Old-Growth CO2 Measurements Reveal High Sensitivity to Climate Anomalies across Seasonal, Annual and Decadal time scales

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Abstract

The traditional hypothesis that old-growth forests are carbon neutral is under debate as recent studies show evidence of net carbon sequestration. Here, we present a decade (1998-2008) of carbon dioxide, water and energy fluxes from an old-growth stand in the American Pacific Northwest to identify ecosystem-level responses to climate variability, including teleconnection patterns. This study provides the longest, continuous record of old-growth eddy flux data to date. From 1998-2008, average annual net ecosystem exchange ($F_{\text{NEE}}$) was $-49 \pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$ (a small net carbon sink) while interannual variability was high ($\sim 300 \text{ g C m}^{-2} \text{ yr}^{-1}$) and indicated that the stand is able to switch from net carbon sink to source in response to climate forcing. Seasonal and annual $F_{\text{NEE}}$ variability was strongly linked to climate anomalies associated with major teleconnections and the subsequent responses of driving mechanisms (e.g., water use efficiency, light use efficiency, canopy conductance) to local weather (e.g., cloudiness). Biometric measurements of aboveground net primary productivity ($F_{\text{ANPP}}$) provided a ~60 year record of growth, recruitment, and mortality responses to a longer range of climatic conditions, including shifts in the Pacific Decadal Oscillation (PDO). A negative trend in $F_{\text{ANPP}}$ generally matched the warm PDO phase shift starting in 1977. As climate models predict future warming in the Pacific Northwest, our results suggest that any perturbations towards a warmer, drier state, such as would occur during positive climate phases, may have significant impacts on regional terrestrial carbon budgets through increasing respiration without subsequent, offset increases in carbon assimilation in these old-growth forests.
1.1 Introduction

Fluxes of energy, water, and carbon at forest ecosystems have been extensively studied with the eddy covariance (EC) technique over the last couple of decades. At present, over 150 FLUXNET sites have long enough (ten years or more) records to examine the influence of interannual climate variability on net ecosystem exchange of carbon ($F_{\text{NEE}}$). Some of the longest, continuous data records for forest sites include: Harvard forest, Massachusetts, USA since 1991 (Goulden et al. 1996, Urbanski et al. 2007); Takayama, Japan (Saigusa et al. 2002) since 1993; BOREAS NSA-Old Black Spruce, Manitoba, Canada (Dunn et al. 2007), BOREAS SSA-Old Black Spruce, Saskatchewan, Canada (Amiro et al. 2006, Bergeron et al. 2007) and SSA-Old Jack Pine, Saskatchewan, Canada (Amiro et al. 2006) since 1994; Camp Borden, Ontario, Canada (Lee et al. 1999, Barr et al. 2002), Loobos, The Netherlands (Dolman et al. 2002, Gusev et al. 2005) and Howland, Maine, USA (Hollinger et al. 1999, 2004) since 1995; Brasschaat, Belgium (Janssens et al. 2001, Carrara et al. 2003), Vielsalm, Belgium (Valentini et al. 2000, Aubinet et al. 2001), SSA-Old Aspen, Saskatchewan, Canada (Amiro et al. 2006, Barr et al. 2007), Sorø-LilleBogeskov, Denmark (Pilegaard et al. 2001), Hyytiälä, Finland (Markkanen et al. 2001, Kolari et al. 2009), Hesse Forest, France (Granier et al. 2000), Tharandt-Anchor Station, Germany (Grunwald 2003), Castelporziano, Italy (Valentini et al. 2000, Reichstein et al. 2003), Flakaliden, Sweden (Lindroth et al. 1998), and Norunda, Sweden (Lindroth et al. 1998) since 1996 (http://www.fluxnet.ornl.gov/fluxnet/viewstatus.cfm).

Many of these EC studies have focused on the role of climate variability on interannual $F_{\text{NEE}}$ although capturing the true range of flux response to climate anomalies has often been hampered by concurrent biological changes or disturbances in the ecosystem or by the lack of strong climate fluctuations during the measurement record. For example, year-to-year changes
in $F_{\text{NEE}}$ at some forests appear to be partially linked to structural changes (Urbanski et al. 2007) or to variations in biotic responses (Richardson et al. 2007) in addition to changes in climate. Forest stand properties such as biomass growth, successional changes, or increases in mortality may change over relatively short time scales after a natural disturbance or from altered management practices. These factors make it difficult to isolate the effects of climate variability on $F_{\text{NEE}}$ at many sites. For example, year-to-year changes in annual $F_{\text{NEE}}$ at a ~100 year old mixed deciduous forest were uncorrelated to environmental drivers, and instead, linked to increases in tree biomass, successional changes in forest species composition, and disturbance, while short term (from hours to months) CO$_2$ flux perturbations appeared to be caused by the changing environment (e.g., warmer temperatures or increased light levels) (Urbanski et al. 2007).

EC measurements are regularly taken over stands of managed, even-aged forests of less than 100 years old (e.g., Arain & Restrepo-Coupe 2005, Markkanen et al. 2001, Morgenstern et al. 2004) while less is known about the seasonal dynamics and interannual variability of fluxes in a complex, old-growth forest ecosystem such as the one investigated here. Pacific Northwest old-growth Douglas-fir forests, including our site, have large, live old trees (175–350+ years old), tall canopy height (> 50 m), large snags, and large logs on the ground (Franklin et al. 1981; Franklin & Spies 1991). These old-growth stands once covered large parts of the Pacific Northwest before the onset of industrial timber operations. Today, they represent a small fraction of western North America: in Oregon and Washington about 10% (1.1 million hectares) of the original old-growth forests remain (Franklin & Spies 1991). While these old-growth forests are small in land coverage, they represent a significant pool of carbon that has been stored
for centuries in the soil, aboveground biomass, and woody debris that could be released into the atmosphere after a disturbance, such as clear-cut harvesting or one induced by climate change.

It had been assumed that mortality balances growth in old-growth forests making them carbon neutral (Odum, 1965, Franklin et al. 1981), although a number of EC (Hollinger et al. 1994, Anthoni et al. 2002, Griffis et al. 2003, Knohl et al. 2003, Loescher et al. 2003, Desai et al. 2005, Tan et al. 2011) and recent forest inventory (Hudiburg et al. 2009, Lichstein et al. 2009) studies in mature and old-growth stands are showing that the late seral class may in fact be a significant net sink of atmospheric CO$_2$. From studying a combination of EC fluxes, biometric, and modeled data, Luyssaert et al. (2008) suggest that forests older than 200 years old sequester on average 240 ± 80 g C m$^{-2}$ yr$^{-1}$, with half of that amount stored belowground in the roots and soil organic matter. Furthermore, old-growth forests may have the potential to sequester carbon at higher rates (> 300 g C m$^{-2}$ yr$^{-1}$) similar to younger forests if climatic conditions are favorable.

This behavior has been observed at La Selva, an old-growth forest in Costa Rica. During relatively wet and cool dry seasons in La Niña years the tropical forest sequestered 310-792 g C m$^{-2}$ yr$^{-1}$ (Loescher et al. 2003).

Biometric measurements from old-growth trees have also shown climate-related variability. Tree ring measurements taken from a Manitoba, Canada old-growth spruce forest indicated a periodicity of approximately 7 years and suggest a link between tree growth and oscillating environmental factors while variation in ring width could not be linked directly to annual changes in temperature and precipitation (Rocha et al. 2006). Such multi-year measurements from Loescher et al. and Rocha et al. illustrate the significance of weather anomalies associated with climate periodicities (i.e., teleconnection patterns). In the western Americas, climate is influenced by major Pacific ocean-atmospheric oscillations. These include...
the 40-50 day Madden and Julian Oscillation (Madden & Julian 1971), 2-7 year El Nino-Southern Oscillation (Rasmusson & Wallace 1983), 10 year Pacific/North American Oscillation (Wallace & Gutzler 1981), and 20-30 year Pacific Decadal Oscillation (Mantua & Hare 2002).

Here, we present a decade (1998-2008) of carbon dioxide, water and energy fluxes from a low elevation, old-growth forest with no recent major disturbances, biomass, or structural changes that has been exposed to a wide spectrum of climate variability including recent phase shifts of the PDO, ENSO and PNA. In addition, biometric data provided an independent, long-term (1947-2004) measurement record of growth, recruitment, and mortality responses to a longer range of climatic conditions including the 1977 major PDO phase change. Our objectives were to: (1) test the traditional ecological hypothesis that an old-growth forest is an insignificant net annual carbon sink and is carbon neutral, (2) investigate the response of old-growth carbon exchange to changing environmental and climatic factors across seasonal, annual and decadal time scales by utilizing eddy covariance and biometric forest inventory data, and (3) identify the mechanistic drivers of interannual CO$_2$ flux variability.

1.2 Site Description

The Wind River Field Station (formerly the Wind River Canopy Crane Research Facility) is located in a 500-hectare old-growth, evergreen needleleaf forest in the T.T. Munger Research Natural Area (RNA), a protected section of the Gifford Pinchot National Forest in southern Washington State, USA (45° 49' 13.76'' N; 121° 57' 06.88'' W, 371 m above sea level). The stand has never been managed and is thought to have originated after a natural fire around the year 1500. Stand characteristics are briefly given here while Shaw et al. (2004) provide a detailed ecological description. Unique stand properties include large standing biomass and
large amounts of coarse woody debris on the forest floor. Total estimated biomass is 619 Mg C ha\(^{-1}\), of which 398 Mg C ha\(^{-1}\) is stored in live biomass and 221 Mg C ha\(^{-1}\) in soil and coarse and fine woody debris (Harmon et al. 2004). Maximum rooting depth is 1-2 m for the tallest, dominant Douglas-fir trees although most of the root biomass is concentrated in the first 0.5 m. The water table depth is seasonally variable and ranges from 0.3 to 0.5 m in the wet winter months to a depth of 2.0-2.4 m in the summer and early autumn.

The old-growth forest is dominated by evergreen conifer species. Douglas-fir (\textit{Pseudotsuga menziesii} (Mirbel) Franco) represent the largest trees in diameter and height, while western hemlock (\textit{Tsuga heterophylla} (Raf.) Sarg), a shade-tolerant species, will eventually outnumber all other species in the stand. Average tree heights are 52 m for Douglas-fir and 19 m for western hemlock (Ishii et al. 2000). Deciduous vegetation is not a significant component of stand biomass comprising no more than 15% of canopy structure during the summer months (Thomas & Winner 2000). Stand density is approximately 427 trees per hectare, tree ages range from 0 to ~500 years (Shaw et al. 2004), and leaf area index (LAI) measurements range from 8.2 to 9.2 m\(^2\) m\(^{-2}\) with little seasonality (Thomas & Winner 2000, Roberts et al. 2004, Parker et al. 2002).

1.3 Climate

The climate is characterized by wet and mild winters interspersed with a strong, seasonal summer drought (Shaw et al. 2004, Falk et al. 2005). Meteorological records are available from the nearby USFS Wind River Ranger Station (1919-1977) (45º 28' 47" N, 121º 33' 36" W, 351.1 m a.s.l) and Carson Fish Hatchery NOAA weather station (1977-2008) (45º 31' 12" N, 121º 34' 48" W, 345.6 m a.s.l). Historical mean annual air temperature is 8.8 °C and total water-year
precipitation is 2338 mm, of which on average only 322 mm falls from July through October. Due to strong seasonality, total precipitation is defined here by water-year (November-October) instead of annually (January-December).

Regional interannual and decadal climate variability is driven by the presence and magnitude of interrelated equatorial and extratropical ocean-atmospheric oscillations, including the Pacific Decadal Oscillation (PDO), Pacific/North American Oscillation (PNA), and El Niño-Southern Oscillation (ENSO) (Mote et al. 2003). Positive phases of the PDO index, PNA index, and Multivariate ENSO index (MEI) bring significantly warmer and drier winters to Wind River while negative phases bring cooler and wetter conditions (Wharton et al. 2009). To take advantage of in-phase additive teleconnection patterns, a single climate index, the Composite Climate Index (CCI), was developed by Wharton et al. (2009). In brief, CCI is calculated from the sum of autumn-winter-spring PDO, PNA, and MEI magnitudes. Years with CCI values below -1.0 are classified as negative or cool phase years, years with CCI values above +1.0 are positive or warm phase years, and years with CCI values between -1.0 and +1.0 are neutral phase years. The CCI intrinsically contains information about cloudiness, temperature, vapor pressure deficit, light levels, and moisture as the Pacific Oscillation Indices are calculated from large-scale perturbations in atmospheric pressure (PNA and MEI), sea surface temperature (PDO and MEI), surface wind (MEI), air temperature (MEI), and cloudiness (MEI).

2. Materials and Methods

2.1 Biometric data

The T.T. Munger RNA has 40 ha of permanent plots in nine parallel belt transects. These plots were established in 1947 and are remeasured approximately every six years to gather data
on tree recruitment, growth, and mortality. The last remeasurement was done in 2004. Average Aboveground Net Primary Productivity ($F_{ANPP}$) ($\text{g C m}^{-2} \text{y}^{-1}$) was calculated as the mean change in live tree carbon storage plus tree mortality and recruitment over the remeasurement interval following methods in Harmon et al. (2004). In contrast to the eddy flux measurements, $F_{ANPP}$ does not include heterotrophic respiration fluxes, belowground autotrophic respiration, or belowground carbon storage (e.g., changes in root biomass).

2.2 Micrometeorological data

Site specific micrometeorological measurements were collected as 30-minute averages from July 1998 through December 2008 at the Wind River AmeriFlux tower. Radiation measurements included above canopy (70m) incoming photosynthetic photon flux density ($Q_p$) ($\mu\text{mol quantum m}^{-2} \text{s}^{-1}$) (190SB, LI-COR, Lincoln, Nebraska, USA) and below canopy (2m) $Q_p$. Air temperature ($T_a$) (°C) and relative humidity (RH) (%) (HMP-35C, Vaisala, Inc., Oy, Finland) were measured at 2 m and 70 m. Soil temperature ($T_s$) (°C) was measured at depths of 0.05, 0.15 and 0.30 m (CS106B, Campbell Scientific Inc., Logan, Utah, USA).

Measurements of water availability included precipitation ($P$) (mm) and volumetric soil moisture ($\theta_v$) ($\text{m}^3 \text{m}^{-3}$). $\theta_v$ was measured at depths from 0.2 m to 2 m (4 replicates) using soil moisture probes (EnviroSMART, Sentek Sensor Technologies, Stepney, Australia). Precipitation was measured using a rain and snow gauge 5 km away at the Carson Fish Hatchery at a similar elevation as the site.

The Standardized Precipitation Index (SPI) was calculated to compare precipitation amounts during the flux years to the long-term meteorological record (1919-1997) following McKee et al. (1993). Positive SPI values indicate above normal precipitation while negative SPI
values indicate below normal. By definition, the SPI ranges from -3 (extremely dry) to +3 (extremely wet). A drought event is defined when the SPI is continuously negative at a value of -1 or less over the time scale of interest. We calculated two standard precipitation indices: a 6-month SPI to identify longer-term precipitation anomalies that may reflect anomalies in soil reservoir storage and a 3-month SPI to determine shorter drought features.

2.3 Ecosystem CO₂, H₂O, and energy fluxes

Half-hour fluxes of carbon dioxide (Fₐ) (μmol m⁻² s⁻¹), water vapor (F_H₂O) (mmol m⁻² s⁻¹), latent energy (λE) (W m⁻²), and sensible heat (H) (W m⁻²) were measured continuously with the EC method since July 1998 at the tower. The system consisted of a 3-dimensional sonic anemometer/thermometer (HS-100 until March 2009, GILL Instruments, Lymington, UK; CSAT3 after March 2009, Campbell Scientific Inc.) and a closed path infrared gas analyzer (IRGA) (LI-6262 until February 2006; LI-7000 after February 2006, LI-COR). The EC system is located above the canopy at a height of 68.4 meters above ground.

10 Hz wind data were rotated to align the streamwise velocity (u) with the mean wind direction and corrected for lateral momentum transfer (Schotanus et al. 1983), high frequency loss (Moore 1986, Leuning & Judd 1996), and sensor separation between the sonic anemometer and IRGA air inlet (Moore 1986, Massman & Lee 2002). Footprint modeling following Wilson & Swaters (1991) indicated that fetch was good in all directions during strongly convective atmospheric conditions, but inadequate under strongly stable conditions. For the remaining stability regimes, footprint homogeneity was sensitive to wind direction and source fluxes originating from northeast-to-southeast wind sectors were removed due to heterogeneous (age fragmented) land cover.
Following Falk et al. (2005, 2008), half-hour net ecosystem exchange fluxes ($F_{\text{NEE}}$) (μmol m$^{-2}$ s$^{-1}$) were calculated to include storage CO$_2$ fluxes ($F_s$) as well as the direct EC measurement ($F_c$):

$$F_{\text{NEE}} = F_c + F_s$$  \hspace{1cm} (1)

### 2.4 Data exclusion criteria for eddy fluxes

The CO$_2$ and H$_2$O fluxes were averaged over 30-minutes and flagged if the data met any one of the following criteria: (1) an incomplete half-hour, (2) instrument failure, (3) wind direction from 45-135 degrees, (4) major rain or snow, or (5) significant flux outliers (magnitudes above or below the 95% confidence interval). Flagged data were removed and gap-filled using techniques described in Section 2.6. Percentage of flagged data ranged from 14% in 2002 to 71% in 2005. High data losses in 1998 and 2005 were due to instrument failure. In addition, nighttime CO$_2$ fluxes were screened to ensure that they were measured during adequate turbulence conditions using the methodology described in Section 2.5. Nighttime turbulence screening resulted in an additional 55% (2006) to 77% (2003) of nocturnal data requiring correction.

### 2.5 Nighttime $F_c$ corrections and $F_{\text{Reco}}$

A stable atmosphere, which commonly occurs at night, causes the suppression of turbulence leading to laminar flow regimes, intermittent turbulence, or the presence of gravity waves. During these conditions, the theoretical assumptions of eddy-covariance are violated and measurements of mass and energy exchange are problematic. Nighttime CO$_2$ fluxes must be “corrected” in order to calculate defensible sums of annual $F_{\text{NEE}}$. We used the $u^*$
correction method to replace nighttime $F_c$ during periods of inadequate turbulence in combination with a respiration model based on air temperature and soil moisture. Half-hour, nighttime $F_c$ were included in the respiration model if all of the following criteria were met: (1) incoming shortwave radiation $< 1 \text{ W m}^{-2}$, (2) $u^* > 0.3 \text{ m s}^{-1}$ (called the $u^*$ critical threshold), (3) $F_c > -25 \mu\text{mol m}^{-2} \text{s}^{-1}$ or $F_c < 35 \mu\text{mol m}^{-2} \text{s}^{-1}$ (negative fluxes were kept so not to artificially bias the dataset towards positive only values), and (4) $F_c$ flux was in the 95% confidence interval.

The half-hour carbon dioxide fluxes were then binned into 0.5 °C temperature classes and fitted with exponential temperature and moisture attenuation functions (see Falk et al. 2005, 2008 for further details).

2.6 Gap filling methods

We implemented two gap filling strategies, which vary in degrees of sophistication, to model half-hour $F_{\text{NEE}}$. Following the mean diurnal variation method described in Falge et al. (2001), our first gap filling method used a FORTRAN90 code with a fixed 14 day time window to fill any missing or flagged $F_{\text{NEE}}$ half-hours. This method is able to reproduce non-linearity ecosystem responses due to diurnal changes, but can also introduce errors during short-term gap filling periods when unusual weather conditions arise and the appropriate corresponding plant functional responses are not well represented by the mean diurnal fluxes.

Our second method, following Reichstein el al. (2005), used both a temporal auto-correlation of fluxes with a time window of ± 7 days and the covariance of fluxes with meteorological variables, i.e. “look-up” tables (http://gaia.agraria.unitus.it/database/eddyproc/). Instrument failure and subsequent large data gaps in 1998 and 2005 caused these years to be gap-
filled additionally with the process-based ecosystem model Biome-BGC (v4.1.2) (Thornton et al. 2002). Ecophysiological parameter values for Wind River were based on Thornton et al. (2002).

2.7 Daily, monthly, and annual $F_{\text{NEE}}$, $F_{\text{Reco}}$, and $F_{\text{GPP}}$

Partitioning $F_{\text{NEE}}$ into the larger component fluxes respiration ($F_{\text{Reco}}$) and photosynthesis (or gross primary production, $F_{\text{GPP}}$) is essential for understanding the drivers of seasonal and interannual $F_{\text{NEE}}$ variability (Baldocchi 2008). Daily integrated $F_{\text{NEE}}$ and $F_{\text{Reco}}$ were used to estimate $F_{\text{GPP}}$ (g C m$^{-2}$ day$^{-1}$):

$$F_{\text{GPP}} = F_{\text{NEE}} - F_{\text{Reco}}$$

(2)

$F_{\text{Reco}}$ and $F_{\text{GPP}}$ are always assigned positive values such that if $F_{\text{NEE}}$ is negative, carbon uptake by photosynthesis is greater than carbon loss by ecosystem respiration. Monthly and annual fluxes were calculated from daily sums.

We estimated uncertainty in annual $F_{\text{NEE}}$ using the bootstrapping technique with the Monte Carlo approach following methodology in Ma et al. (2007). Here, uncertainties in annual $F_{\text{NEE}}$ were based on the 95% confidence interval from running 5000 simulations of daily $F_{\text{NEE}}$.

2.8 Bulk canopy and efficiency parameters: $G_c$, WUE, LUE

Canopy conductance ($G_c$) (m s$^{-1}$), light use efficiency (LUE) (g C MJ$^{-1}$), and water use efficiency (WUE) (g C kg$^{-1}$ H$_2$O) were derived using a combination of micrometeorological and EC data to investigate mechanistic responses to weather and climate anomalies. Following Stewart (1988), $G_c$ was estimated using the inverted Penman-Monteith equation (Monteith 1964):
\[ G_c = \left[ \frac{\rho c_p \delta e}{\gamma \lambda E} + \frac{\Delta}{\gamma} \frac{\beta - 1}{G_a} \right]^{-1} \]

where \( \rho \) is air density (kg m\(^{-3}\)), \( c_p \) is specific heat (J kg\(^{-1}\) K\(^{-1}\)), \( \delta e \) is vapor pressure deficit (kPa), \( \gamma \) is the psychrometric constant (kPa K\(^{-1}\)), \( \Delta \) is slope of the saturation vapor pressure curve (kPa K\(^{-1}\)), \( \beta \) is Bowen ratio (\( \frac{H}{\lambda E} \)), and \( G_a \) is aerodynamic conductance for momentum transfer (\( G_a = \frac{u^2}{U} \)) (m s\(^{-1}\)).

LUE describes how efficient plants are at using light for carbon assimilation (Monteith 1972, 1977) and was calculated based on the mass of carbon assimilated (g C) for every megajoule (MJ) of light intercepted by the canopy (\( Q_{p,i} \)):

\[ LUE = \frac{F_{GPP}}{Q_{p,i}} \]

Where \( Q_{p,i} \) (MJ m\(^2\) day\(^{-1}\)) was calculated using above canopy \( Q_p \), LAI, and a varying light extinction coefficient (see Wharton et al. 2009). Because diffuse radiation measurements were not available, we were unable to identify any ecophysiological response differences to direct versus diffuse radiation. Instead, we categorized daily incoming \( Q_p \) data into dark and cloudy, cloudy, partly cloudy, and sunny periods based on a clear sky fraction (CSF):

\[ CSF = \frac{Q_p}{Q_{p,max}} \]
CSF by definition ranges from 0 (minimum brightness, cloudy sky) to 1 (maximum brightness, clear sky). The advantage of CSF is that it implicitly provides information about wavelength, intensity, and scattering of light as well as temperature, moisture, and vapor pressure deficit.

WUE is defined as the total mass of dry matter (g C) produced by photosynthesis for every kilogram of water lost by vegetation through transpiration (Rosenberg et al. 1983). Continuous measurements of transpiration (e.g., from sap-flow measurements) were not available. Therefore, WUE was modified to represent the total mass of carbon assimilated for every gram of water lost by the ecosystem through evapotranspiration ($E_T$):

$$WUE = \frac{F_{GPP}}{E_T} \quad (6)$$

3. Results

3.1 Climate variability

3.1.1 Seasonal and annual trends

Climate seasonality is historically strong at Wind River: on average more than 60% of water-year precipitation falls between November-March, 25% between April-June, and less than 15% between July-October. The dry season usually begins in late June to early July and ends in late September to mid-October. During the flux period (1998-2008), conditions were generally warmer and drier than the historical (1919-1997) mean (8.8 °C, 2338 mm water-year$^{-1}$). From 1998-2008, mean annual air temperature was 9.0 °C and total water-year precipitation was 2142 mm.

Interannual and interseasonal climate variability was large during the flux period (Figure 1). Annual mean air temperature varied from 8.09 °C in 2008 to 9.75 °C in 1998. 1998, 2003,
and 2004 were more than 0.70 °C warmer than the historical average. In addition, these years were in the upper 90th percentile for mean minimum temperature. Total water-year precipitation varied by more than 1500 mm and ranged from 1334 mm in 2000-2001 to 2878 mm in 1998-1999. 2000-2001 had the lowest measurable precipitation since records began in 1919, while 1998-1999 was in the upper 20th percentile of historically wettest years. Below normal water-years were mostly due to dry March-June conditions although unusually dry winters were also observed in 2001 and 2005. Dry season (July-October) precipitation was below the historical mean (322 mm) during all flux years except 2004 (492 mm).

3.1.2 Influence of teleconnections

Negative CCI phase years included 1999, 2000, and 2008, positive CCI years included 1998, 2003, and 2005, and 2001, 2002, 2004, 2006, and 2007 were classified as neutral. Positive CCI years were on average warmer and drier than normal and include the strong El Niño event of 1998, moderate El Niños in 2003 and 2005, and warm, winter-time phases of the PDO and PNA. Negative CCI years were on average cooler and wetter and include in-phase La Niña, cool PDO and cool PNA events (Table 1 and Figure 1).

3.1.3 Standardized Precipitation Index and summer drought

Significant anomalies in the 6-month SPI occurred during the rainy season (November-April) in 1999 (moderately wet, SPI = +1.4), 2001 (extremely dry, - 2.9), 2005 (severely dry, -1.9) and growing season (March-August) in 2006 (moderately dry, - 1.3) and 2007 (extremely dry, - 2.5) (Figure 2). A long-term drought event lasted from November 2000-July 2001 and the 6-month SPI averaged -2.1. The 3-month SPI indicated significant precipitation anomalies in
June-August 1998 (moderately dry, -1.5), March-May 2001 (severely dry, -1.6), July-September 2002 (severely dry, -1.9a), July-September 2003 (extremely dry, -2.2), April-June 2007 (extremely dry, -2.5), as well as very wet conditions in June-August 2004 (+1.7). Short-term drought events occurred at the end of summer/early autumn in 2002, 2003 and 2006, and during early summer in 2007.

The average summer dry season resulted in very low soil moisture with values as low as 10-15% in the upper 20 cm of the soil in August and September before rains returned in early autumn. In 2002 and 2006, very dry near-surface $\theta_v (<15\%)$ conditions extended into October. The deeper soil layers, for comparison, were wetter throughout the dry season: the 50 cm soil layer (within reach of most of the coarse root biomass) was generally 10% wetter than the near-surface, while the 150 cm depth (within reach of the tallest, dominant Douglas-fir trees) was 15-20% wetter than near-surface conditions.

### 3.2 Seasonal patterns in $F_{\text{NEE}}, F_{\text{GPP}}, F_{\text{Reco}}$

Maximum monthly carbon uptake occurred in April in all years except for 2000, 2004 and 2005 (May) (Table 2) and averaged -71 g C m$^{-2}$ mo$^{-1}$. On average, net sink months included February through June while all other months were a small to moderate net carbon source (up to +22 g C m$^{-2}$ mo$^{-1}$ in July). $F_{\text{GPP}}$ on average peaked in May while $F_{\text{Reco}}$ showed a clear seasonal pattern with temperature and peaked in July. Average key seasonal carbon flux transitions at Wind River include:

1. The transition from winter with low light levels ($Q_p < 60$ MJ m$^{-2}$ mo$^{-1}$), saturated soil conditions ($\theta_v > 0.3$ m$^3$ m$^{-3}$), low air temperatures ($T_{\text{air}} < 5^\circ$C), and low vapor pressure deficit (maximum daily $\delta e < 0.3$ kPa) to spring with the highest rates of daily $F_{\text{NEE}}$ under cool ($5 < T_{\text{a}} < 15^\circ$C), wet ($\theta_v > 0.25$ m$^3$ m$^{-3}$), adequate light ($100 < Q_p < 200$ MJ m$^{-2}$ mo$^{-1}$).
\[ \text{and low-to-moderate } \delta_e (< 1.5 \text{ kPa}) \text{ conditions. Springtime conditions favor} \]

photosynthesis and the greatest difference between daily \( F_{\text{GPP}} \) (larger flux) and \( F_{\text{Reco}} \) (smaller flux) is observed in April-May.

(2) The end of the cool, rainy season in June and start of the warm, dry season with air temperatures above 15 °C, low soil moisture (\( \theta_v < 0.25 \text{ m}^3 \text{ m}^{-3} \)), high light levels (\( Q_p > 200 \text{ MJ m}^{-2} \text{ mo}^{-1} \)), and high vapor pressure deficit (maximum daily \( \delta_e > 1.5 \text{ kPa} \)). The old-growth forest transitions to a net carbon source due to reduced photosynthesis caused by low water availability (low precipitation, low \( \theta_v \)) and high water demand (high \( \delta_e \)) and enhanced respiration due to higher temperatures.

(3) The end of drought in September-October when rains return and maximum air temperatures drop below 15 °C, vapor pressure deficit decreases (\( \delta_e < 1 \text{ kPa} \)), soil moisture increases (\( \theta_v > 0.25 \text{ m}^3 \text{ m}^{-3} \)), and light levels moderate (\( Q_p < 150 \text{ MJ m}^{-2} \text{ mo}^{-1} \)). Water availability does not immediately bring high rates of \( F_{\text{GPP}} \) indicating that the ecosystem needs time to recover from summer drought stress and the forest ecosystem remains a net carbon source.

(4) The transition back to winter conditions.

These features are highlighted in Figure 3. The timing of transition #2 (i.e., shift from a continuous net daily carbon sink to a continuous net carbon source) had significant implications on whether the old-growth stand was an annual net sink or source of carbon. In the 11 years of data collection, the timing between the earliest and latest occurrence of maximum cumulative \( \text{CO}_2 \) uptake (i.e., most negative \( \Sigma F_{\text{NEE}} \)) varied by 72 days and occurred as early as May 21 (2003) and as late as August 1 (2006). The average occurrence of maximum cumulative net carbon uptake was June 24 (transition #2 in Figure 3) and coincided with the end of the average rainy season.
3.3 Interannual F\textsubscript{NEE}, F\textsubscript{GPP}, and F\textsubscript{Reco} variability

Average annual F\textsubscript{NEE} was -49 g C m\textsuperscript{-2} yr\textsuperscript{-1} ± 40 g C m\textsuperscript{-2} yr\textsuperscript{-1}, indicating that the forest was on average an annual net sink of carbon from 1998-2008. Interannual variability was high for annual F\textsubscript{NEE} (on the order of 300 g C m\textsuperscript{-2} yr\textsuperscript{-1}) and resulted from variability in the larger component fluxes F\textsubscript{GPP} and F\textsubscript{Reco} (Figure 4). Annual F\textsubscript{NEE} ranged from -217 (1999) to +100 (2003) g C m\textsuperscript{-2} yr\textsuperscript{-1}, F\textsubscript{GPP} from 1229 (2002) to 1635 (2003) g C m\textsuperscript{-2} yr\textsuperscript{-1}, and F\textsubscript{Reco} from 1122 (2002) to 1735 (2003) g C m\textsuperscript{-2} yr\textsuperscript{-1}. Years with greater than average F\textsubscript{Reco} included 1998, 2003, 2004, and 2006. Years with greater than average F\textsubscript{GPP} included 2003, 2004, and 2006. Significant net carbon sink years (F\textsubscript{NEE} > - 50 g C m\textsuperscript{-2} yr\textsuperscript{-1}) included 1999, 2002, 2006, 2007, and 2008. Strong sink years in 1999 and 2002 largely resulted from reduced respiration fluxes instead of increased F\textsubscript{GPP}. Significant net carbon source years (F\textsubscript{NEE} > + 50 g C m\textsuperscript{-2} yr\textsuperscript{-1}) included 1998 and 2003 and were driven by greater than normal respiration fluxes.

Annual anomalies in F\textsubscript{Reco} and F\textsubscript{GPP} were generally well correlated (R\textsuperscript{2} = 0.82, P < 0.001) and each year was usually associated with either having both below normal or both above normal component fluxes (slope = + 0.72). Highest net annual carbon uptake in 1999 was caused by attenuated respiration driven by cooler and wetter than normal temperatures in the spring and relatively cool conditions in the summer, while wetter than normal spring conditions did not lead to a substantial increase in F\textsubscript{GPP}. Moderate net annual carbon loss in 2003 was related to an increase in respiration rates driven by higher than normal temperatures in winter and spring and near-normal rainfall (i.e., there were no significant moisture limitations until the end of summer). Temperature anomalies in 2003 appeared to increase photosynthesis but at lower rates than respiration. Very low rates of F\textsubscript{Reco} and F\textsubscript{GPP} in 2002 were likely related to water stress during the summer, and possibly, from a delayed forest recovery after the very dry 2000-2001 year.
We found a significant ($P < 0.01$) relationship between annual $F_{\text{NEE}}$ and the Composite Climate Index as indicated in Figure 5. Strong positive (or warm) phases of the CCI ($> +1$) were linked to near-neutral (2005) or moderate CO$_2$ source years (1998, 2003) while strong negative (or cool) phases of the CCI ($< -1$) resulted in weak (2000), moderate (2008), and strong (1999) carbon sink years. From 1999-2003, the climate indices transitioned to a more positive state whilst annual carbon uptake at the old-growth forest declined on average and the stand was a significant source of CO$_2$ in 2003. Since 2006, the climate indices have transitioned back towards more negative phases and carbon uptake has increased over the last couple of years as compared to 2003–2005.

### 3.4 Interdecadal $F_{\text{NEP}}$ and $F_{\text{ANPP}}$ variability

To extend the EC flux record and examine the role of multi-decadal climate variability on stand carbon response, we present over 50 years of biometric, aboveground net primary productivity at Wind River and modeled net CO$_2$ fluxes in Figure 6. Modeled fluxes were calculated using the linear regression fit from Figure 5 which predicted annual CO$_2$ exchange based on the annual CCI. Modeled (1952-1997) and measured (1998-2008) carbon fluxes are presented here as net ecosystem production ($F_{\text{NEP}}$, where $+ F_{\text{NEP}} = - F_{\text{NEE}}$) so that positive $F_{\text{NEP}}$ represents a net carbon sink. This was done so that the carbon flux sign notation agreed with $F_{\text{ANPP}}$. In Figure 6 we also illustrate key exogenous factors on stand carbon dynamics: the 6-month SPI, a major Douglas-fir beetle infestation and tree kill in 1950-1951, a less severe but significant beetle outbreak and tree kill in 1971, a major shift of the PDO in 1977, and smaller, and less certain, PDO shifts in 1998 and 2003. From 1950-1977, the PDO was in a dominant negative phase. These decades were associated with a mean positive SPI value of $+ 0.45$ (i.e.,
wetter than normal conditions), and higher than average net carbon uptake (modeled mean $F_{\text{NEP}} = +101.6 \text{ g C m}^{-2} \text{ yr}^{-1}$) and aboveground net primary productivity (measured mean $F_{\text{ANPP}} = 288 \text{ g C m}^{-2} \text{ yr}^{-1}$) (Figure 6). In contrast, the dominant positive PDO phase from 1977-1998 led to drier than normal conditions (mean SPI = -0.20), and smaller net carbon uptake carbon fluxes ($F_{\text{NEP}} = +24.9 \text{ g C m}^{-2} \text{ yr}^{-1}$) and ANPP (mean measured $F_{\text{ANPP}} = 238 \text{ g C m}^{-2} \text{ yr}^{-1}$).

$F_{\text{ANPP}}$ was in part difficult to interpret because it included tree mortality as well as carbon assimilation for recruitment and growth. Maximum annual $F_{\text{ANPP}}$ during the 1949-1952 remeasurement was likely due to the beetle tree kill in 1950-1951 and associated increases in coarse woody debris. The second $F_{\text{ANPP}}$ peak in 1971 was also likely due to increased tree mortality and coarse woody debris from beetle infestation. Since no major disturbances have occurred since, the later remeasurement periods likely indicate increased growth and recruitment and reduced mortality during wetter than normal conditions, while decreased growth and recruitment occurred during drier conditions. The $F_{\text{ANPP}}$ trends are in rough agreement with the modeled and measured $F_{\text{NEP}}$ data (Figure 6).

3.5 Mechanistic drivers and efficiency parameters

In Figure 7, daily $F_{\text{NEE}}$, $F_{\text{GPP}}$, and $F_{\text{Reco}}$ were segregated by season, annual climate phase, and daily clear sky fraction to examine the effects of light conditions on ecosystem carbon exchange. In general, maximum (most negative) spring and summer $F_{\text{NEE}}$ occurred during cloudy or partly cloudy conditions while maximum winter net uptake occurred on sunny or partly cloudy days. Distinct CSF-flux differences were also observed by climate phase. Dark, cloudy spring days were on average net carbon sources (0.3 g C m$^{-2}$ day$^{-1}$) during positive CCI years but net carbon sinks (-1.0 g C m$^{-2}$ day$^{-1}$) in negative CCI years. Partly cloudy summer days
were net carbon sources (0.54 g C m$^{-2}$ day$^{-1}$) during positive CCI years but net carbon sinks (-0.23 g C m$^{-2}$ day$^{-1}$) during negative CCI years.

Sunny conditions led to higher average rates of both $F_{\text{GPP}} (\Delta = + 1.1 \text{ g C m}^{-2} \text{ day}^{-1})$ and $F_{\text{Reco}} (\Delta = + 1.6 \text{ g C m}^{-2} \text{ day}^{-1})$ during positive phase years as compared to sunny days in negative phase years. To tease out the mechanisms specifically controlling $F_{\text{GPP}}$, vapor pressure deficit, light use efficiency, and water use efficiency are plotted in Figure 8 as a function of CSF.

Canopy conductance responses to CSF are plotted in Figure 9. Figure 8a shows a systematic increase in springtime $\delta e$ as cloudiness decreases regardless of whether the year was in a positive, negative or neutral CCI phase, although positive CCI years had slightly lower (but insignificant) springtime $\delta e$ values during all light environments. During the summer, in contrast, positive CCI years experienced on average higher $\delta e$ ($\Delta = + 0.55 \text{ kPa}$) during partly cloudy and sunny days than during any other climate phase although no concurrent decrease in $F_{\text{GPP}}$ is apparent in Figure 7e. It appears that a high atmospheric water demand did not lead to a significant reduction in photosynthesis during 2003 and 2005 summers.

Light use efficiency, in contrast to $\delta e$, increased with increasing cloudiness. LUE on average peaked during dark and cloudy (1.66 g C MJ$^{-1}$) and cloudy days (1.29 g C MJ$^{-1}$) (Figure 8b and 8e) illustrating the higher efficiency of the needleleaf canopy to utilize diffuse radiation for photosynthesis. Springtime LUE was higher during positive phase years (Figure 8e) and coincided with lower than average vapor pressure deficit levels (Figure 8a). In the summer, minimal differences in LUE were observed between climate phase years (8e) and the largest decline in LUE occurred between cloudy and partly cloudy skies. Water use efficiency, in a similar manner, also increased with cloudiness (Figure 8c and 8f). Positive climate years were more water use efficient than either neutral or negative climate years during the dry season.
Canopy conductance responses to clear sky fraction were distinct in both the spring and summer. Figure 9 shows mean afternoon $G_c$ according to season and clear sky fraction (cloudy, partly cloudy, or sunny) for all flux measurement years. Maximum afternoon canopy conductance universally peaked during cloudy conditions ($\text{mean } G_c = 8.23 \text{ mm s}^{-1}$) and declined as sky brightness increased ($\text{mean } G_c = 3.80 \text{ mm s}^{-1}$ during sunny conditions). Summertime $G_c$ rates were slightly higher during cool phase years ($G_c = 5.75 \text{ mm s}^{-1}$) than during either positive ($G_c = 4.76 \text{ mm s}^{-1}$) or neutral ($G_c = 5.19 \text{ mm s}^{-1}$) phase years. Significant deviations in $G_c$ occurred in spring 1999 ($\Delta G_c = +1.33 \text{ mm s}^{-1}$), spring 2003 ($\Delta G_c = +1.93 \text{ mm s}^{-1}$), spring 2006 ($\Delta G_c = -1.29 \text{ mm s}^{-1}$), and summer 2000 ($\Delta G_c = +1.00 \text{ mm s}^{-1}$). The largest anomalies in $G_c$ were not correlated to precipitation-based drought (i.e., the 3-month SPI) although $G_c$ was less than normal during the summer droughts of 2002 and 2003. Declined $G_c$ rates in summer 2003 corresponded to higher than normal air temperatures and water vapor pressure deficits. $G_c$ rates were more sensitive to shorter-term weather anomalies (e.g., cloudiness, air temperature) associated with dominant climate phase than precipitation.

4. Discussion

4.1 Old-growth carbon dynamics across multiple temporal scales

As successional endpoints, old-growth forests are predicted to be near carbon neutral (Odum 1965). Early studies suggested that as forests age, photosynthesis decreases while respiration continues to increase (Kira & Shidei 1967). As such, it was hypothesized that any increase in net carbon uptake in old-growth stands implies a change to exogenous factors (e.g., climate, atmospheric $\text{CO}_2$ concentration) (Graumlich et al. 1989) as aboveground production in these ancient forests remains relatively constant after crown closure (Grier et al. 1981). Our
study sheds important insights into the magnitude and uncertainty of old-growth forests as net carbon sinks as we presented over a decade of CO₂ exchange measurements under a full range of climate conditions for a 500 year old forest with limited recent disturbance. This paper provides the longest, continuous record of old-growth eddy flux exchange to date. To extend the time series and look at multi-decadal climate variability on forest carbon response, we also presented over 50 years of biometric measurements of growth, recruitment and mortality and 50 years of modeled CO₂ flux exchange.

On average Wind River was a small annual net sink of carbon equaling $49 \pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 1998-2008 (the eddy covariance record) and an estimated net sink of $65 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 1952-1997 (the modeled CO₂ flux record). Our EC estimates are in agreement with the biometric estimates of Harmon et al. 2004 for Wind River ($F_{\text{NEP}} = +20 \pm 130 \text{ g C m}^{-2} \text{ yr}^{-1}$). Between 1952 and 1997 a significant climate event occurred: the PDO switched from a dominant negative phase to a dominant positive phase in mid-1977. The consequences of this phase shift lasted for decades and were captured by our modeled carbon exchange ($1952-1977 \text{ mean } F_{\text{NEE}} = -101 \text{ g C m}^{-2} \text{ yr}^{-1}$, 1977-1997 mean $F_{\text{NEE}} = -25 \text{ g C m}^{-2} \text{ yr}^{-1}$), $F_{\text{ANPP}}$ measurements ($1952-1977 \text{ mean } = 288 \text{ g C m}^{-2} \text{ yr}^{-1}$, 1977-1997 mean = 238 g C m⁻² yr⁻¹), local climatological records (1952-1977 mean SPI = +0.45, 1977-1997 mean SPI = -0.2), and Composite Climate Index (1952-1977 mean CCI = -1.12, 1977-1997 mean CCI = +1.03). Our SPI record agrees with findings by Mantua et al. (1997) and Mote et al. (2003) who showed that negative phases of the PDO bring wetter than normal conditions while positive phases bring drier conditions to the Pacific Northwest and by Wharton et al. (2009) who found a strong link between local Wind River climatology and the three dominant Pacific Ocean oscillations. Our results strongly...
suggest that Wind River is a stronger net carbon sink during negative climate years, coinciding with wetter, cooler, and cloudier than normal conditions.

Low-elevation Douglas-fir stands in the western Cascade Mountains were once assumed to be relatively insensitive to climate when compared to subalpine species, but Case & Peterson 2005 suggest that radial growth in low elevation Douglas-fir is limited by low summer precipitation and high summer temperatures linked to positive PDO and warm ENSO events. Furthermore, Graumlich et al. (1989) from tree ring analysis studied how variation in F_{ANPP} of old-growth Douglas-fir forests from 1880-1979 is related to long-term trends in temperature and precipitation. They found that F_{ANPP} was significantly correlated with summer temperatures at lower frequencies (> 6 years) and significantly correlated with annual precipitation at higher frequencies (< 3 years). Their results suggest that links between temperature and F_{ANPP} may be driven by longer climate phases such as the PDO while precipitation and F_{ANPP} may be driven by ENSO. Correlations between climate data and F_{ANPP} measurements at Wind River were difficult to interpret because high F_{ANPP} in 1951 and 1971 appeared to be linked to the immediate effects of beetle disturbance and associated increases in mortality and coarse woody debris. The decline in F_{ANPP} ~five years later in 1958 and 1977 suggests that negative impacts of insect infestation on stand carbon uptake were evident during these remeasurements. The timing of this lag between insect disturbance and decreased F_{ANPP} agrees with other forest inventory observations (e.g., Campbell et al. 2009, Pfeifer et al. 2010). Although it is common belief that beetle kill events are higher during drought conditions because of increased tree stress, at Wind River beetle kill events may be uncoupled from weather and instead are correlated with fungal pathogens which thrive during wet events (K. Bible, personal communication). This could
explain why we observed higher F_{ANPP} in 1952 and 1971; a multi-decadal period of wetter conditions during the dominant negative PDO.

Our study showed a strong link between the SPI and CCI, between the SPI and modeled F_{NEE}, and a less certain link between the SPI and measured F_{ANPP} from 1952-1997 which suggests that teleconnection-induced variability in precipitation is a strong driver of net ecosystem exchange at Wind River. Small PDO switches likely occurred in mid-1998 (from positive to negative) and again in mid-2002 (from negative to positive). The 1998 PDO shift corresponded with a simultaneous strong ENSO phase change from El Niño to La Niña (warm to cool) in 1998-1999. Less significant, in-phase switches of the PNA were also observed in 2002.

Coinciding with the 1998 PDO phase change, the old-growth forest was a strong carbon sink in 1999 (F_{NEE} = -217 g C m^{-2} yr^{-1}) as compared to the preceding carbon source year (F_{NEE} = +50 g C m^{-2} yr^{-1}). Carbon flux shifts were also observed between 2002 (F_{NEE} = -98 g C m^{-2} yr^{-1}) and 2003 (F_{NEE} = +100 g C m^{-2} yr^{-1}) corresponding to the negative to positive PDO shift.

El Niño-La Niña impacts on forest carbon exchange have been studied over a young-to-intermediate Douglas-fir stand (~60 years old) in coastal British Columbia (Morgenstern et al. 2004, Krishnan et al. 2009), a managed Ponderosa pine stand in the Sierra Nevada, California (Goldstein et al. 2000, Misson et al. 2005), and a mixed needleleaf forest in Howland, Maine (Zhang et al. 2011). In California, where El Niño brings cooler and wetter conditions than normal, maximum sink years occurred during El Niño events due to an increase in F_{GPP} from the wetter winter and spring months (Goldstein et al. 2000). In British Columbia, which has similar ENSO-related weather patterns as Wind River, Morgenstern et al. (2004) found that variance in annual F_{NEE} was linked to air temperature anomalies during the 1997–1999 period. During the
1997-1998 El Niño, they observed lower annual F$_{\text{NEE}}$ (i.e., reduced net carbon uptake) in 1998 than during the following La Niña in 1999, likely due to higher F$_{\text{Reco}}$ in 1998 than in 1999.

We noted a strong asymmetric pattern in peak F$_{\text{GPP}}$ and F$_{\text{Reco}}$ at Wind River. Maximum photosynthesis normally occurred in May while maximum ecosystem respiration occurred two months later in July-August. This 60-day lag between peak F$_{\text{GPP}}$ and F$_{\text{Reco}}$ is longer than observed in other mid-latitude and younger forests. For example, Krishnan et al. (2009) report less asymmetry in the 60 year old Douglas-fir stand in British Columbia and F$_{\text{GPP}}$ and F$_{\text{Reco}}$ both peaked between July and August. Our strong asymmetry in the component fluxes is likely an adaptive feature of old growth ecology and physiology to the strong seasonal climate whereby F$_{\text{GPP}}$ is optimized during the wetter, cloudier spring months and F$_{\text{Reco}}$ follows a close trend with temperature and peaks in the summer.

4.2 Mechanistic drivers of CO$_2$ flux variability

While trends in F$_{\text{NEE}}$, F$_{\text{GPP}}$, and R$_{\text{eco}}$ appear to be linked to longer-scale teleconnection patterns and perturbations in seasonal temperature and precipitation, the mechanisms which control fluxes are also sensitive to environmental drivers across shorter-term scales. Numerous studies have shown that tree canopy photosynthesis is more efficient under cloudy skies (e.g., Baldocchi 1997, Gu et al. 2002). Cloudy conditions are a common occurrence at Wind River except during mid-summer and early autumn when a Pacific high pressure cell dominants the region. We generally found higher rates of F$_{\text{GPP}}$ on cloudy or partly cloudy days, likely because of the associated changes in canopy light scattering, vapor pressure deficit, canopy temperature, and water availability on photosynthesis. Clouds had a negative effect on daily F$_{\text{Reco}}$ in late spring, summer, and early autumn as the intensity and scattering of light affects how much
radiation hits the ground surface. This alters soil temperature and surface moisture, both of
which affect rates of heterotrophic and belowground autotrophic respiration. Cloudiness also
alters canopy albedo and leaf and bole temperatures affecting autotrophic respiration rates in the
canopy. Clouds had the effect of increasing net carbon uptake at Wind River except during very
dark and cloudy conditions which led to light limitations and substantially lower $F_{GPP}$.

In the tallest Douglas-fir trees at Wind River, the hydrological path length between the
roots and upper canopy stomata is greater than 50 m. This distance results in a decline in whole-
plant hydraulic conductance with height regardless of soil moisture (Ryan et al. 2000) which is
most attenuated on days with higher vapor pressure deficit (Waring & Franklin 1979). Lower $G_c$
rates restrict gas exchange (i.e., decreasing rates of transpiration and carbon assimilation) while
increasing leaf temperature and autotrophic respiration rates which result in a decrease in net
$CO_2$ uptake through lower light and water use efficiencies and higher autotrophic respiration
rates. We found that WUE was lowest on sunny days regardless of climate phase. This agrees
with other findings that WUE is a plastic characteristic for Douglas-fir trees and increases with
increasing light availability (Winner et al. 2004) and is inversely proportional to $\delta e$ (Lindroth &
Cienciala 1996, Berbigier et al. 2001). LUE was also highest on cloudy days and suggests, in
lieu of diffuse radiation measurements, that the old-growth canopy is efficient at scattering
isotropic radiation.

We caution that a complete understanding of the mechanistic drivers of carbon exchange
is limited by the fact that most of the derived parameters used here ($G_c$, WUE, and LUE, and $\delta e$)
provide little insight into the drivers of ecosystem respiration and in particular, to the drivers of
heterotrophic versus autotrophic respiration. This is especially critical at Wind River
considering that total soil respiration scales from 67% to 79% of $F_{Reco}$ (Falk et al. 2005).
Ongoing δC\textsuperscript{13} research at Wind River may provide additional clues to the importance of climate variability on F\textsubscript{NEE} as estimates of ecosystem respiration and its components can be derived via isotopic signatures of the canopy boundary layer and background air (Keeling 1958).

5. Conclusions

The biometric and eddy covariance data presented here suggest that Wind River is not a strong continuous sink of carbon as other recent EC and forest inventory studies have found in mature and old-growth forest stands although on average it is a small net sink. This is in agreement with recent modeling for old-growth stands done by Turner et al. 2011 and by the biometric estimates at Wind River taken by Harmon et al. (2004). At Wind River the lack of strong significant carbon sink activity may be attributable to the large amount of coarse woody debris and subsequent large pool of potentially respiring carbon, and to restrictions on gas exchange inhibiting photosynthesis in the upper canopy when atmospheric water demand is high during the summer drought. We found that anomalies in annual F\textsubscript{NEE} and to a lesser extent F\textsubscript{ANPP} were linked to climate perturbations driven by Pacific teleconnection events. Considering that Pacific Northwest forests store more carbon per unit area than any other forest in North America (Turner et al. 1995) and many climate models predict greatest future warming in the Pacific Northwest to occur in the summer months with as much as a 20-40\% decrease in summer precipitation (Mote & Salathe 2010), our results suggest that any perturbations in climate towards a warmer, drier state, such as would occur during dominant positive climate phases, will have significant regional impacts on terrestrial carbon exchange and possibly global atmospheric CO\textsubscript{2} concentration as respiration may increase without subsequent, offset increases in carbon assimilation in these forests.
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Table 1: Mean annual and seasonal air temperature and precipitation associated with the composite climate index (CCI) during flux measurement years (1998-2009) as well as the historical (1919-1997) mean. Positive CCI years are generally warmer and drier than average while negative CCI years are cooler and wetter. Water-year is November-October, peak growing season is March-June, and dry season is July-October.

<table>
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<th>Neutral CCI years</th>
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Table 2: Timing of maximum monthly net ecosystem exchange, gross primary productivity, and ecosystem respiration in comparison to annual $F_{\text{NEE}}$ and CCI. Note that 1998 and 2005 were partially gap-filled using Biome-BGC because of high amounts of missing data.
Figure 1: Seasonal total precipitation (top panel) and mean air temperature (bottom panel) for each of the flux measurements years as well as the historical mean and annual Composite Climate Index (CCI) phase. Precipitation is based on the water-year. Important climate anomalies included: cold winters in 2001 and 2004, a warm winter in 2003, a cold spring 2008, a warm summer 2003, dry summers in 2002 and 2006, a wet summer 2004, a dry spring 2007, dry winters in 2001 and 2005, and a wet winter 1999.

Figure 2: Time series of (a) monthly CCI, (b) running 6-month SPI, (c) running 3-month SPI, and monthly precipitation for all flux years. The SPI is based on the 1919-2008 precipitation record. Gray panels show 3-month drought events in winter 2001, summer/autumn 2002, autumn 2003, winter 2005, and spring 2007. Positive CCI values are generally linked to drier than normal precipitation conditions and negative SPI while negative CCI values are generally linked to above normal precipitation and positive SPI.

Figure 3: Average (a) daily $F_{GPP}$ and $F_{Reco}$ and (b) cumulative daily $F_{NEE}$ and monthly mean $Q_p$ and $\delta_e$ during neutral climate years show a typical asymmetric pattern in the timing of peak $F_{GPP}$, $F_{Reco}$, and $F_{NEE}$. This asymmetry is likely driven by relatively high light levels in spring and low vapor pressure deficit which leads to peak rates of $F_{GPP}$ and moderate $F_{Reco}$, resulting in maximum net carbon uptake.
Figure 4: A decade of annual (a) $F_{\text{Reco}}$, (b) $F_{\text{GPP}}$, and (c) $F_{\text{NEE}}$ estimates at Wind River show high interannual variability. The old-growth forest has switched from a moderate net sink of carbon (1999) to a moderate net source (2003) coinciding with a climate phase shift from positive to negative. The dotted lines represent the long-term mean.

Figure 5: Annual $F_{\text{NEE}}$ (1998-2008) as a function of the CCI shows that net carbon sink years are generally associated with more negative (cool) climate phases while net carbon source years are associated with strongly positive (warm) climate phases. Data are fit with a linear regression line (Pearson’s r value = 0.78, P < 0.005, y-intercept = -57 g C m$^{-2}$ yr$^{-1}$).

Figure 6: Time series of (a) running 3-month SPI and (b) modeled $F_{\text{NEP}}$ (1952-1997) based on the CCI, measured EC $F_{\text{NEP}}$ (1998-2008), and measured biometric $F_{\text{ANPP}}$ (1952-2004). $F_{\text{NEP}} = -F_{\text{NEE}}$, so that positive $F_{\text{NEP}}$ represents a net carbon sink year. Arrows represent significant external events including a large Douglas-fir beetle tree kill in 1951, a smaller but significant beetle tree kill in 1971, a major PDO switch (cool to warm) in 1977, and less certain and smaller PDO switches in 1998 and 2003. The SPI data show wetter conditions (positive values) than average from 1952-1977, coinciding with higher net carbon uptake in the modeled $F_{\text{NEP}}$ series. As the climate state has become drier over the last 30 years it also appears that $F_{\text{ANPP}}$ has decreased following the SPI and modeled $F_{\text{NEP}}$ trend.

Figure 7: Mean daily $F_{\text{NEE}}$, $F_{\text{GPP}}$, and $F_{\text{Reco}}$ by season, climate phase and clear sky fraction (CSF). Maximum carbon uptake occurred on spring-time cloudy or partly cloudy days during negative
climate phase years. This was driven by a combination of higher rates of $F_{GPP}$ and attenuated $F_{Reco}$.

Figure 8: Seasonal mean daily maximum vapor pressure deficit, midday light use efficiency and midday water use efficiency as a function of CSF during negative, positive, and neutral phase years. Sunny days led to significantly higher $\delta e$, lower LUE, and slightly lower WUE during all light levels and seasons, while $\delta e$, WUE and LUE were generally lower during negative climate phases regardless of light conditions or season.

Figure 9: Mean afternoon canopy conductance rates ($G_c$) by CSF in (a) spring and (b) summer with the annual climate phase indicated. Dotted lines are the 1999-2008 mean, **** represent annual mean. Year to year as well as light-related differences are apparent and $G_c$ rates on average are lower than the long-term mean during drought events based on the 3-month SPI. The highest $G_c$ rates are observed in 1999 and 2003 in spring and in 2000 in summer and correspond to non-drought conditions.
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(a) March - May

(b) June - September

$G_c$ (mm s$^{-1}$)

Year

- cloudy
- partly cloudy
- sunny
- average
- 1999-2008 average
- drought