borer Domec et al. (2005) found an approximately 20% decrease in sapwood RWC from winter to summer in ponderosa pine. Using a 4.3-mm borer Waring and Running (1978) found a decrease of up to 50% in sapwood RWC from winter to summer in old growth Douglas-fir. We used a 5-mm borer to collect tissue samples for gravimetric analysis of RWC, and seasonal patterns were indiscernible (Figure 2). A seasonal pattern of increasing RWC during early summer was evident from the ThetaProbe data, so the high variability in the gravimetric samples likely masked any seasonal pattern.

Consistent with our findings, increased bole water content during the growing season has been reported in other species based on periodic measurements with TDR probes. In Pinus sylvestris L., sapwood water content increased about 4% (v/v) from spring to early August as soil water content decreased (Irvine et al. 1998). Similar patterns were found in four species of deciduous hardwoods in which tissue water content was measured monthly over a span of two years (Wullschleger et al. 1996).

Bole RWC peaked and began to decrease as ASW decreased to about 60 mm in the upper 0.6 m of soil, generally in early August. Fine root production at this site followed the same general pattern as RWC, increasing from spring to early summer, peaking near, or slightly before RWC peaked in the summer, and declining with decreasing ASW (Tingey et al. 2005). Although the trees may have had access to deep water, a threshold of water depletion in the upper profile could affect water use via root activity in combination with stomatal control. Roots in the upper soil layers appear to affect stomatal closure as soil dries (Irvine et al. 1998, Domec et al. 2004, Warren et al. 2005, MeInzer et al. 2006), even when water remains in the lower soil profile (Brooks et al. 2006). This similarity in timing supports the concept that fine roots in the upper soil layers are involved in signaling impending soil water depletion.

The relatively small seasonal variation in RWC observed in our study trees may reflect tight control of water loss, particularly as the soil dried during summer drought. Bole tissue water content can be fairly stable throughout the year if the prevailing weather conditions result in low vapor pressure deficits, or in areas with cold winters and moderately dry summers (Waring et al. 1979). As in most plants, conifers can avoid xylem conduit cavitation by controlling water potential via stomata (Irvine et al. 1998, Kavanagh et al. 1999, Utsumi et al. 2003, Domec et al. 2004). Stomatal control in Douglas-fir is implicated in maintaining bole water potential above that leading to cavitation (Lassioie and Salo 1981, Bond and Kavanagh 1999, Domec and Gartner 2002a). Therefore, bole tissue water...
content does not appear to act as a buffer during a drought. The annual change in bole water volume was estimated from the probes on the south side of the boles to be 0.07 m³ for Tree 544 and 0.12 m³ for Tree 545 (Table 3). For perspective, Phillips et al. (2003) determined, based on sap flow measurements, that a large Douglas-fir (DBH of 1.57 m) can transpire an average of 0.205 m³/night during the summer. The annual changes in bole water amount to not more than a day’s transpiration.

Water loss from phloem tissue increases as soil water content decreases, although partial refilling occurs during the night (Zweifel et al. 2005). In our study, diurnal changes in PH + SW RWC were not seen. The PH + SW RWC as measured by the ThetaProbes includes the water in the phloem, but is dominated by the water in the sapwood because of the relative amounts of PH and SW tissue (Table 2). Seasonal changes in phloem RWC were indiscernible from the gravimetric data (Figure 2b). Consequently, changes in the phloem RWC resulting from soil drying, although expected, are unresolved by our data.

The lack of water loss immediately after winter freezing events suggests that freezing-induced xylem embolisms, if they occurred, had no effect on bole RWC (Figure 1). The sharp decreases in RWC after freezing events are probably due to the formation of ice in the tissues. The dielectric constant of ice is about 4 compared with 80 for liquid water, resulting in an apparent drop in water content as water in the tissue freezes (Sparks et al. 2001). This effect was visible in late January 2002, early January 2004 and again in December 2005 when freezing temperatures lasted more than a week. In contrast, freezing air temperatures occurred in early December 2004 and again in early January 2005, but the temperature did not stay below freezing for more than a day, and had no effect on apparent tissue water content.

**Tissue water, growth and phenology**

Although small, the changes in bole RWC appear primarily related to tree growth and phenology. Marked increases in RWC began with the onset of cambial and shoot activity in late-spring. Decreases were associated with latewood formation in summer, and minimum values were reached in the fall.

Changes in relative basal area increment (BAIr) derived from dendrometric measurements were used to couple growth and phenology data with bole RWC data in order to identify corresponding seasonal patterns. Basal area increment can be affected by short-term reversible changes associated with diurnal water use and weather conditions (Dobbs and Scott 1971, Zaerr 1971, Lassoie and Salo 1981, Irvine and Grace 1997, Zweifel and Häsl er 2001). It can also be affected by longer-term reversible changes resulting from water stress (Herzog et al. 1995, Zweifel et al. 2005) and sugar concentration in the phloem (Gall et al. 2002, Sevento et al. 2002, McLaughlin et al. 2003). However, over a number of years, BAl provides a relative measure of annual growth patterns and timing (Bormann and Kozlowski 1962, Kozlowski 1972). Based on our findings, monthly measurements of BAl provide information on the timing of annual growth and reflect phenological changes in cambial activity and shoot growth triggered by changes in soil water content.

The annual pattern of increasing RWC from spring to summer coincided with the phenological phases of bud swell, earlywood formation and bud break and is reflected in the rapid increase in BAl, (Figures 3 and 4). Earlywood is responsible for conducting most of the water through the bole (Domec and Gartner 2002b) and, consequently, this period of active growth may be responsible for increased RWC in the boles. The BAl, began to slow with stem elongation (Figure 4). During this time ASW was rapidly decreasing (Figure 1b).

The onset of water stress limits shoot growth and is signaled by the formation of transition and latewood (Domec and Gartner 2002b). Decreasing bole RWC corresponded to the formation of transition and latewood. Both BAl, and RWC began to decrease in early August of 2002, 2003 and 2005 as ASW reached ~60 mm (Figures 1 and 3). This decrease coincided with the end of shoot expansion and the formation of transition and latewood based on patterns of BAl, (Figure 4).

During late summer, bole RWC decreased, reaching a minimum before the cambium became inactive and buds hardened in the fall. As water stress develops in late summer, cambial growth slows (Lassoie 1982). Bole RWC continued to decrease even as soil water began to recharge during September of 2002, 2003 and 2005 (Figure 1) and latewood continued to form (Figure 4). Lateward in Douglas-fir has a lower water content than earlywood at xylem water potentials commonly encountered in the field (Domec and Gartner 2002b). The cambium became inactive during the October–November period in 2004 and 2005 (Figure 5). Although determining precisely when the cambium becomes inactive in Douglas-fir is difficult because activity tends to slow throughout the fall depending on temperature and water conditions (Emmingham 1977, Grotta et al. 2005), a similar time period can be assumed for 2002 and 2003 based on the BAl, data for those years (Figure 3).

In conclusion, we hypothesized that bole water content changes directly with, and in proportion to, soil water content, starting in the spring and continuing through the summer drought, and increasing following the onset of fall rains and peaking in the winter. We found that seasonal changes in bole RWC are small relative to changes in soil water—roughly 5% compared with over 60% in soil—and appear to be primarily related to tree growth and phenology. Rather than maximum bole water content occurring in winter after soil water was recharged, maximum RWC occurred in midsummer when soil water content was approaching minimum values. Marked increases in RWC began with the onset of cambial and shoot activity in late-spring. Decreases were associated with latewood formation in summer, and minimum values were reached in the fall.

**Acknowledgments**

The authors thank J. Irvine, R.H. Waring and S.D. Wullschleger for...
their thoughtful reviews and helpful suggestions. Special thanks to E. H. Lee for help with the soil water data. The research described in this article has been funded wholly by the U.S. Environmental Protection Agency. It has been subjected to review by the National Health and Environmental Effects Research Laboratory’s Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the Agency, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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