

Stand-level gas-exchange responses to seasonal drought in very young versus old Douglas-fir forests of the Pacific Northwest, USA

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Received October 10, 2008; accepted May 11, 2009; published online June 5, 2009

Summary This study examines how stand age affects ecosystem mass and energy exchange response to seasonal drought in three adjacent Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. The sites include two early seral (ES) stands (0–15 years old) and an old-growth (OG) (~450–500 years old) forest in the Wind River Experimental Forest, Washington, USA. We use eddy covariance flux measurements of carbon dioxide (F_{NEE}), latent energy (E) and sensible heat (H) to derive evapotranspiration rate (E_T), Bowen ratio (B), water use efficiency (WUE), canopy conductance (G_c), the Priestley-Taylor coefficient (x) and a canopy decoupling factor (λ). The canopy and bulk parameters are examined to find out how ecophysiological responses to water stress, including changes in relative soil water contents (θ) and vapour pressure deficit (de), differ among the two forest successional stages. Despite different rainfall patterns in 2006 and 2007, we observed site-specific diurnal patterns of E_T , x , G_c , λ and θ during both years. The largest stand differences were (1) at the OG forest high morning G_c ($> 10 \text{ mm s}^{-1}$) coincided with high net CO_2 uptake ($F_{\text{NEE}} = -9$ to $-6 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$), but a strong negative response in OG G_c to moderate de was observed later in the afternoons and subsequently reduced daily E_T and (2) at the ES stands total E_T was higher ($+72 \text{ mm}$) because midday G_c did not decrease until very low water availability levels ($\theta < 30\%$) were reached at the end of the summer. Our results suggest that ES stands are more likely than mature forests to experience constraints on gas exchange if the dry season becomes longer or intensifies because water conserving ecophysiological responses were observed in the youngest stands only at the very end of the seasonal drought.

Keywords: AmeriFlux, canopy conductance, eddy covariance, evapotranspiration, the Priestley-Taylor coefficient, *Pseudotsuga menziesii*, Wind River.

Introduction

The landscape of the Pacific Northwest, USA is dominated by tall, long-lived evergreen conifer species that are well adapted to a distinct seasonal climate. This climate regime includes a cool and wet season, and a warm and dry season that are determined by the locations of the Aleutian low during the wet winter months and the Pacific high during the dry summer. Climate change scenarios currently predict that while the Pacific Northwest region will likely receive more precipitation during the winter than it does now, the summers are expected to be warmer and drier creating ecophysiological stress on forest communities and species (Mote et al 2005). Some ecologists predict that a more intense summer drought will generally have a greater impact on Pacific Northwest tree species, including the dominant low-elevation species Douglas-fir (*Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), than the expected annual temperature increases (Mote et al 2003). Enhanced water stress is a particular concern for the regeneration of Douglas-fir stands in the Western Cascade Mountains. This is an area where the youngest age class makes up 40% of the total forest coverage on harvested lands (Cohen et al 1996). Mature trees in intact, closed stands will likely be partially buffered from increased drought stress (Waring and Franklin 1979), but early seral (ES) conifer species (< 15 years old) may have trouble surviving prolonged, extremely dry summers.

In Douglas-fir/western hemlock forests, stomatal conductance and net photosynthesis are strongly dependent on the canopy's microclimate and decline throughout the course of the drought season as vapour pressure deficit (de) increases and soil water content (θ_v) decreases (e.g., Waring and Franklin 1979, Winner et al 2004, Falk et al. 2008), although stand age certainly affects this response. Stomatal control is an important driver of variation in the surface

energy budget of forests (Stewart 1988) because stomatal aperture controls how available energy is partitioned between sensible heat and latent heat (or transpiration). Partial stomatal closure restricts water vapour exchange between the leaf and atmosphere and consequently increases leaf temperature and sensible heat transfer. Douglas-fir and western hemlock foliage have the ability to induce stomatal closure and conserve water in the short term by limiting transpiration but this occurs at the expense of reducing the photosynthetic rate, and over the long term, it also reduces tree growth and wood production (Bower et al. 2005).

In developing forest stands, productivity is closely dependent on available soil water because (1) soil moisture determines the growth of foliage biomass and (2) soil moisture stress affects the photosynthetic efficiency of that foliage (Jarvis and Mullins 1987). Prior studies give us an idea of how evergreen needleleaf trees in southern Washington survive the annual, 5-month drought event. Site water availability and tree water use and demand measurements have been taken in a 20-year-old Douglas-fir and the 450-year-old Douglas-fir/western hemlock forest in the Wind River Experimental Forest, Washington, USA. Warren et al. (2005) showed that soil moisture in the shallow 0.15–0.60 m soil layer declined by 40–45% during the summer drought period, while deep soil (2 m) released only 5% of its original volume. The importance of hydraulic redistribution (HR) at these forest sites, whereby roots are able to lift water from deeper, moist soil horizons and release it into shallower, drier soil portions is reinforced in the work by Domec et al. (2004). Their data showed that HR at the highest rates replenished 60% of the previous day's water use and was critical for maintaining shallow root function and preventing total stomatal closure during drought conditions in the Douglas-fir stands. Brooks et al. (2002) further found that the effects of summer drought in the 20-year-old Douglas-fir forest were partially muted by HR, which accounted for an additional 16 days of stored water to remain in the upper soil horizons after a 60-day drought.

Although experiments have shown that mature stands have access to deep water reserves during drought periods, foliage at the top of very tall trees often exist near critical values for cavitation, a condition largely set by the distance between the water table and the hydraulic capacity of the xylem (Ryan and Yoder 1997, Ryan et al. 2006). High hydraulic path-length resistance may decrease productivity in taller, older trees because stomata in tall trees are more often closed than in the younger, shorter trees and consequently carbon gain is reduced during the midday hours (see 'hydraulic limitation hypothesis', Ryan and Yoder 1997). Several branch-level, gas-exchange studies have shown that stomatal conductance decreases with increasing tree age and height (Yoder et al. 1994, Ryan et al. 2000), while other studies have shown that stomatal conductance measurements fail to conclusively support the hydraulic limitation to gas-exchange hypothesis (Bauerle et al. 1999,

Phillips et al. 2002, McDowell et al. 2005). Identifying any universal stand age-effect responses from these types of studies needs to be done with caution because 'branch-level' data are scaled up to the 'stand level' based on short measurement periods and small sampling sizes (e.g., Raulier et al. 2000).

Our study uses the eddy covariance (EC) technique that makes measurements of microclimate, and mass and energy fluxes between the whole forest ecosystem and the atmosphere. We collected stand-level data over two growing seasons (May to October 2006 and 2007) at the Wind River old-growth (OG) forest and at Early Seral North (ESN) in 2006 and Early Seral South (ESS) in 2007. All our study sites were either dominated (the ES stands) or co-dominated (the OG stand) by Douglas-fir, an extremely long-lived (maximum age ~ 1000 years old) pioneering species and the three stands are representative of the youngest and oldest Douglas-fir successional stages. Our objectives were to (1) assess how summer-time reductions in soil moisture availability and increases in vapour pressure deficit influence ecosystem-atmospheric carbon dioxide (F_{NEE})' evapotranspiration rate (E_T) and energy exchange in two distinct forest age classes and (2) compare site ecophysiological responses (e.g., canopy conductance, the Priestley-Taylor coefficient and canopy decoupling factor) to microclimate conditions during the seasonal drought period.

Materials and methods

Site description

OC forest and canopy crane The 87-m-tall canopy crane is in the Thorton T. Munger Research Natural Area (RNA) (45°49'13.76" N and 121°57'06.88" W; 371 m a.s.l.), a preserved 478 ha section of OG forest in the Gifford Pinchot National Forest, Washington, USA. The RNA is classified as part of the Western Cascades Lowlands and Valleys ecoregion with a wet, mild climate and forests that are dominated by Douglas-fir and western hemlock (Thorson et al. 2003). Topography within the RNA is gentle and elevations range from 335 to 610 m (Shaw et al. 2004). The stand is co-dominated by Douglas-fir (mean height = 52 m and maximum height = 65 m), the colonizing tree species, and western hemlock (mean height = 19 m and maximum height = 55 m) (Ishii et al. 2000), a shade tolerant, climax species, which will eventually dominate the stand. Other tree species found in the T.T. Munger RNA include the conifers: western red cedar (*Thuja plicata* Donn.), noble fir (*Abies procera* Rehd.), grand fir (*Abies grandis* (Dougl.) Forbes), western white pine (*Pinus monticola* Dougl.), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) and Pacific yew (*Taxus brevifolia* Nutt.); and the angiosperms: cascara buckthorn (*Rhamnus purshiana* (DC.) Cooper), Pacific dogwood (*Comus nuttallii* (Aud.) Torr.) and red alder (*Alnus rubra* Bong.). Ground species

include salal (*Gaultheria shallon* Pursh), vine maple (*Acer circinatum* Pursh), Oregon-grape (*Berberis nervosa* Pursh), vanillaleaf (*Achlys triphylla* (Smith) DC.), bracken fern (*Pteridium aquilinum* (L.) Kuhn), sword fern (*Polystichum munitum* (Kaulf.) C. Presl) and deer fern (*Blechnum spicant* (L.) Roth) (Franklin 1972, DeBell and Franklin 1987, Harmon et al. 2004).

The vertical canopy is structurally complex due to a mixture of tree ages (0 to ~500 years old) among shade-tolerant and shade-intolerant species. Strong vertical temperature and humidity gradients are periodically present (paw U et al. 2004, Pyles et al. 2004, Falk et al. 2005) and are indicative of low aerodynamic mixing conditions throughout the canopy and high boundary-layer resistance around the foliage. Overhead canopy gap fraction is 0.52 (Parker et al. 2002) and leaf area index (LAI) measurements range from 8.2 to 9.2 m² m⁻² (Thomas and Winner 2000, Parker et al. 2004) and are divided unevenly among the middle and upper canopy (4.8 m² m⁻²), lower canopy (2.1 m² m⁻²) and understory (1.7 m² m⁻²). Western hemlock and western red cedar represent more than half (55%) of the stand LAI but Douglas-fir foliage dominate the upper canopy (Thomas and Winner 2000), the driest and brightest microenvironment, and have disproportionate control over ecosystem mass and energy exchange, including transpiration (Lewis et al. 2000, Winner et al. 2004). Deciduous vegetation are insignificant components of stand biomass and during the summer months are no more than 15% of the canopy LAI (Thomas and Winner 2000).

ES canopies The ESN (45°49'37.2 N and 121°57'39.6" W; 361 m a.s.l.) is a re-established evergreen needleleaf forest on a 7 ha clear-cut patch, 1.25 km northwest of the canopy crane. This stand represents a third generation Douglas-fir ecosystem: the original OG forest was logged in 1920 and a clear-cut harvest was done in 1994 on the 80-year-old Douglas-fir trees. In 1997, the stand was seeded with Douglas-fir saplings at 741 trees ha⁻¹. The second most common tree was the deciduous species red alder, which was found predominately in the southern portion of the stand. Western hemlock and western white pine seedlings were also present but in insignificant amounts. Douglas-fir height and diameter at breast height (d.b.h.) measurements were taken in September 2005: mean height = 4.4 m, height range = 1.2–5.3 m and mean d.b.h. = 5.7 cm. Ground cover species were diverse in the summer months and included salal, Oregon-grape, bracken fern, sword fern and blackberry (*Rubus ursinus* Cham. & Schltdl.).

The ESS stand (45°48'47.4" N and 121°57'32.9" W; 371 m a.s.l.) is an abandoned clear-cut patch (1990), 1.1 km southwest of the canopy crane, and was naturally established with Douglas-fir from surrounding cone crops. In July 2007, the average Douglas-fir tree height was 3.58 ± 0.84 m and d.b.h. was 4.47 ± 1.6 cm (*n* = 95 trees). The estimated tree density was 1063 trees ha⁻¹

(biomass survey included eight plots of 100 m² each). Tree cores showed that stand-representative Douglas-fir trees were between 9 and 12 years of age in 2007 (*n* = 10 trees). Other tree species included western white pine, red alder, and planted Pacific silver fir and Pacific yew seedlings, each in insignificant amounts. Bracken fern was the dominant ground species from May to September. Grasses and scotch broom bushes (*Cytisus scoparius* (L.) Link) were also common in the more open areas.

LAI at the ES canopies LAI was indirectly measured at the ES stands using digital hemispheric photography (DHP), and estimated using HemiView 2.1 (Delta-T Devices Ltd., Cambridge, UK) and the following equation (Chen 1996, Chen et al. 1997):

$$\text{LAI} = \frac{(1 - \alpha) \text{LAI}_{\text{eff}} \gamma_E}{\Omega_E} \quad (1)$$

LAI_{eff} is effective, single-sided LAI and was calculated using the software program, *x* is woody-to-plant ratio and was set at 0.20, *YE* is needle-to-shoot ratio and was set at 1.61 and γ_E is the foliage element clumping index and was set at 0.91 (parameter values were based on the measurements taken by Chen 1996, Chen et al. 2006). The hemispheric photographs were taken at a height of 10 m with a Nikon COOLPIX E4300 digital camera adapted with a Nikon Fisheye Converter lens (Nikon Inc., Melville, NY). For logistical reasons DHP surveys were done just once at both sites. The photographs were taken just past sunset on 1 September 2006 at ESN and 30–31 August 2007 at ESS07. Fern and other ground species were cleared before the photographs were taken to ensure that only trees were included in the canopy LAI estimates. At ESN, 15 images were taken along a 150 m west-to-east transect (centred on the flux tower) at 10 m intervals. At ESS, 17 images were taken along a 170 m west-to-east transect at 10 m intervals. DHP average estimates of canopy LAI were 1.5 m² m⁻² at ESN and 0.9 m² m⁻² at ESS. Separate LAI measurements of the herbaceous/understory species were not taken at ESN. ESS LAI of ground species (predominately bracken fern) was estimated from DHP and was between 0.4 and 0.5 m² m⁻².

Belowground description Coarse roots of mature Douglas-fir extend 1–2 m deep although most root biomass in the OG stand is concentrated within the first 0.5 m of the soil profiles (Shaw et al. 2004). At the ES stands coarse roots were observed down to 0.5 m and fine roots were primarily in the 0–0.3 m soil layer. Area soils are medial, mesic, Entic Vitrandis and are 2–3 m deep, well drained and derived from volcanic material (Shaw et al. 2004). These soils are classified as silt loams and are generally stone-free, high in organic material and nitrogen deficit in the root zone at the Wind River sites. Stand-specific soil properties are listed in Table 1. The water table depth is

Table 1. Stand descriptions for the three forest sites.

	ESN	ESS	OG stand
<i>Measurement period</i>			
2006	May–October		May–October
2007		May–August (flux data); May–October (meteorological data)	May–October
<i>Stand properties</i>			
Stand area (ha)	7	10	478
Site preparation	Minimal: post-harvest coarse woody debris (CWD) piles, snags, logs; no fertilization	Extensive: no CWD; mechanically homogenized soil to 1 m; no fertilization	None: natural fire recovery
Maximum tree age (years)	10	14	~ 450–500
Mean tree height (m)	4.4	3.6	52 (Douglas-fir) 19 (western hemlock)
Stand density (trees ha ⁻¹)	741 ¹	1063	427 (Shaw et al. 2004)
LAI (m ² m ⁻²)	1.1–1.8	0.6–1.1	8.2–9.2 (Parker et al. 2002)
Foliar C:N	44:1 ± 3	37:1 ± 3	41:1 (Klopatek et al. 2006)
<i>Soil properties</i>			
0–0.15 m			
Sand:silt:clay	66:28:6	60:32:8	60:30:10 (Shaw et al. 2004)
C:N	27:1 ± 6	26:1 ± 3	28:1 ± 1 (Klopatek 2002)
Organic C (%)	3.4	2.2	5–10 (Shaw et al. 2004)
Bulk density (g cm ⁻³)	0.94	1.07	0.83
0.15–0.30 m			
Sand:silt:clay	68:26:6	62:29:9	60:31:9 (Shaw et al. 2004)
C:N	28:1 ± 5	26:1 ± 4	25:1 ± 1 (Klopatek 2002)
Organic C (%)	2.9	3.9	5–10 (Shaw et al. 2004)
Bulk density (g cm ⁻³)	0.94	1.07	0.83

¹Note that stand density is an underestimate at ESN because it only includes planted trees and not naturally established trees that are present as well.

both spatially and temporally heterogeneous at the OG forest and ranges from 0.3 to 0.5 m in the winter months to 2.0–2.4 m in the dry summer months (Shaw et al. 2004). Water table depth was not measured at the ES stands but is assumed to be within the range found at the OG forest. Field capacity (0v–10 kPa, 0v at matrix potential = -10 kPa) for this soil type is 0.30 m³ m⁻³, permanent wilting point (0v–1500 kPa, 0v at matrix potential = -1500 kPa) is 0.14 m³ m⁻³ and volumetric available water content of the soil (0v, where 0v = 0v–10 kPa – 0v–1500 kPa) is 0.16 m³ m⁻³ (Lambers et al. 2008). For root-zone depths of 1.5 and 0.6 m, respectively, at the OG forest and ES stands, maximum available water storage was estimated to be 240 mm (OG) and 96 mm (ES) (By multiplied by root-zone depth).

Instrumentation and flux calculations

OG forest Ecosystem carbon dioxide, water vapour and energy fluxes were measured using EC methodology (see, e.g., Wofsy et al. 1993, Hollinger et al. 1994, Goulden et al. 1996, Paw U et al. 2000, Baldocchi 2003). The EC system consisted of a sonic anemometer (Solent HS, Gill Instruments, Lymington, UK) and a closed-path infrared

gas analyser (IRGA) (LI-7000, Li-Cor Inc., Lincoln, NE), which measured the wind velocity vectors and air temperature, and concentrations (mixing ratios) of water vapour (H₂O) and carbon dioxide (CO₂), respectively, at 10 Hz. The IRGA and sonic anemometer were mounted on a horizontal boom extending off the canopy crane at a height of 67 m so that the anemometer faced west, the predominant wind direction and direction of greatest homogenous fetch (> 1 km). Carbon dioxide (F_{CO_2} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), sensible heat (H , W m^{-2}) and latent energy (ΛE , W m^{-2}) fluxes were computed with FORTRAN90 code using a 30-min averaging period and a horizontal coordinate rotation. The rate of change in CO₂ concentration (storage flux, Sea , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) within the canopy volume was estimated using 30-min changes in the mean CO₂ mixing ratio measured at the top of the canopy (Falk et al. 2008). To account for any CO₂ stored within the canopy and below the detection height of the instruments, Sco , was added to F_{CO_2} to estimate the net ecosystem exchange of carbon (F_{NEE} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) on a half-hourly basis. Half-hour measurements of F_{NEE} and ΛE were further screened for outliers and gap-filled (16% of data in 2006 and 11% in 2007) using a running-mean and look-up table approach

(Reichstein et al. 2005). We report no nighttime flux data in this study except in the daily evapotranspiration sums. For further details on the EC post-processing, refer to Paw U et al. (2004) and Falk (2005).

Meteorological instrumentation at the canopy crane included air temperature/relative humidity (sheltered *HMP-35C*, Vaisala Oyj, Helsinki, Finland) and incident photosynthetically active radiation sensors (PAR) (190-SB, Li-Cor Inc.) mounted at heights of 2 (below canopy measurement) and 70 (above canopy measurement) m along the crane tower, and a four-stream (up- and down-welling and short- and long-wave radiation) net radiometer (CNR 1, Kipp and Zonen, Delft, The Netherlands) was mounted at a height of 85 m. Additionally, soil temperature was measured at depths of 0.05, 0.10 and 0.15 m (CS106B, Campbell Scientific Inc., Logan, UT). Ground heat flux was measured with a HFT-3.1 soil heat flux plate (Radiation and Energy Systems, REBS, Seattle, Washington) buried 0.075 m below the surface. The meteorological measurements were collected as 30-min averages and were logged continuously from May 2006 to October 2007.

ESN and ESS Ten hertz measurements of horizontal (u and v) and vertical (w) wind velocity and air temperature were made using a CSAT-3 sonic anemometer (Campbell Scientific Inc.), and densities of CO_2 and H_2O vapour were measured with an open-path fast response IRGA (LI-7500, Li-Cor Inc.). F_{co_2} , ΔE and H were calculated in real time using a 30-min averaging period with the CRI000 EC program (Campbell Scientific Inc.). F_{co_2} , and ΔE were also corrected for any measurement errors associated with density fluctuations (Webb et al. 1980, referred to as WPL80 corrections). During post-processing, all scalar and energy fluxes were re-calculated after the mean cross-wind (v) and vertical wind (w) velocities were rotated to zero (following the natural wind coordinate system). The rate of change of CO_2 concentration (S_{co_2}) within the canopy was estimated using the half-hourly changes in the CO_2 mixing ratio measured at the top of the canopy and was added to F_{co_2} to estimate F_{NEE} . Half-hour scalar and energy fluxes were quality controlled for non-preferred wind directions, inadequate fetch (using a parameterized footprint model), low turbulence conditions (determined by a ratio of mean wind velocity to a turbulent energy velocity scale; methodology described in Wharton et al. 2009), heavy precipitation events and times of general instrument failure. Missing or excluded scalar and energy fluxes were gap-filled using a running-mean approach (Reichstein et al. 2005).

At ESN, the sonic anemometer was mounted facing west-southwest with a fetch of 210 m over homogeneous Douglas-fir trees. Both LI-7500 and CSAT-3 were mounted at 5.5 m a.g.l., 1.1 m above the ESN canopy, on a boom extending from a 6 m tall tower. Tower-based micrometeorological data included half-hour measurements of air temperature/relative humidity (sheltered *HMP-35C*,

Vaisala Oyj), net radiation (Q7.1, REBS) and soil temperature (0.05, 0.10 and 0.15 m) (CS106B, Campbell Scientific Inc.). Ground heat storage was calculated from the soil temperature profiles. Fluxes and micrometeorological data were collected at ESN from May to October 2006. The instrument setup at ESS was identical except that the LI-7500 and CSAT-3 were mounted at 5 m a.g.l., 1.4 m above the canopy facing south (170°) and up- and down-welling PAR sensors (190-SB, Li-Cor Inc.) were added at the top of the tower at a height of 6 m a.g.l. EC data at ESS were collected May to August 2007 (EC fluxes end in August due to instrument failure) and meteorological data from May to October 2007.

A simple, parameterized footprint model (Kljun et al. 2004, <http://www.footprint.kljun.net/index.php>) was used to determine the extent of which measured turbulent fluxes were influenced by scalar sources outside the ES stands. The model showed that daytime (10:00–14:00) footprint estimates ranged from 75 m (east upwind direction) to 100 m (north upwind direction) at ESN and 77 m (east upwind direction) to 118 m (north upwind direction) at ESS, translating into fetch-to-be instrument height ratios of 14:1–23:1. Available (i.e., homogeneous vegetation) fetch-to-EC instrument height ratios averaged 33:1 and 34:1 at ESN and ESS, respectively, but ranged from 10:1 to 44:1 depending on the wind direction. Half-hour fluxes taken under inadequate fetch conditions were removed from the data series, as well as wind directions at ESN where red alder made up a significant portion of the flux footprint.

Water supply and demand measurements

Direct measurements of canopy water availability included precipitation and volumetric soil moisture. Precipitation (P , mm day^{-1}) was measured at the Carson Fish Hatchery (CFH) National Oceanic and Atmospheric Administration (NOAA) weather station (45°31'12"N and 121°34'48"W; 345.6 m a.s.l.) using a rain and snow gauge (385 heated, Met One Instruments, Inc., Grants Pass, Oregon). The NOAA weather station is located 5 km north of the canopy crane in the Wind River Valley at a similar elevation. Soil water content ($0v$, $\text{m}^3 \text{m}^{-3}$) at the OG forest was measured over an integrated depth of 0–0.30 m (three replicates) in 2006 with a time-domain reflectometry (TDR) system (TDR100, Campbell Scientific Inc.) and in staggered depths down to 2 m in 2007 with Sentek soil moisture probes (four replicates) (Sentek EnviroSMART, Sentek Sensor Technologies, Stepney, Australia). At ESN, $0v$ was measured with the TDR100 system over integrated depths of 0–0.30 and 0.30–0.60 m (two replicates). The TDR100 system was moved to ESS in 2007, where $0v$ was measured over integrated depths of 0–0.30, 0.30–0.60 and 0.60–0.90 m (two replicates). Our study reports soil moisture measurements in relative soil water content ($0v_r$), where $0v_r = (0v - 0v_{-1500} \text{ kPa}) / (0v_{-10} \text{ kPa} - 0v_{-1500} \text{ kPa})$. $0v_r$ is a dimensionless number that ranges from 0 to 1 and represents the fraction of available water in the soil root zone.

Water vapour loss from the canopy was estimated using the 30-min averaged ΔE to calculate the evapotranspiration rate (E_T , mm half hour⁻¹), and summed over daily and monthly intervals. Equilibrium evapotranspiration rate (E_{Teq} , mm half hour⁻¹) was calculated based on the energy-balance technique ($\Delta E + H = R_n - S$, where S = energy storage flux) and a modification of the Penman equation (Penman 1948) following Denmead and McIlroy (1970),

$$E_{Teq} = \left(\frac{\Delta}{\Delta + \gamma} \right) (R_n - S_g). \quad (2)$$

In Eq. (2), Δ is the slope of the saturation vapour pressure curve (kPa K⁻¹), γ is the psychrometric constant (kPa K⁻¹), R_n is the net radiation (W m⁻²) and S_g is the ground heat storage flux (W m⁻²). Equilibrium E_T is a measure of the climatologically expected evapotranspiration rate over a moist surface based only on temperature and available energy. The Priestley-Taylor coefficient, α , a ratio of measured E_T to equilibrium E_{Teq} , was calculated using (Priestley and Taylor 1972)

$$\alpha = \frac{E_T}{E_{Teq}}. \quad (3)$$

The Priestley-Taylor coefficient is site dependent and varies with surface vegetation (Denmead 1969) and microclimate conditions, including soil water availability (Slatyer and Denmead 1964, Priestley and Taylor 1972, Black 1979). Equation (3) gives a maximum α value of 1 assuming that there is no upwind advection of heat added to the system (e.g., an 'oasis effect'). Magnitudes of α approach one as E_T approaches E_{Teq} , and measured evapotranspiration is largely controlled by aerodynamic resistance ($R_a = 1/G_a$) and the subsequent water vapour gradient between the canopy surface and atmosphere, and less by canopy resistance ($R_c = 1/G_c$) to water vapour transfer. As α approaches zero, the measured evapotranspiration rate is less than the expected, energy-limited rate (E_{Teq}) and ecosystem water loss is strongly controlled by canopy resistance (i.e., the degree of stomatal closure) to surface-atmospheric water exchange.

Bulk canopy and mechanistic measurements

Bulk canopy and mechanistic variables including water use efficiency (WUE), canopy conductance and a canopy decoupling factor were calculated for daytime (downwelling shortwave radiation > 10 W m⁻²) half-hour periods only. The WUE is defined as the total mass of dry matter produced by photosynthesis for every kilogram of water lost by vegetation through transpiration (e.g., Rosenberg et al. 1983). Here, we defined a midday WUE as the ratio of F_{NEE} (g C m⁻² half hour⁻¹) to E_T (kg H₂O m⁻² half hour⁻¹), averaged between the hours of 10:00 and 15:00 when ΔE was greater than zero (following Berbigier et al. 2001). Following Stewart (1988), canopy conductance (G_c) was estimated using the inverted Penman-Monteith equation (Monteith 1964):

$$G_c = \left[\frac{\rho c_p \delta e}{\gamma \lambda E} + \frac{\Delta \beta - 1}{G_a} \right]^{-1}. \quad (4)$$

In Eq. (4), G_c is canopy conductance (m s⁻¹), ρ is air density (kg m⁻³), c_p is specific heat (J kg⁻¹ K⁻¹), δe is vapour pressure deficit (kPa), ΔE is latent energy (W m⁻²), β is the Bowen ratio ($H/\Delta E$) and G_a is aerodynamic conductance for momentum transfer ($G_a = u^2/U$, m s⁻¹, where u^* is friction velocity, m s⁻¹ and U is mean wind speed, m s⁻¹). Equation (4) includes both a canopy conductance-driven component (first term, right-hand side (RHS) of Eq. (4)) and a radiation-driven component (second term, RHS of Eq. (4)) so that the proportion of E_T controlled by the two drivers can be represented by a canopy decoupling factor, Ω (Jarvis and McNaughton 1986):

$$\Omega = \frac{\frac{\Delta}{\gamma} + 1}{\frac{\Delta}{\gamma} + 1 + \frac{G_a}{G_c}}, \quad (5)$$

where Ω is a dimensionless number that ranges from 0 to 1 depending on whether E_T is controlled strongly by G_c and δe (Ω approaches 0) and is an aerodynamic-driven process, or whether E_T is determined by the amount of available energy ($R_n - S$) to the canopy (Ω approaches 1). If a canopy is completely dry at the surface and one assumes that E_T is approximately equal to the transpiration flux, then Ω refers to the degree to which transpiration is uncoupled to atmospheric δe . In a forest canopy where surface roughness is high, Ω is mostly dependent on wind speed, and gas exchange will be strongly coupled to atmospheric saturation conditions ($\Omega < 0.2$). As soil moisture decreases, Ω also decreases and canopy air coupling is enhanced (Jarvis and McNaughton 1986).

Results

Climate and stand microenvironments

Water-year precipitation was 2361 mm from October 2005 to September 2006 and 2129 mm in 2006-2007. Although the water year totals were equal, the timing of precipitation varied among years. May to June was wetter (112 mm) in 2006 than in 2007 (64 mm), while July and August were dramatically wetter in 2007 (34 mm) than in 2006 (2 mm). Overall, 2006 experienced a wet spring which led into a very dry summer season, while 2007 received less rain in the spring but experienced periodic rain events throughout the summer (Table 2).

Above canopy air temperatures were warmer ($T_{a\max}$ was 1-2°C higher) on most summer days at the ES stands than at the dense OG forest. The OG forest (2006 and 2007) and ESN canopies were generally cooler than the local air temperature (CFR NOAA meteorological station data), while cooler conditions were not measured at ESS. Larger site temperature differences were observed in the soil temperature measurements. At ESS, the daily maximum soil

(Reichstein et al. 2005). We report no nighttime flux data in this study except in the daily evapotranspiration sums. For further details on the EC post-processing, refer to Paw U et al. (2004) and Falk (2005).

Meteorological instrumentation at the canopy crane included air temperature/relative humidity (sheltered HMP-35C, Vaisala Oyj, Helsinki, Finland) and incident photosynthetically active radiation sensors (PAR) (190-SB, Li-Cor Inc.) mounted at heights of 2 (below canopy measurement) and 70 (above canopy measurement) m along the crane tower, and a four-stream (up- and down-welling and short- and long-wave radiation) net radiometer (CNR 1, Kipp and Zonen, Delft, The Netherlands) was mounted at a height of 85 m. Additionally, soil temperature was measured at depths of 0.05, 0.10 and 0.15 m (CS106B, Campbell Scientific Inc., Logan, UT). Ground heat flux was measured with a HFT-3.1 soil heat flux plate (Radiation and Energy Systems, REBS, Seattle, Washington) buried 0.075 m below the surface. The meteorological measurements were collected as 30-min averages and were logged continuously from May 2006 to October 2007.

ESN and ESS Ten hertz measurements of horizontal (u and v) and vertical (w) wind velocity and air temperature were made using a CSAT-3 sonic anemometer (Campbell Scientific Inc.), and densities of CO_2 and H_2O vapour were measured with an open-path fast response IRGA (LI-7500, Li-Cor Inc.). F_{CO_2} , E and H were calculated in real time using a 30-min averaging period with the CR1000 EC program (Campbell Scientific Inc.). F_{CO_2} and E were also corrected for any measurement errors associated with density fluctuations (Webb et al. 1980, referred to as WPL80 corrections). During post-processing, all scalar and energy fluxes were re-calculated after the mean cross-wind (v) and vertical wind (w) velocities were rotated to zero (following the natural wind coordinate system). The rate of change of CO_2 concentration (S_{CO_2}) within the canopy was estimated using the half-hourly changes in the CO_2 mixing ratio measured at the top of the canopy and was added to F_{CO_2} to estimate F_{NEE} . Half-hour scalar and energy fluxes were quality controlled for non-preferred wind directions, inadequate fetch (using a parameterized footprint model), low turbulence conditions (determined by a ratio of mean wind velocity to a turbulent energy velocity scale; methodology described in Wharton et al. 2009), heavy precipitation events and times of general instrument failure. Missing or excluded scalar and energy fluxes were gap-filled using a running-mean approach (Reichstein et al. 2005).

At ESN, the sonic anemometer was mounted facing west-southwest with a fetch of 210 m over homogeneous Douglas-fir trees. Both LI-7500 and CSAT-3 were mounted at 5.5 m a.g.l., 1.1 m above the ESN canopy, on a boom extending from a 6 m tall tower. Tower-based micrometeorological data included half-hour measurements of air temperature/relative humidity (sheltered HMP-35C,

Vaisala Oyj), net radiation (Q7.1, REBS) and soil temperature (0.05, 0.10 and 0.15 m) (CS106B, Campbell Scientific Inc.). Ground heat storage was calculated from the soil temperature profiles. Fluxes and micrometeorological data were collected at ESN from May to October 2006. The instrument setup at ESS was identical except that the LI-7500 and CSAT-3 were mounted at 5 m a.g.l., 1.4 m above the canopy facing south (170°) and up- and down-welling PAR sensors (190-SB, Li-Cor Inc.) were added at the top of the tower at a height of 6 m a.g.l. EC data at ESS were collected May to August 2007 (EC fluxes end in August due to instrument failure) and meteorological data from May to October 2007.

A simple, parameterized footprint model (Kljun et al. 2004, <http://www.footprint.kljun.net/index.php>) was used to determine the extent of which measured turbulent fluxes were influenced by scalar sources outside the ES stands. The model showed that daytime (10:00-14:00) footprint estimates ranged from 75 m (east upwind direction) to 100 m (north upwind direction) at ESN and 77 m (east upwind direction) to 115 m (north upwind direction) at ESS, translating into fetch-to-EC instrument height ratios of 14:1-23:1. Available (i.e., homogeneous vegetation) fetch-to-EC instrument height ratios averaged 33:1 and 34:1 at ESN and ESS, respectively, but ranged from 10:1 to 44:1 depending on the wind direction. Half-hour fluxes taken under inadequate fetch conditions were removed from the data series, as well as wind directions at ESN where red alder made up a significant portion of the flux footprint.

Water supply and demand measurements

Direct measurements of canopy water availability included precipitation and volumetric soil moisture. Precipitation (P , mm day^{-1}) was measured at the Carson Fish Hatchery (CFH) National Oceanic and Atmospheric Administration (NOAA) weather station ($45^\circ 31' 12''$ N and $121^\circ 34' 48''$ W; 345.6 m a.s.l.) using a rain and snow gauge (385 heated, Met One Instruments, Inc., Grants Pass, Oregon). The NOAA weather station is located 5 km north of the canopy crane in the Wind River Valley at a similar elevation. Soil water content ($0v$ $\text{m}^3 \text{m}^{-3}$) at the OG forest was measured over an integrated depth of 0-0.30 m (three replicates) in 2006 with a time-domain reflectometry (TDR) system (TDR100, Campbell Scientific Inc.) and in staggered depths down to 2 m in 2007 with Sentek soil moisture probes (four replicates) (Sentek EnviroSMART, Sentek Sensor Technologies, Stepney, Australia). At ESN, $0v$ was measured with the TDR100 system over integrated depths of 0-0.30 and 0.30-0.60 m (two replicates). The TDR100 system was moved to ESS in 2007, where $0v$ was measured over integrated depths of 0-0.30, 0.30-0.60 and 0.60-0.90 m (two replicates). Our study reports soil moisture measurements in relative soil water content (0_r), where $0_r = (0v - 0v_{-1500}) / (0c - 0c_{-1500})$. 0_r is a dimensionless number that ranges from 0 to 1 and represents the fraction of available water in the soil root zone.

Water vapour loss from the canopy was estimated using the 30-min averaged ΔE to calculate the evapotranspiration rate (E_T , mm half hour⁻¹), and summed over daily and monthly intervals. Equilibrium evapotranspiration rate (E_{Teq} , mm half hour⁻¹) was calculated based on the energy-balance technique ($\Delta E + H = Rn - S$, where S = energy storage flux) and a modification of the Penman equation (Penman 1948) following Denmead and McIlroy (1970),

$$E_{Teq} = \left(\frac{\Delta}{\Delta + \gamma} \right) (Rn - S_g). \quad (2)$$

In Eq. (2), Δ is the slope of the saturation vapour pressure curve (kPa K⁻¹), γ is the psychrometric constant (kPa K⁻¹), Rn is the net radiation (W m⁻²) and S_g is the ground heat storage flux (W m⁻²). Equilibrium E_T is a measure of the climatologically expected evapotranspiration rate over a moist surface based only on temperature and available energy. The Priestley-Taylor coefficient, α ; a ratio of measured E_T to equilibrium E_T , was calculated using (Priestley and Taylor 1972)

$$\alpha = \frac{E_T}{E_{Teq}}. \quad (3)$$

The Priestley-Taylor coefficient is site dependent and varies with surface vegetation (Denmead 1969) and microclimate conditions, including soil water availability (Slatyer and Denmead 1964, Priestley and Taylor 1972, Black 1979). Equation (3) gives a maximum α value of 1 assuming that there is no upwind advection of heat added to the system (e.g., an 'oasis effect'). Magnitudes of α approach one as E_T approaches E_{Teq} , and measured evapotranspiration is largely controlled by aerodynamic resistance ($Ra = 1/G_a$) and the subsequent water vapour gradient between the canopy surface and atmosphere, and less by canopy resistance ($Rc = 1/G_c$) to water vapour transfer. As α approaches zero, the measured evapotranspiration rate is less than the expected, energy-limited rate (E_{Teq}) and ecosystem water loss is strongly controlled by canopy resistance (i.e., the degree of stomatal closure) to surface-atmospheric water exchange.

Bulk canopy and mechanistic measurements

Bulk canopy and mechanistic variables including water use efficiency (WUE), canopy conductance and a canopy decoupling factor were calculated for daytime (downwelling shortwave radiation > 10 W m⁻²) half-hour periods only. The WUE is defined as the total mass of dry matter produced by photosynthesis for every kilogram of water lost by vegetation through transpiration (e.g., Rosenberg et al. 1983). Here, we defined a midday WUE as the ratio of F_{NEE} (g C m⁻² half hour⁻¹) to E_T (kg H₂O m⁻² half hour⁻¹), averaged between the hours of 10:00 and 15:00 when ΔE was greater than zero (following Berbigier et al. 2001). Following Stewart (1988), canopy conductance (G_c) was estimated using the inverted Penman-Monteith equation (Monteith 1964):

$$G_c = \left[\frac{\rho c_p \delta e}{\gamma \Delta E} + \frac{\Delta \beta - 1}{G_a} \right]^{-1}. \quad (4)$$

In Eq. (4), G_c is canopy conductance (m S⁻¹), ρ is air density (kg m⁻³), c_p is specific heat (J kg⁻¹ K⁻¹), e is vapour pressure deficit (kPa), ΔE is latent energy (W m⁻²), β is the Bowen ratio ($H/\Delta E$) and G_a is aerodynamic conductance for momentum transfer ($G_a = u^* 2/U$, S⁻¹, where u^* is friction velocity, m S⁻¹ and U is mean wind speed, m S⁻¹). Equation (4) includes both a canopy conductance-driven component (first term, right-hand side (RHS) of Eq. (4)) and a radiation-driven component (second term, RHS of Eq. (4)) so that the proportion of E_T controlled by the two drivers can be represented by a canopy decoupling factor, Λ (Jarvis and McNaughton 1986):

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where Λ is a dimensionless number that ranges from 0 to 1 depending on whether E_T is controlled strongly by G_c and Λ approaches 0 and is an aerodynamic-driven process, or whether E_T is determined by the amount of available energy ($Rn - S$) to the canopy (Λ approaches 1). If a canopy is completely dry at the surface and one assumes that E_T is approximately equal to the transpiration flux, then Λ refers to the degree to which transpiration is uncoupled to atmospheric de. In a forest canopy where surface roughness is high, Q is mostly dependent on wind speed, and gas exchange will be strongly coupled to atmospheric saturation conditions ($Q < 0.2$). As soil moisture decreases, Λ also decreases and canopy air coupling is enhanced (Jarvis and McNaughton 1986).

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Table 2. Monthly micrometeorological data at the tower sites and total precipitation and mean maximum temperature at CFH NOAA weather station.

	Ta _{max} (°C)	Tsoil _{max} (°C)	δe _{max} (kPa)	θ _r	Ta _{max} (°C)	Tsoil _{max} (°C)	δe _{max} (kPa)	θ _r	P (mm)	Ta _{max} (°C)
2006	ESN				OG				CFH	
May	20.0	—	1.5	1.0	18.6	11.7	1.3	1.0	59.2	19.3
June	25.8	19.6	2.5	1.0	22.0	14.8	1.6	1.0	52.3	23.1
July	27.2	21.6	2.6	0.44	25.6	17.7	2.1	0.63	1.0	28.8
August	27.1	19.9	2.6	0.27	25.3	17.3	2.2	0.28	1.3	27.5
September	24.0	16.7	2.2	0.28	22.4	15.1	1.8	0.26	14.2	24.5
October	15.6	12.3	1.1	0.55	14.6	10.6	0.9	0.51	55.6	16.6
Average	23.3	18.0	2.1	0.59	21.4	14.5	1.7	0.63	183.6 ¹	23.3
2007	ESS				OG				CFH	
May	21.0	22.9	2.2	1.0	18.7	13.0	1.5	1.0	34.3	19.8
June	21.6	24.5	1.9	1.0	19.1	14.4	1.4	0.87	30.0	21.3
July	28.8	30.9	2.9	0.89	26.0	18.8	2.2	0.72	18.8	27.8
August	25.1	27.4	2.3	0.73	22.8	16.9	1.8	0.52	15.5	25.4
September	23.0	22.2	—	0.71	19.0	14.2	1.3	0.56	57.7	21.6
October	15.1	11.3	—	1.0	11.6	9.7	0.5	0.94	223.5	12.1
Average	22.4	23.2	2.3	0.88	19.5	14.5	1.5	0.78	379.8 ¹	21.3

¹Total precipitation.

temperature (0.05 m) was often 10°C higher than at OG on 2007 sunny summer days. Maximum daily δe was also higher at the ES stands than at the OG forest. June to August mean daily maximum δe was 2.6 kPa at ESN and 1.9 kPa at OG (2006), and 2.4 kPa at ESS and 1.8 kPa at OG (2007) (Table 2).

Relative available soil water content also varied among stands and years although the seasonal drought pattern remained a dominant feature. In 2006, near-surface (0–0.30 m) θ_r equaled one at both ESN and OG during the spring months and began declining between June and July. Relative water availability dropped to a minimum of 0.27 in August at ESN and to 0.26 in September at OG (Table 2). During the 2007 summer months, near-surface θ_r did not reach these low levels. θ_r dropped to a weekly minimum value of 0.67 at ESS in September and 0.52 at OG in August. While the near-surface water availability was less at the OG stand than at the ES stand, the 0.9–2.0 m depth θ_v measurements in 2007 revealed that deeper soil layers were not water deficient ($\theta_r = 1$) at OG. At ESS, the deepest θ_v measurements (0.6–0.9 m) showed that relative water availability was not significantly higher in this soil layer and available water content was nearly identical to the near-surface measurements from July to September.

Diurnal and monthly fluxes

Net radiation was higher at the OG stand than at either ES stand during the months of May to August. Monthly R_n averaged 470 MJ m⁻² mo⁻¹ in 2006 and 468 MJ m⁻² mo⁻¹ in 2007 at OG, and 410 MJ m⁻² mo⁻¹ at ESN and 393 MJ m⁻² mo⁻¹ at ESS (Tables 3 and 4).

During the summer months at the OG stand, a greater amount of available energy was on average partitioned into sensible heat (average daily maximum = 350 W m⁻²) than latent heat (average daily maximum = 200 W m⁻²). The May to August Bowen ratios at OG were higher than those observed at either ES stand and ranged from 2.05 (June) to 2.61 (July) in 2006 and 1.94 (June) to 2.58 (May) in 2007. Peak daytime latent heat fluxes were constant at the OG stand from May to August with the exception of a midday λE decline in July 2006. A more distinct λE pattern was observed at the ES stands with peak λE occurring in June and July (Figures 1B and 2B). July E_T in 2006 was nearly twice as great at ESN (103 mm mo⁻¹) than at OG (53 mm mo⁻¹) (Table 3), while a smaller increase over 2007 OG E_T was also measured at ESS (Table 4).

During May, midday CO₂ fluxes were more than twice as great at the OG stand as at either ES stand (Figures 1C and 2C). Midday net CO₂ uptake at the OG stand peaked in June and declined throughout the latter summer months at OG. At the ES stands, the greatest differences in midday CO₂ fluxes occurred between the months of May and June. Mean midday F_{NEE} increased from -3.2 to -9.0 μmol m⁻² s⁻¹ at ESN and from -4.6 to -8.7 μmol m⁻² s⁻¹ at ESS during this period. A lag of ~2 h occurred in the timing between daily peak flux exchange at ESS and OG in 2007 but not at ESN and OG in 2006. This time lag created a longer period of net CO₂ uptake in May at the OG stand but a reduced period of CO₂ uptake at OG during July as compared to ESS (compare boxed regions in Figure 2C). Peak λE at ESS also occurred later in the afternoon than at OG from May to August 2007 resulting in higher total daily E_T at the younger stand.

Table 3. Monthly total net radiation, mean Bowen ratio, total evapotranspiration, mean ratio of precipitation to E_T , mean Priestley–Taylor coefficient, and mean midday CO_2 flux, WUE, canopy conductance and canopy decoupling coefficient at ESN and OG forest in 2006.

	ESN						OG							
	May	June	July	August	September	October	May–October	May	June	July	August	September	October	May–October
R_n (MJ m ^{−2} mo ^{−1})	302	454	467	417	279	172	350	394	495	525	465	312	202	400
β ($H/\lambda E$)	2.82	0.94	0.78	1.26	1.60	1.30	1.51 ± 0.35	2.23	2.05	2.61	2.18	1.92	1.46	2.07 ± 0.45
E_T (mm mo ^{−1})	49	86	103	68	44	39	388 ± 17	60	67	53	51	41	31	303 ± 13
P/E_T	1.22	0.61	0.01	0.02	0.32	1.44	0.60	0.98	0.78	0.02	0.03	0.35	1.78	0.66
α (E_T/E_{Treq})	0.55	0.69	0.74	0.65	0.52	0.62	0.65	0.42	0.47	0.35	0.43	0.36	0.49	0.42
F_{NEE} (μmol m ^{−2} s ^{−1})	−3.2	−9.0	−10.2	−8.0	−3.4	−2.2	−6.0 ± 1.8	−9.3	−11	−9.2	−7.3	−5.8	−6.9	−8.3 ± 2.0
WUE (g C kg H ₂ O ^{−1})	2.1	1.6	1.7	1.8	1.2	1.8	1.6 ± 1.0	2.3	2.1	2.7	2.5	2.2	2.9	2.5 ± 1.1
G_c (mm s ^{−1})	8.2	9.4	9.7	8.7	7.9	8.5	8.9 ± 3.3	5.7	7.8	5.9	5.4	4.3	6.7	6.0 ± 3.4
Ω	0.16	0.21	0.23	0.18	0.12	0.09	0.18	0.17	0.27	0.17	0.15	0.15	0.12	0.18

Bold values show site significant differences at $P < 0.001$.

Ecosystem response to water stress

Precipitation. *On and de effects on E_T* A ratio of precipitation to evapotranspiration (P/E_T) showed that all forest canopies lost more water via evapotranspiration than gained from precipitation during the months of June to August (Tables 3 and 4). Precipitation was assumed equal at all stands so any differences were due only to variations in canopy evapotranspiration. In 2006, we observed very low (P/E_T) values of just 0.01 at the young stand and 0.02 at the older forest in July and August due to nearly zero precipitation. The ESN was likely water stressed by September 2006 as relative soil moisture fell to 20% in the root zone. Near-surface θ_r at the OG stand was also extremely low and deeper water measurements were not made that year to accurately determine water availability throughout the entire root zone. On average, the 2007 summer was wetter and larger stand differences were observed between the OG and ES stand. From May to August, (P/E_T) was 0.35 (more water limited) at ESS and 0.42 (less water limited) at OG.

A time series of daily maximum de and daily total E_T at ESS and the OG forest is shown in Figure 3. de was consistently higher at ESS during the 2007 summer, often by > 1 kPa (circled data points in Figure 3). In June, higher de coincided with increased canopy water loss ($1\text{--}2 \text{ kg H}_2\text{O m}^{-2} \text{ day}^{-1}$) at the ES stand, while in August, daily E_T was moderate and closer to E_T observed at OG (e.g., compare squared data points in Figure 3) even though de remained higher at the ES site. Figure 4 shows that E_T was not related to de at the OG forest ($R^2 = 0.0$) during the month of June in both 2006 and 2007 while a stronger relationship between E_T and be was observed at ESN ($R^2 = 0.47$) and ESS ($R^2 = 0.78$). E_T at the OG forest was more closely linked to vapour pressure deficit in August ($R^2 = 0.6$ in 2006 and $R^2 = 0.34$ in 2007) than during early summer. For equivalent daily maximum de (e.g., 2 kPa) total daily E_T was smaller in August ($1.5\text{--}2.5 \text{ kg H}_2\text{O m}^{-2} \text{ day}^{-1}$) than in June ($2.5\text{--}3.5 \text{ kg H}_2\text{O m}^{-2} \text{ day}^{-1}$) at all forests.

Summer x ranged from a low of 0.35 at OG (July) to a high of 0.74 at ESN (July) in 2006 and from 0.39 (July) at OG to 0.63 (June) at ESS in 2007 (Tables 3 and 4). Overall, both ES stands had higher Priestley–Taylor coefficients ($\sim 0.5\text{--}0.6$) than the OG forest (~ 0.4) during the drought seasons. The Priestley–Taylor coefficient increased logarithmically with canopy conductance in all stands (e.g., $R^2 = 0.34$ at ESN) so that measured E_T was closer to equilibrium E_T at the higher G_c values. The relationship between x and relative available soil water was less straightforward (Figure 5). At the OG forest and ESS a correlation between the Priestley–Taylor coefficient and θ_r was not found ($R^2 = 0.0$). At ESN x dropped from an average of 0.73–0.55 as θ_r conditions decreased and approached 20%.

Bulk canopy parameter and mechanistic responses We measured higher WUE at the OG stand than at either of the ES stands. Mean midday WUE during the summer

Table 4. Monthly total net radiation, mean Bowen ratio, total evapotranspiration, mean ratio of precipitation to E_T , mean Priestley–Taylor coefficient, and mean midday CO_2 flux, WUE, canopy conductance and canopy decoupling coefficient at ESS and OG forest in 2007.

2007	ESS					OG				
	May	June	July	August	May–August	May	June	July	August	May–August
R_n ($\text{MJ m}^{-2} \text{mo}^{-1}$)	408	361	435	368	393	494	445	523	411	468
β ($H/\lambda E$)	1.28	0.82	0.94	1.36	1.10 ± 0.65	2.58	1.94	2.22	2.20	2.23 ± 0.71
E_T (mm mo^{-1})	68	78	85	58	289 ± 14	53	64	63	51	230 ± 11
P/E_T	0.51	0.38	0.22	0.27	0.35	0.65	0.47	0.29	0.30	0.43
α (E_T/E_{Teq})	0.53	0.63	0.57	0.52	0.56	0.43	0.46	0.39	0.40	0.42
F_{NEE} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	−4.6	−8.7	−7.2	−6.5	$−6.7 \pm 1.0$	−10.4	−10.8	−5.7	−7.9	$−8.7 \pm 2.7$
WUE ($\text{g C kg H}_2\text{O}^{-1}$)	1.1	1.8	1.5	1.8	1.5 ± 0.7	2.5	2.3	1.9	2.1	2.2 ± 1.0
G_c (mm s^{-1})	6.1	7.1	5.4	5.0	5.8 ± 2.7	6.2	6.9	5.0	5.7	5.9 ± 4.0
Ω	0.15	0.21	0.16	0.13	0.16	0.31	0.33	0.31	0.29	0.31

Bold values show site significant differences at $P < 0.001$.

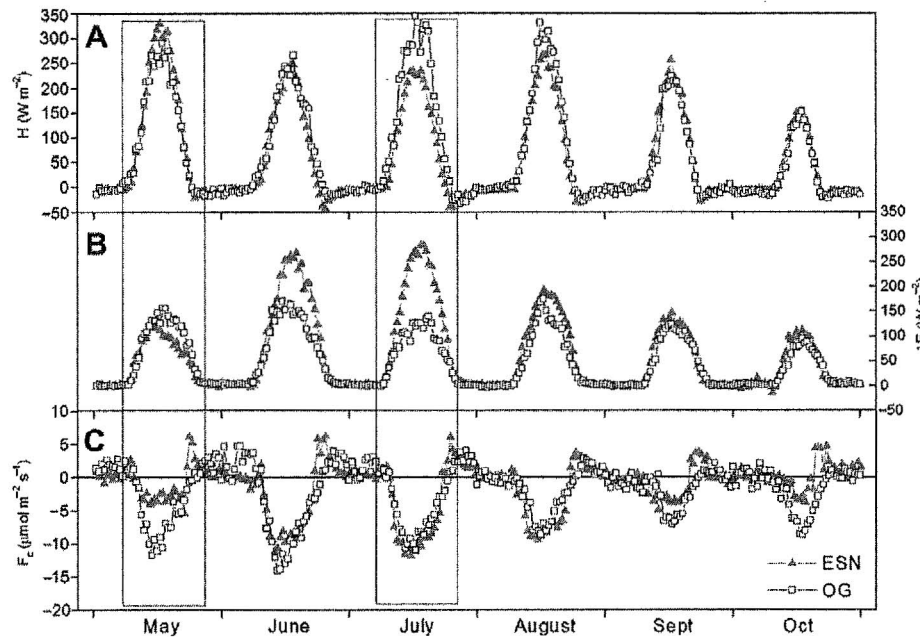


Figure 1. Mean monthly diurnal plots of sensible heat (A), latent energy (B) and carbon dioxide flux (C) at ESN and OG in 2006. The boxes highlight that site differences in ecosystem fluxes change dramatically from May to July.

drought was 2.5 ± 1.1 g C kg^{−1} H₂O at OG and 1.6 ± 1.0 g C kg^{−1} H₂O at ESN in 2006 (Table 3), and 2.2 ± 1.0 g C kg^{−1} H₂O at OG and 1.5 ± 0.7 g C kg^{−1} H₂O at ESS in 2007 (Table 4). The OG stand was slightly more water use efficient in 2006 than in 2007 and consistently more water use efficient than either of the ES stands. Figure 6 shows average canopy conductance from May to October at the OG and ES stands in 2006 and 2007. Overall, higher values of G_c were observed in 2006 than in 2007 and G_c magnitudes were higher at the beginning of the drought season than at the end. Site differences in diurnal G_c values were also observed. Canopy conductance was higher at the ES stands during the afternoon hours than at the OG forest, while morning G_c was often higher at the mature forest. Canopy conductance began declining

earlier in the day at OG suggesting that stomates are shutting down at lower levels in the OG Douglas-fir/western hemlock forest than in the 4 m tall ES Douglas-fir trees. Figure 7 further details the difference between mean canopy conductance in May and July 2007 at ESS and OG during the hours of 10:00, 13:00 and 16:00. In May, G_c declined at similar rates (~ 0.2 mm S^{−1} per half hour) at both stands and averaged 7.4 mm s^{−1} (OG) and 7.6 mm S^{−1} (ESS) at 10:00, 6.4 mm S^{−1} (OG) and 6.5 mm S^{−1} (ESS) at 13:00, and 4.7 mm s^{−1} (OG) and 4.6 mm s^{−1} (ESS) at 16:00. In contrast, August G_c declined more rapidly at the OG stand (0.3 mm s^{−1} per half hour) than at ESS (0.1 mm S^{−1} per half hour) beginning at the noon hour. By early evening, G_c averaged less than 4 mm S^{−1} at OG but remained around 6 mm s^{−1} at ESS.

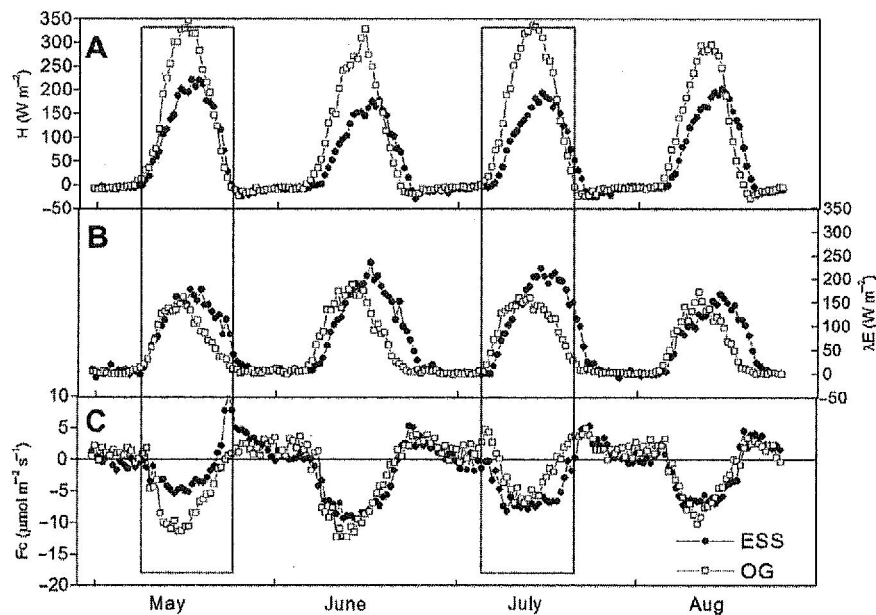


Figure 2. Mean monthly diurnal plots of sensible heat (A), latent energy (B) and carbon dioxide flux (C) at ESS and OG in 2007. The boxes highlight that site differences in April were greatest for CO_2 flux and in July for energy fluxes.

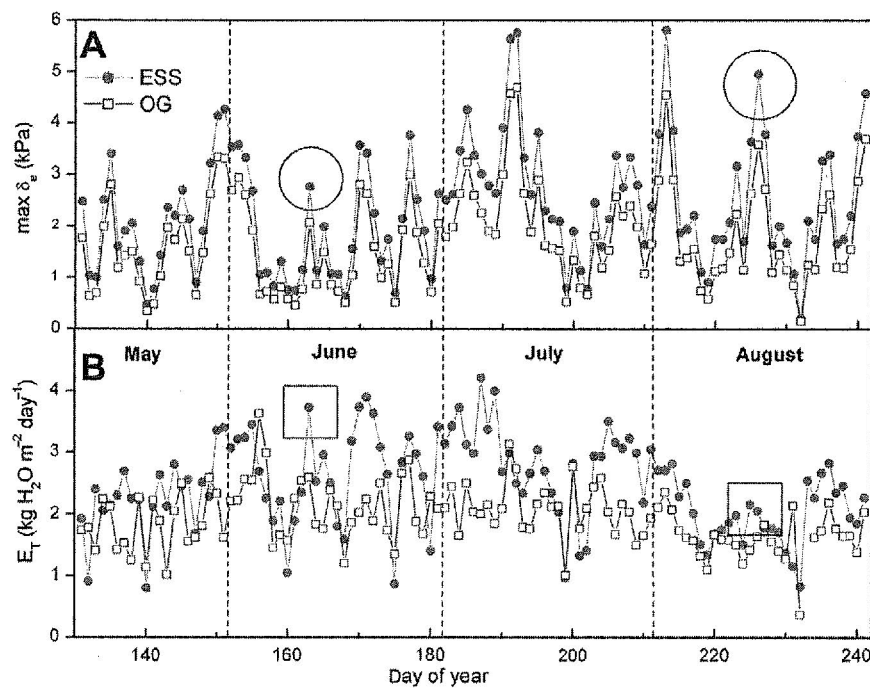


Figure 3. Time series of daily maximum δe and total E_T at ESS and OG during the seasonal drought in 2007. The circled points show two peaks in δe in June and August at ESS and illustrate that δe is largely greater at the ES stand than at OG. Corresponding to the same 2 days, the squares show that E_T was twice greater at ESS than OG in June but no large E_T difference was observed on the selected day in August even though δe was 1 kPa higher at ESS.

A close look at canopy conductance in Figure 8 reveals both site and monthly differences in leaf-atmosphere gas-exchange response to evaporative demand at ESS and OG. At low δe values (< 0.5 kPa), the OG stand had higher G_c ($> 2\text{--}3$ mm S^{-1}) than the young stands but beyond values of 1–1.5 kPa, G_c at OG rapidly declined with increasing δe . Even though available soil moisture was not low (e.g., $\theta_r < 50\%$) in May and June. In general, G_c was lower in July and August than in May and June at both

stands for all vapour pressure deficit levels below 2.5 kPa. Beyond 2.5 kPa, the rate of canopy conductance decline with increasing vapour pressure deficit was strongest at OG. The minimum δe threshold to produce very little response in G_c (i.e., G_c approaches 0) was 3 kPa and 4 kPa at ESS in May to June and in July to August. The OG stand had no observable δe – G_c threshold response in May to June but was 3.5 kPa in July to August. Figure 9 illustrates how the δe – G_c responses at OG and ESS differ

Table 4. Monthly total net radiation, mean Bowen ratio, total evapotranspiration, mean ratio of precipitation to E_T , mean Priestley–Taylor coefficient, and mean midday CO_2 flux, WUE, canopy conductance and canopy decoupling coefficient at ESS and OG forest in 2007.

2007	ESS					OG				
	May	June	July	August	May–August	May	June	July	August	May–August
R_n ($\text{MJ m}^{-2} \text{mo}^{-1}$)	408	361	435	368	393	494	445	523	411	468
β ($H/\lambda E$)	1.28	0.82	0.94	1.36	1.10 ± 0.65	2.58	1.94	2.22	2.20	2.23 ± 0.71
E_T (mm mo^{-1})	68	78	85	58	289 ± 14	53	64	63	51	230 ± 11
P/E_T	0.51	0.38	0.22	0.27	0.35	0.65	0.47	0.29	0.30	0.43
α (E_T/E_{Teq})	0.53	0.63	0.57	0.52	0.56	0.43	0.46	0.39	0.40	0.42
F_{NEE} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	−4.6	−8.7	−7.2	−6.5	$−6.7 \pm 1.0$	−10.4	−10.8	−5.7	−7.9	$−8.7 \pm 2.7$
WUE ($\text{g C kg H}_2\text{O}^{-1}$)	1.1	1.8	1.5	1.8	1.5 ± 0.7	2.5	2.3	1.9	2.1	2.2 ± 1.0
G_c (mm s^{-1})	6.1	7.1	5.4	5.0	5.8 ± 2.7	6.2	6.9	5.0	5.7	5.9 ± 4.0
Ω	0.15	0.21	0.16	0.13	0.16	0.31	0.33	0.31	0.29	0.31

Bold values show site significant differences at $P < 0.001$.

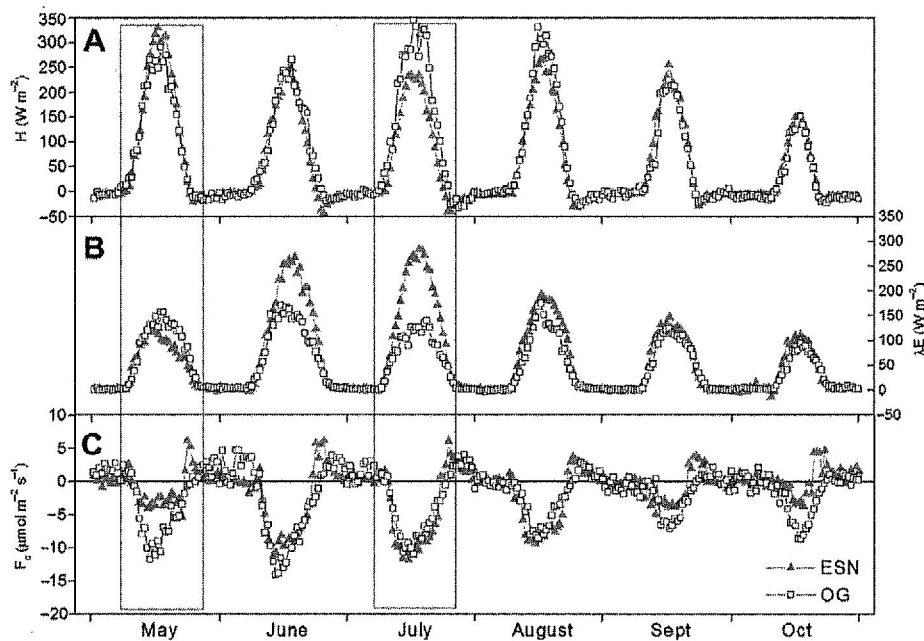


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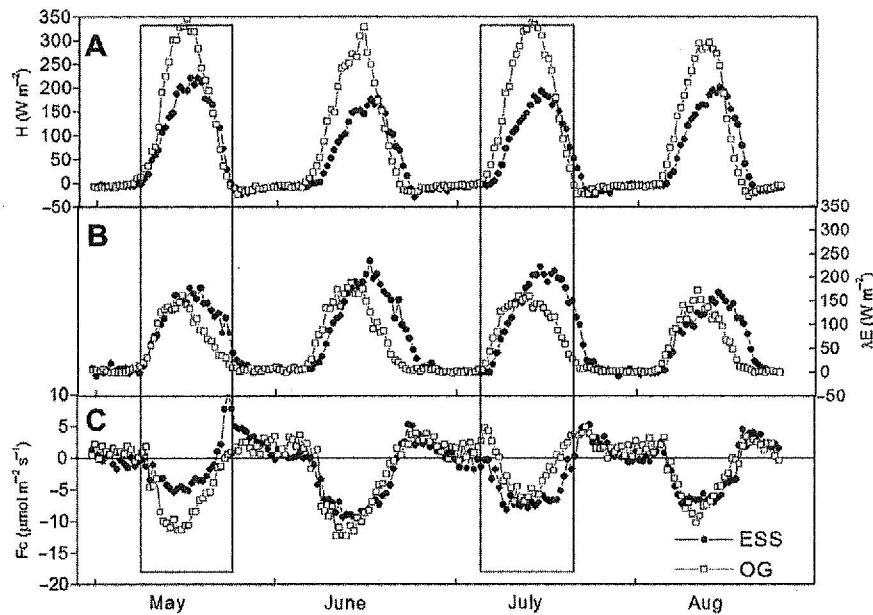


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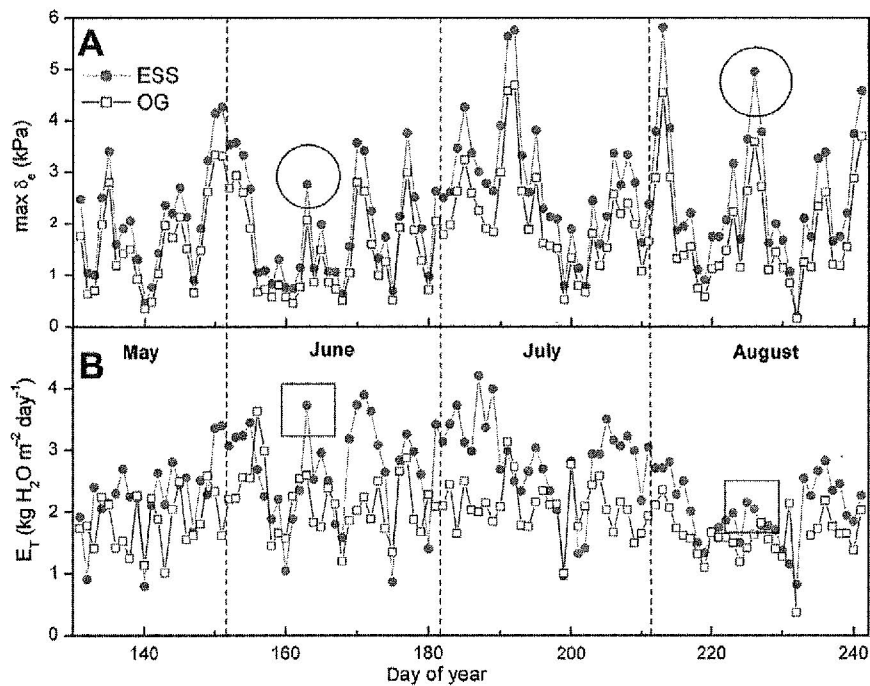


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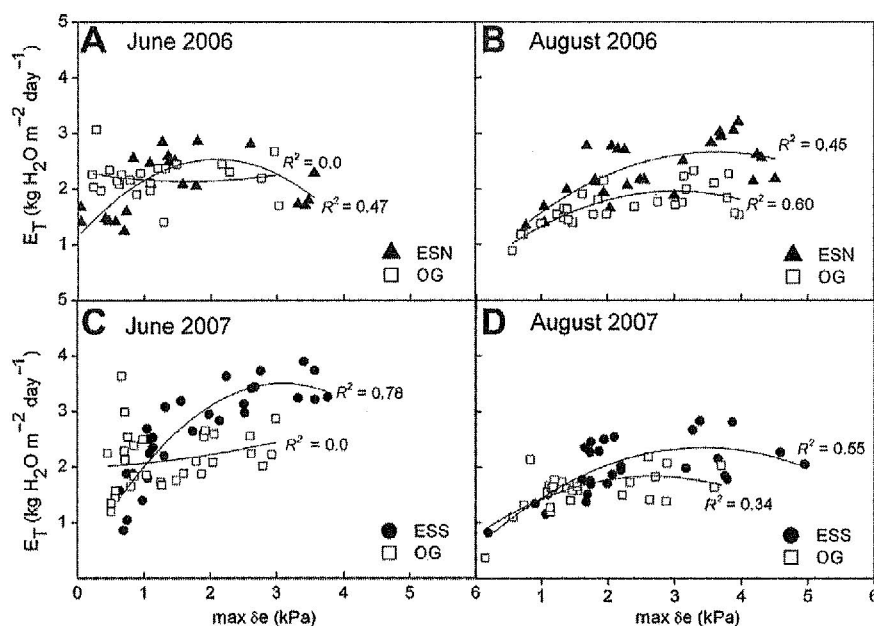


Figure 4. Relationship between daily maximum δe and daily total E_T in June at ESN and OG (A) and ESS and OG (C) and in August at ESN and OG (B) and ESS and OG (D). Daily E_T was not correlated to vapour pressure deficit at the beginning of the summer at the OG stand but a correlation was found between the two variables at the end of the summer. At the ES stands, a significant correlation was found during both months.

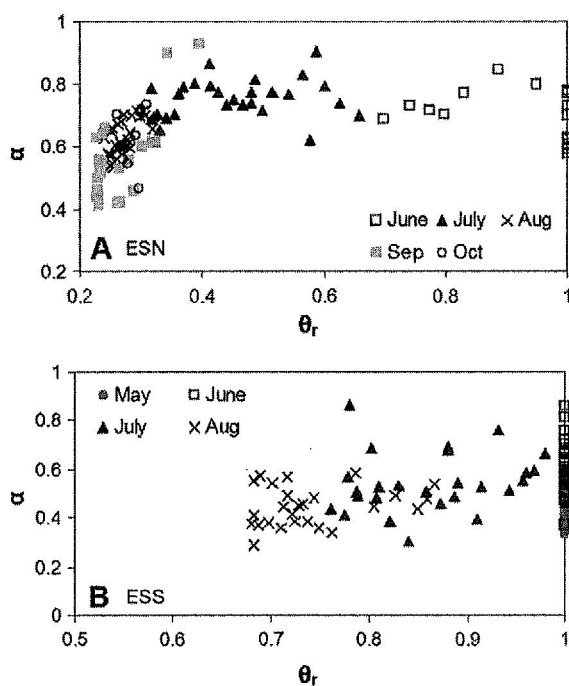


Figure 5. Daily mean Priestley–Taylor coefficient and relative soil water content grouped by month at the ESN (A) and ESS (B). Although θ_r was high at ESS, α tended to be lower at this site. A θ_r threshold is clearly visible in the ESN data, available water content < 30% ($\theta_r = 0.3$) led to a sharp decline in actual E_T as compared to the equilibrium E_T or low α values.

from the beginning of the drought season to conditions at the end. In May and June 2007, canopy conductance declined sharply at OG from 4 to 1 mm s⁻¹ across the

highest δe levels (2–3.5 kPa), while ESS G_c dropped only from 5 to 3 mm s⁻¹ (grey triangles in Figure 9). In contrast, in July and August, ESS G_c declined sharply from 4 to 2 mm s⁻¹ across the highest δe levels (3.0–4.5 kPa), while G_c remained at 2 mm s⁻¹ at the OG forest (grey circles in Figure 9).

At very high δe (> 4.5 kPa), canopy conductance was low (about 2 mm s⁻¹) in all stands but we found that evapotranspiration was more directly related to available energy than to stomatal control as shown by higher decoupling coefficients (e.g., at ESN, $\Lambda = 0.27$ for $\delta e > 4.5$ kPa and $\Lambda = 0.14$ for $2.5 < \delta e < 3.5$ kPa). The decoupling coefficients at the OG stand in 2006 were on average ($\Lambda = 0.18$) equal to those at ESN ($\Lambda = 0.18$), while OG Λ values in 2007 were significantly higher ($\Lambda = 0.31$) than in 2006 and higher than those found at ESS ($\Lambda = 0.16$).

Discussion and conclusions

Douglas-fir/western hemlock stands in the Pacific Northwest have adapted to seasonal moisture constraints on photosynthesis by assimilating large amounts of carbon during the wetter and cooler spring months while during the summer, stomatal closure is induced as vapour pressure gradients between the leaf and atmosphere increase (Waring and Franklin 1979). Our study showed that G_c was notably reduced after the noon hour in mid-summer at the OG forest regardless of soil moisture availability. While relative near-surface soil moisture was noticeably lower at the OG forest in 2006 ($\theta_r \sim 25\%$) than in 2007 ($\theta_r \sim 55\%$), the mature stand likely had access to deep soil water supplies during both drought seasons because (1) relative soil

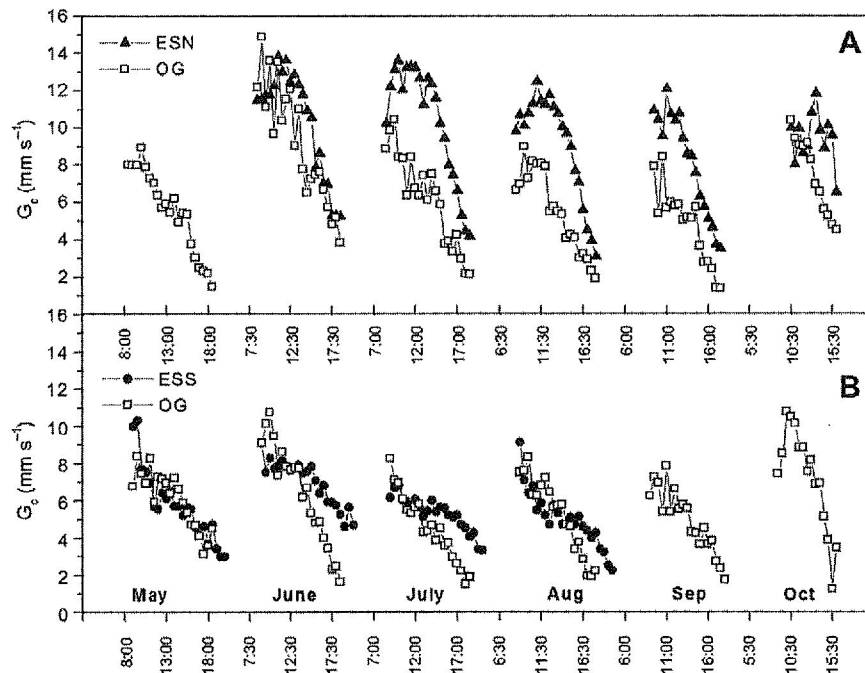


Figure 6. Average canopy conductance by site and month for the hours of 8:00 until 19:30. Overall, G_c was higher in 2006 than in 2007 and greater at the ES sites than at the OG stand during the afternoon hours.

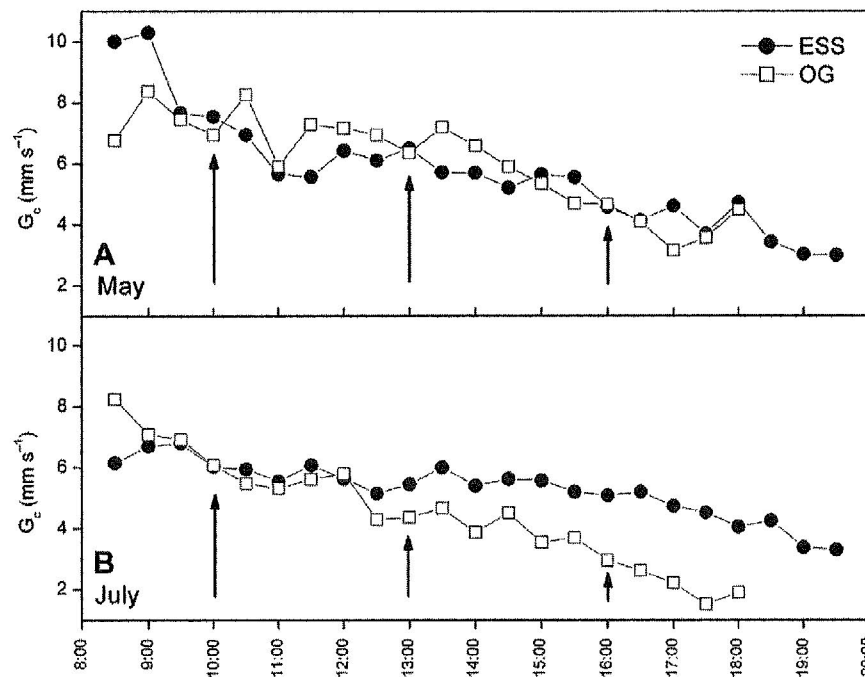


Figure 7. A close examination of mean canopy conductance in May (A) and July (B) at ESS and OG in 2007. The arrows highlight three half hours showing the differences in morning, midday and afternoon G_c among stands at the beginning of the drought season (May) and in the middle of the drought season (July).

moisture never dropped below 90% at the 1 m depth when these measurements were available, (2) the root zone extends down to 2 m for the oldest trees and (3) there is prior evidence of HR in the soils at this stand (Brooks et al. 2002, Warren et al. 2005). The phenomenon of stomatal closure in OG trees regardless of soil moisture has also

been noted by Zweifel et al. (2002) in a 250-year-old Norway Spruce stand, whereby they observed midday stomatal closure on most sunny days during permanently wet soil conditions.

Even under moderate de levels, foliage at the tops of tall evergreen conifer trees often reach near critical values for

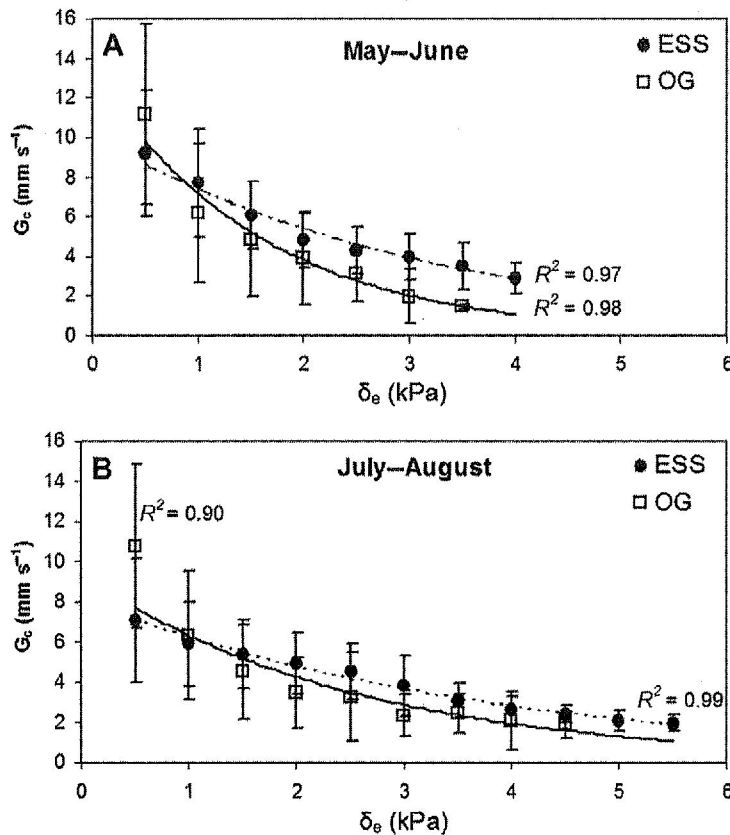


Figure 8. Mean midday canopy conductance binned by vapour pressure deficit in May to June (A) and July to August (B) at ESS and OG. G_c decreases logarithmically with increasing δ_e at all sites. At the OG stand, G_c is significantly greater between 0 and 1 kPa than at either ES stand but as δ_e reaches 2 kPa, G_c is systematically lower at the mature forest. The error bars are ± 1 standard deviation from the mean.

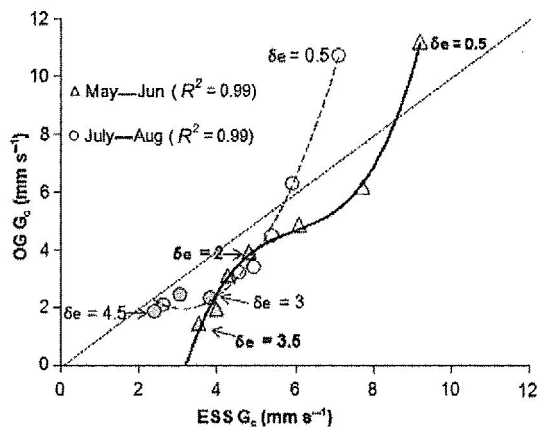


Figure 9. Canopy conductance at ESS and OG grouped by δ_e bins (0.5 kPa intervals from 0.5 to 4.5 kPa) at the beginning (May–June) and middle (July–August) of the 2007 drought season. G_c decreases with increasing δ_e so that the lowest δ_e bins are found at the top-right of the figure (starting at 0.5 kPa) and increase along the fitted lines to a maximum δ_e level (up to 4.5 kPa) in the bottom-left of the figure. The grey-filled symbols show mean G_c at each site at the four highest vapour pressure deficit levels per drought period. Bolded δ_e bins correspond to May to June data and the dotted line represents a 1:1 fit.

cavitation due to a long path distance between the water table and the hydraulic capacity of the xylem, and as a result shut their stomata frequently (Ryan and Yoder 1997). Our observation of a rapid decline in G_c between 0.5 and 1.0 kPa in the older forest is consistent with the findings of Ryan and Yoder (1997) as well as with the observations of a diurnal hysteresis in sap flow measurements taken at the bottom and top of tall Douglas-fir trees at Wind River by Cermak et al. (2007). Taken together, these datasets suggest that upper canopy Douglas-fir foliage are driving our observed monthly and diurnal fluxes of mass and energy at the OG forest. At the ES stands, we found that canopy conductance was also inhibited by vapour pressure deficit but not until later in the afternoon hours when the highest δ_e levels were reached and later in the drought season when relative soil moisture was low. Our overall G_c observations (e.g., canopy conductance was 2–4 mm S⁻¹ higher at the ES stands than at the OG agree with branch-level measurements taken by Yoder et al. (1994), whereby they found that stomatal conductance is lower in the Wind River OG trees than in the younger Douglas-fir stands, and by Fessenden and Ehleringer (2002) who, using $d^{13}\text{C}$ isotopes, found evidence that

decreased hydraulic conductance in the 450-year-old stand led to lower stomatal conductance in the mature forest than in the younger, shorter trees. The B_{e} was almost always lower at the top of the OG forest than over the ES stands suggesting that the upper canopy stomates are generally closing at lower d_e levels in the older stand.

In addition to our successional-stage research, gas-exchange studies comparing a Wind River 20-year-old Douglas-fir stand and the OG forest were made in 1998 and 1999 by Chen et al. (2002, 2004). In their study, Chen et al. (2002) report higher WUE ($1.7 \text{ g C kg}^{-1} \text{ H}_2\text{O}$) and Bowen ratio (2.9) at a Wind River 20-year-old stand than at the OG forest ($\text{WUE} = 1.0 \text{ g C kg}^{-1} \text{ H}_2\text{O}$, $B = 1.6$), while total E_T was greater at OG. In contrast, we found higher B , higher WUE and lower E_T at the OG forest than the ES stands. Lower WUE values have also been measured for the 10-year-old Douglas-fir age class by Thomas and Winner (2002), whereby they found that WUE was twice as high at the OG forest than at nearby younger trees using 'branch-level' measurements. We suggest that the conflicting nature of succession-stage, gas-exchange results at Wind River is a consequence of (1) a rapidly growing Douglas-fir canopy during the first 0–20 years, (2) a rapid shift in secondary species distributions in the first 0–20 years and (3) different measurement techniques (e.g., 'stand-level' versus 'branch-level') and measurement periods were used in the studies.

It is important to note that other plant species, particularly bracken fern, were a non-negligible component of ecosystem biomass at the younger stands during the summer months. Ground species certainly played a role in determining the carbon, water and energy budgets at the ES stands although we were not able to quantify how significant that role might be. At the OG forest, the canopy is diverse (eight evergreen conifer and three angiosperm species are present) and structurally complex because of this mixture of shade-tolerant and shade-intolerant species. Our measurements of gas exchange are for the forest ecosystem as a whole and as such we were not able to determine what contribution each species made to ecosystem fluxes. Therefore, we are making the following conclusions based on the two successional stages investigated in this study and not specifically on tree species, tree height or tree age:

- (1) Total evaporation (and fraction of expected E_T) is higher in ES stands than at the OG forest during the summer months as a result of higher soil temperatures, higher air temperatures and higher vapour pressure deficits in the open canopies during the mid-afternoon hours. Available soil moisture limited E_T at the ES stands but only when θ_r dropped below 30%. Total E_T was limited at the OG stand during moderate vapour pressure deficits and moderate soil water availability.
- (2) The ES stands are likely to be more susceptible to increased water stress than mature stands if the Pacific

Northwest drought season becomes longer or more intense due to the young stand's open canopy and extreme microclimate, limited root system (i.e., lack of access to deeper water), and inability to induce stomatal closure and conserve water under moderate levels of vapour pressure deficit.

Our results have impacts beyond our specific sites since Pacific Northwest forest productivity during the drought season is strongly coupled with evapotranspiration through stomatal control on water vapour loss. Since forest productivity models are often used to estimate present and future carbon stocks and hydrological processes for this region (see, e.g., Thornton et al. 2002, Law et al. 2004, Turner et al. 2006), our results show the critical need for using stand-specific, ecophysiological response functions in these models, especially for properly capturing the ecosystem-level impacts of drought. We found significant differences in the timing, magnitude and environmental controls of ecosystem exchange between the OG and the ES stands, indicating the presence of distinct successional-stage mechanisms between the microenvironments and the canopies. Considering that Pacific Northwest forests are characterized by regular silviculture harvest rotations and are predicted to have strong water availability changes in the future from regional climate change, we suggest that more successional-stage studies are needed to properly predict future CO_2 , water and energy fluxes in these evergreen conifer forests.

Acknowledgments

S.W. would like to especially thank Mark Creighton and Annie Hamilton at the Wind River Canopy Crane Research Facility for their hospitality and assistance with logistics throughout this project. The authors also thank Dr. Dennis Baldocchi and Youngryel Ryu (UC Berkeley) and Dr. Susan Ustin (UC Davis) for their technical advice and help in the preparation of this manuscript, and the Editor and the two anonymous reviewers for their beneficial critiques and suggestions. This research was supported by the Office of Science, US Department of Energy, through the Western Regional Center of the National Institute for Global Environmental Change (Cooperative Agreement No. DE-FC03-90ER61010) and the Jastro Shields Research Scholarship (UC Davis). Any opinions, findings and conclusions or recommendations expressed herein are those of the authors and do not necessarily reflect the view of the DOE. The Wind River Canopy Crane Research Facility is operated under joint sponsorship of the University of Washington and the USDA Forest Service/PNW Station and we acknowledge both for significant support. Lawrence Livermore National Laboratory is operated by Lawrence Livermore National Security, LLC, for the US Department of Energy, National Nuclear Security Administration under Contract DE-AC52-07NA27344.

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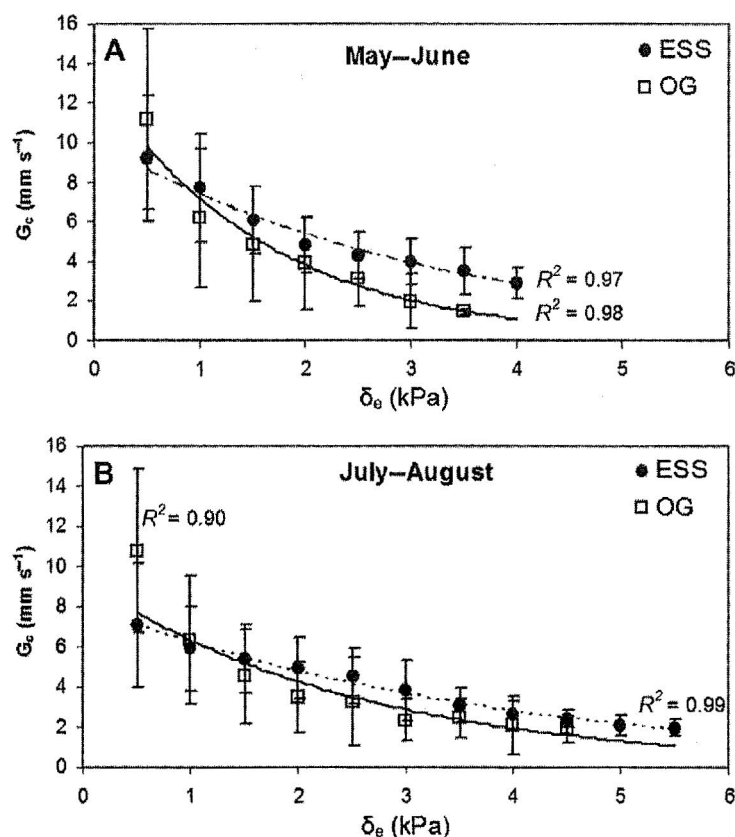


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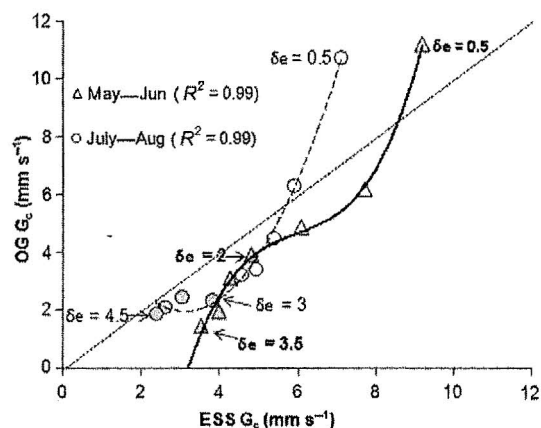


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- (2) The ES stands are likely to be more susceptible to increased water stress than mature stands if the Pacific

Northwest drought season becomes longer or more intense due to the young stand's open canopy and extreme microclimate, limited root system (i.e., lack of access to deeper water), and inability to induce stomatal closure and conserve water under moderate levels of vapour pressure deficit.

Our results have impacts beyond our specific sites since Pacific Northwest forest productivity during the drought season is strongly coupled with evapotranspiration through stomatal control on water vapour loss. Since forest productivity models are often used to estimate present and future carbon stocks and hydrological processes for this region (see, e.g., Thornton et al. 2002, Law et al. 2004, Turner et al. 2006), our results show the critical need for using stand-specific, ecophysiological response functions in these models, especially for properly capturing the ecosystem-level impacts of drought. We found significant differences in the timing, magnitude and environmental controls of ecosystem exchange between the OG and the ES stands, indicating the presence of distinct successional-stage mechanisms between the micro environments and the canopies. Considering that Pacific Northwest forests are characterized by regular silviculture harvest rotations and are predicted to have strong water availability changes in the future from regional climate change, we suggest that more successional-stage studies are needed to properly predict future CO_2 water and energy fluxes in these evergreen conifer forests.

Acknowledgments

S.W. would like to especially thank Mark Creighton and Annie Hamilton at the Wind River Canopy Crane Research Facility for their hospitality and assistance with logistics throughout this project. The authors also thank Dr. Dennis Baldocchi and Youngryel Ryu (UC Berkeley) and Dr. Susan Ustin (UC Davis) for their technical advice and help in the preparation of this manuscript, and the Editor and the two anonymous reviewers for their beneficial critiques and suggestions. This research was supported by the Office of Science, US Department of Energy, through the Western Regional Center of the National Institute for Global Environmental Change (Cooperative Agreement No. DE-FC03-90ER61010) and the Jastro Shields Research Scholarship (UC Davis). Any opinions, findings and conclusions or recommendations expressed herein are those of the authors and do not necessarily reflect the view of the DOE. The Wind River Canopy Crane Research Facility is operated under joint sponsorship of the University of Washington and the USDA Forest Service/PNW Station and we acknowledge both for significant support. Lawrence Livermore National Laboratory is operated by Lawrence Livermore National Security, LLC, for the US Department of Energy, National Nuclear Security Administration under Contract DE-AC52-07NA27344.

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