Interannual variability of the carbon balance of three different-aged Douglas-fir stands in the Pacific Northwest

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[1] The seasonal and interannual variability of gross ecosystem photosynthesis (P_g) and ecosystem respiration (R_e), and their relationships to environmental variables and stand characteristics were used to explain the variation of eddy-covariance-measured net ecosystem productivity (F_{NEP}) of three different-aged Douglas-fir stands located on the east coast of Vancouver Island in British Columbia, Canada. During the 9-year period, 1998–2006, which included a strong El Niño/La Niña event, the near-end-of-rotation stand (DF49, 57 years old in 2006) was a moderate carbon (C) sink for CO₂ with annual F_{NEP} ranging from 267 to 410 g C m⁻² yr⁻¹ (mean ± SD, 357 ± 51 g C m⁻² yr⁻¹). The pole/sapling stand (HDF88, 18 years old in 2006) was a weak C source (F_{NEP} = -64 ± 75 g C m⁻² yr⁻¹), and the recently harvested stand (HDF00, 6 years old in 2006) was a large C source (F_{NEP} = -515 ± 88 g C m⁻² yr⁻¹) during 2002–2006. Irrespective of stand age, all sites responded quite similarly to changes in environmental variables during each year. Daily total values of P_g and R_e were highest in July–August in all three stands, while daily F_{NEP} peaked during April–June at DF49, May–June at HDF88, and June–July at HDF00. Reductions in root-zone soil water content decreased both P_g and R_e especially during the dry period from May to September, and this effect was more pronounced in the younger stands. Evapotranspiration and dry-foliage surface conductance also decreased with decreasing root-zone soil water content whereas water use efficiency appeared to be conservative, especially at DF49. Increasing spring temperature had a positive effect on annual P_g and R_e but caused a slight decrease in annual F_{NEP} . During the summer to autumn transition period, increases in soil water content resulted in a greater increase in R_e than P_g causing a reduction in F_{NEP} . The interannual variation in the C balance was determined mainly by the interannual variation in R_e for the near-end-of-rotation stand and P_g for the two younger stands. The results indicate that regardless of the stand age, interannual variability in the C balance was mainly determined by year-to-year variability in spring temperature and water availability in late summer.

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1. Introduction

[2] Characterizing the effects of the interannual variability of climate on the carbon (C) balance of ecosystems is necessary for understanding the causes of the interannual variability of global CO₂ budget and also predicting

the consequences of projected climate change in response to increasing global temperature [Barford *et al.*, 2001; Intergovernmental Panel on Climate Change (IPCC), 2007]. Even though the northern high-latitude boreal and temperate forest biomes are known to be sinks for atmospheric CO₂ [Keeling *et al.*, 1996; Myneni *et al.*, 1997; Sellers *et al.*, 1997; Schimel *et al.*, 2001], ecophysiological factors can change an ecosystem from a C sink to a C source or vice versa [Goulden *et al.*, 1996; Lindroth *et al.*, 1998; Dunn *et al.*, 2007]. In addition to climatic variability, land use change, changes in age distribution and species composition, recovery and response time of a forest ecosystem from a past disturbance like fire, harvesting and insect defoliation can alter the magnitude of C gain or loss by an ecosystem over diurnal, seasonal, annual and longer timescales. This suggests that for accurately determining the contribution of forested ecosystems to the global C budget and also for

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assessing the impact of climate change and alternative land use at landscape and regional scales, adequate understanding of the processes that control net CO₂ exchange of different vegetation types over the course of stand development is required [Turner et al., 2000]. This information is also crucial to quantify and predict vegetation feedback on the climate system [Cramer et al., 2001; Heimann and Reichstein, 2008].

[3] The C balance at the ecosystem level (net ecosystem productivity, F_{NEP}) is the difference between gross ecosystem photosynthesis (P_g) and ecosystem respiration (R_e) and is typically almost an order of magnitude smaller than these nearly offsetting components. Assessing the factors controlling F_{NEP} from diurnal to interannual timescales is challenging because of the complexity of the processes controlling its components. Previous studies have reported that both P_g and R_e are highly sensitive to changes in solar irradiance, temperature, water availability and leaf area index (LAI) in temperate [Reichstein et al., 2002, 2007] and boreal [Barr et al., 2007; Krishnan et al., 2006, 2008] stands. There is an ongoing debate about which component largely controls the interannual variation in F_{NEP} for various ecosystems. Studies on southern boreal ecosystems, where the growing season is short, show that an increase in spring temperature causes an increase in annual F_{NEP} by causing earlier leaf emergence in deciduous forest and P_g to increase faster than R_e in coniferous forests [Black et al., 2000, 2005; Barr et al., 2002]. However, Valentini et al. [2000] reported that R_e was the main determinant of the variation in the C balance along a continental gradient in Europe. Studies have shown that the C balance of a forest varies dramatically during stand development by changing its status from a C source in the early stages of development to a C sink in the intermediate and mature stages, and can even maintain its status as a sink or turn into a C source as it ages [Schulze et al., 1999; Amiro et al., 2005; Chen et al., 2002; Clark et al., 2004; Bond-Lamberty et al., 2004; Humphreys et al., 2006; McMillan et al., 2008]. The above studies showed how stand age influences annual F_{NEP} ; however, the information on how climate causes interannual variation in ecosystem C exchange at different stages of development following disturbance is lacking. Long-term measurements are needed to quantify the interannual variability of C exchange at different ages of the stand, to relate these differences to environmental forcings, and to determine the presence of long-term trends. In this context, direct, long-term measurement of CO₂ fluxes using the eddy-covariance (EC) technique permits the assessment of the C exchange at different stages of development.

[4] In this paper, we examine the interannual variation in the C balance of three Pacific Northwest (PNW) Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) stands at different stages of development after harvesting. Coastal Douglas-fir occurs in a large geographical region (>20 million ha) in the PNW from central California to the midcoast of British Columbia (BC) [Hermann, 1985] and likely plays a significant role in the global C cycle. The forests of the PNW, which are often dominated by Douglas-fir, a commercially desirable timber species, store more C per unit area than any other forested area of North America [Turner et al., 1995] and with improved management are capable of storing more C than they do at present [Smithwick et al., 2002]. The climate in the PNW, which is characterized

by wet mild winters and warm and dry summers, contrasts strikingly with other temperate forest regions in eastern United States, eastern Asia and Europe as they have a more even distribution of precipitation during the year with no reduction during the growing season [Waring and Franklin, 1979]. El Niño–Southern Oscillation (ENSO) with a periodicity of 2–7 years [Rasmussen and Wallace, 1983] and Pacific decadal oscillations (PDO), primarily on decade-to-decade timescales, have been identified as key sources of interannual climate variations in the PNW. Warm phases of ENSO (El Niño) and PDO typically induce warmer and drier conditions in the PNW, while cool phases of ENSO (La Niña) and PDO bring cooler, wetter weather to the region [Rasmussen and Wallace, 1983; Case and Peterson, 2005]. In a recent analysis on trends in temperature and precipitation in the PNW, Mote et al. [1999] and Mote [2003] found that temperature and precipitation have increased more than their respective global averages and this is likely to continue with increased precipitation mostly occurring in winter. In this context, it is important to investigate the impact of climate variability on the C balance and how these ecosystems may respond to projected climate change.

[5] The study sites included a young plantation, a pole/sapling stand and a near-end-of-harvest-rotation stand (hereafter referred to as HDF00, HDF88 and DF49, respectively). Previous studies on this chronosequence have focused on the climatic sensitivity and uncertainty of the C balance [Morgenstern et al., 2004], soil and ecosystem respiration [Drewitt et al., 2002; Jassal et al., 2007, 2008a], and variability and controls of sensible heat, latent heat and CO₂ fluxes [Humphreys et al., 2003, 2005, 2006; Jassal et al., 2008b]. In this paper, we focus on the interannual variability in the C balance of the chronosequence. The main objectives of this paper are (1) to examine the seasonal and interannual variation in F_{NEP} , P_g and R_e of the three stands, (2) to determine the responses of P_g and R_e to environmental variables at different stages of stand development, and (3) to understand the processes controlling the interannual variability of F_{NEP} , P_g and R_e .

2. Materials and Methods

2.1. Study Sites

[6] The three stands are located between Buckley Bay and Campbell River within 13 km of Georgia Strait on the east coast of Vancouver Island, BC, Canada. The oldest stand (DF49) was planted with Douglas-fir seedlings in 1949 after the original stand was logged in 1937 and slash-burned in 1943. In 2004, it was composed of 80% Douglas-fir, 17% western red cedar (*Thuja plicata* Donn) and 3% western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) [Humphreys et al., 2006] and its leaf area index (LAI) was 7.3 [Chen et al., 2006]. DF49 is a 130-ha stand on a 5–10° NE facing slope located only 3 km NWN of the plantation (HDF00), which was clear-cut-harvested in the 1999/2000 winter and planted in the spring of 2000 with 1-year-old seedlings (93% Douglas-fir and 7% western red cedar). About 48 km SE of these two sites is the pole/sapling stand (HDF88) established in 1988. This stand was clear-cut in 1987, burned, planted in 1988 with 75% Douglas-fir, 25% western red cedar and 4% grand fir (*Abies grandis* var. *grandis*) and sprayed with herbicide to control competing brush in 1992.

Table 1. Sites Characteristics

	DF49	HDF88	HDF00
Location	49°52'7.8"N, 125°20'6.3"W	49°32'10.49"N, 124°54'7.18"W	49°52'1.08"N, 125°16'43.80"W
Elevation (m)	320	173	188
Slope (deg)	5–10 NE	2–5 SE	0–2
Stand height ^a (m)	34	7	0.8
Distance from coastline (km)	15.7	3.1	11.6
Stand density ^a (trees ha ⁻¹)	1150	1240	1500
Stand area (ha)	130	110	32
80% cumulative flux footprint area (annual average) ^b (ha)	93	17	8
Mean DBH (cm)	28.3	7.3	1.02 (at base)
Woody debris biomass ^c (kg m ⁻²)	0.7–10	3.4–16.5	0.5–2.2
Live aboveground biomass ^c (kg m ⁻²)	8.5–23.0	0.8–2.1	<0.1–0.4
Total aboveground biomass ^d (kg m ⁻²)	13.81	1.139	0.165
Total belowground biomass ^d (kg m ⁻²)	1.25	-	-
Tree cover type	77% Douglas-fir, 18% western red cedar, 4.6% western hemlock	75% Douglas-fir, 21% western red cedar, and 4% grand fir	97% Douglas-fir, 3% western red cedar
Understory	Vanilla leaf deerfoot, Oregon grape, mosses	Salal, Oregon grape, fireweed and bracken fern, huckleberry	Grasses, sword and bracken fern, herbs, woody shrubs: twinflower, honeysuckle rubrus spp., Oregon grape
Stand history	Clear-cut, slash burned, planted stock mixed with natural regeneration	Clear-cut, broadcast burned, planted	Clear-cut, planted
LAI ^{e,f} (m ² m ⁻²)	7.3	3.0–7.2	0.3–2.5
Soil classification	Humo-ferric podzol	Humo-ferric podzol	Humo-ferric podzol
Soil texture	Gravelly loamy sand	Gravelly loam	Gravelly loamy sand to sand
Soil organic layer (cm)	3	4.1	3.6
Flux measurement height (m)	42	12	2.5
u_* threshold (u_{*T}) (m s ⁻¹)	0.30	0.16	0.08
Mean annual temperature ^g (°C)	8.4	9.6	8.9
Mean annual rainfall ^g (mm)	1245	1546	1227

^aStand height and density is for live trees in 2002.

^bChen *et al.* [2009].

^cBoth woody debris and live biomasses are the sum of all aboveground tree components and understory vegetation [Humphreys *et al.*, 2006].

^dTotal aboveground biomass is the sum of tree wood, tree foliage, shrub, nonwoody biomass while total belowground biomass is the sum of fine root and coarse root biomass.

^eLAI at DF49 [Chen *et al.*, 2006].

^fSeasonal range of stand LAI values in 2002 at HDF88 and HDF00 [Humphreys *et al.*, 2006].

^gMean values during 1998–2006 for DF49 and 2002–2006 for HDF88 and HDF00, respectively.

The chronosequence is part of the seasonal dry variety of the temperate rain forest that covers much of North America's PNW in the coastal western hemlock (CWH) biogeoclimatic zone [Meidinger and Pojar, 1991]. Even though the three stands were located in very similar ecosystems and experienced similar weather, there were differences in elevation and soil characteristics between the sites. Key stand and soil attributes, and flux-footprint areas at each site are given in Table 1 and further details are provided elsewhere [Morgenstern *et al.*, 2004; Humphreys *et al.*, 2006; Chen *et al.*, 2009]. The prevailing wind directions at the sites were NE to E during daytime and SW to W during nighttime, and are attributed to the topography and land-sea circulation due to the sites' proximity to Georgia Strait.

2.2. Eddy-Covariance Flux Measurements

[7] Continuous, half-hourly turbulent fluxes of CO₂, water vapor (E) and sensible heat (H) were measured above the canopy using the EC technique [Morgenstern *et al.*, 2004; Humphreys *et al.*, 2005, 2006]. EC fluxes were measured at all sites above the canopy (Table 1) using a three-dimensional sonic anemometer-thermometer (Model R2 or R3, Gill Instruments, Lymington, UK) and a closed-path, temperature-controlled infrared gas (CO₂/H₂O) analyzer (IRGA) (model LI-6262, LI-COR Inc., Lincoln, NE, USA)

or open-path IRGA (HDF88 up to 2003, model LI-7500, LI-COR Inc.). Closed-path IRGA analog signals (CO₂ and H₂O mole fractions) were sampled at 125 Hz with a data acquisition system (Model DaqBook/200, Iotech Inc., Cleveland, OH, USA), digitally filtered and down sampled to 20.83 Hz and transferred every half-hour to a site computer for further flux calculations. Further details on the experimental setup, calibration and eddy flux calculations can be found in the works of Morgenstern *et al.* [2004] and Humphreys *et al.* [2006].

2.3. Supplementary Meteorological Measurements

[8] Meteorological variables continuously measured at all three sites included above-canopy downwelling and upwelling solar and longwave radiation (model CNR1, Kipp and Zonen B.V., Delft, The Netherlands), above-canopy downwelling and upwelling photosynthetically active radiation (PAR) (model 190SB, LI-COR Inc.), above- and within-canopy air temperature and relative humidity (model HMP35CF or HMP45CF, Vaisala Oyj, Helsinki, Finland), rainfall (two tipping-bucket rain gauges, model 2, Texas Electronics, Dallas, TX, USA or model 2501, Sierra Misco, Berkeley, CA, USA), soil temperature at the 2, 5, 10, 20 and 50 cm depths (with copper-constantan thermocouples), soil-heat flux (3 heat-flux plates, model F, Middleton

Instruments, Melbourne, Australia), volumetric soil water content at the depths of 1–2, 10–12, 35–48 and 70–100 cm (with reflectometers model CS-615, Campbell Scientific Inc. (CSI), Logan, UT, USA) at two locations. A precipitation gauge (model I-200B, Geonor A.S., Oslo, Norway) for measuring the liquid-water equivalent of snowfall was installed at HDF00 near the end of 2003.

2.4. Calculation of Annual Totals, Water Use Efficiency, and Surface Conductance

[9] The half-hourly turbulent fluxes were calculated using the covariance of the fluctuations in the vertical wind velocity and scalar quantities, namely, air temperature for sensible heat, molar mixing ratio of CO₂ for CO₂ flux and the molar mixing ratio of water vapor for water vapor flux. The net ecosystem exchange (F_{NEE}) of CO₂ was calculated by adding the turbulent flux of CO₂ to the time derivative of the air-column storage of CO₂ below the EC sensor level (i.e., the storage flux). In this analysis, the storage flux was calculated following *Morgenstern et al.* [2004] using the CO₂ mixing ratio measured at the EC sensor level. F_{NEE} provides a direct measure of F_{NEP} (i.e., $F_{NEP} = -F_{NEE}$). Positive values of F_{NEP} correspond to C gain by the ecosystem and negative values to C loss. *Humphreys et al.* [2006] found that average half-hour energy balance closure was 0.80, 0.90 and 0.91 for DF49, HDF88 and HDF00, respectively, for 2002; however, closure corrections were not applied in this analysis.

[10] A common procedure was applied to all sites to fill half-hour data gaps and to obtain annual estimates of F_{NEP} . This included filling gaps caused by missing data and created by removing nighttime fluxes when turbulence was not fully developed, i.e., friction velocity (u_*) was less than a threshold value (u_{*T}). Values of u_{*T} of 0.30, 0.16 and 0.08 m s⁻¹ were used for DF49, HDF88 and HDF00, respectively [see *Morgenstern et al.*, 2004; *Humphreys et al.*, 2006]. This procedure removed ~60–70% of the nighttime fluxes at each site. Small gaps (i.e., <2 h) in F_{NEP} were filled by linear interpolation. Measured R_e was obtained as $R_e = F_{NEE}$ during periods when P_g was known to be zero, i.e., during night in the growing season and during night and day in the winter when both air (T_a) and shallow soil (T_s) temperatures were less than 0°C. An exponential relationship between measured R_e and T_s at the 2-cm depth for each year was obtained as follows:

$$\ln R_e = A + BT_s \quad (1)$$

This logarithmic transformation of the data minimizes inhomogeneous scatter [*Morgenstern et al.*, 2004] and allows the assumption of normality and homoscedasticity to be valid for linear least squares regression [*Humphreys et al.*, 2005, 2006]. P_g was estimated as $F_{NEP} + \text{daytime } R_e$ (calculated using equation (1) with daytime T_s) and assumed to be zero at night and during periods when both T_a and $T_s < 0^\circ\text{C}$. Gaps in P_g were filled using the rectangular hyperbolic dependence of P_g on PAR (Q) (Michaelis-Menten light-response equation) given by

$$P_g = \frac{\alpha Q P_x}{\alpha Q + P_x} \quad (2)$$

where α is the quantum yield and P_x is the photosynthetic capacity (P_g at light saturation). To account for short-term changes in environmental conditions, a time-varying parameter was determined within a 100-point moving window as the slope of a linear regression, forced through the origin, of the modeled P_g (and R_e) versus measured P_g (and R_e) and was applied as a multiplier to the above relationships [*Barr et al.*, 2004]. Gaps in $F_{NEP} > 2$ h were filled using modeled $P_g - R_e$. Gap-filled values of F_{NEP} , R_e for both nighttime and daytime, and P_g were used to calculate annual totals of F_{NEP} , R_e , and P_g . As mentioned above, the u_{*T} criteria removed 60–70% of the nighttime and hence 30–40% of the total flux data while the original data (before applying u_{*T}) loss was <10% when using the closed-path IRGA and 20–30% when using the open-path IRGA (at HDF88). Uncertainties in annual F_{NEP} associated with the random error in half-hourly fluxes and the gap-filling procedure were obtained by resampling half-hourly fluxes after introducing a 20% random error and also by using Monte Carlo simulation [*Griffis et al.*, 2003; *Morgenstern et al.*, 2004; *Krishnan et al.*, 2006, 2008] by artificially generating gaps (up to 40% of the total half hours in a year, with continuous gaps varying from a half hour to 10 days) using a uniformly distributed random-number generator. This procedure was repeated 1000 times and the 95% confidence levels in the annual estimates of F_{NEP} , P_g and R_e were calculated.

[11] To better understand the physiological response of the ecosystem to changes in soil water content, canopy-level water use efficiency and dry-foliage surface conductance were used. Water use efficiency (WUE), an important indicator of ecosystem function, adaptation and productivity of plants in water-limited areas [*Xu and Hsiao*, 2004], was calculated as the ratio of daily daytime ($Q > 200 \mu\text{mol m}^{-2} \text{s}^{-1}$) average P_g to average evapotranspiration (E), i.e., $\text{WUE} = P_g/E$. The surface conductance to water vapor transfer (g_s) was calculated by rearranging the Penman–Monteith equation [*Monteith and Unsworth*, 1990] as given by *Krishnan et al.* [2006]. The daytime mean value of dry-foliage g_s was calculated by averaging daytime g_s values for $Q > 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ for those days without precipitation.

3. Results

3.1. Seasonal and Interannual Variations in Environmental Variables

[12] Figure 1, which shows the annual cycles of monthly total Q , rainfall (R) and monthly mean above-canopy air temperature (T_a), soil temperature at the 2-cm depth (T_s), daytime ($Q > 0$) atmospheric saturation deficit (D), average soil water content in the 0–30 cm layer (θ) for 2002–2005, indicates that the three sites experienced similar weather with cool and wet winters and dry and warm summers. Q generally peaked during June and July with slightly higher values at HDF88. The variations in T_s and D closely followed those in T_a , all being highest in July and August with the highest values occurring at HDF00 as expected being a recently clear-cut site. However, winters were slightly warmer at HDF88 than at the other two sites. More than 75% of the annual rainfall occurred between October and March leading to high θ during these months. The low rainfall rates during May to September resulted in dry

Figure 1. Average monthly values of (a) total downwelling PAR (Q), (b) mean above-canopy air temperature (T_a), (c) mean soil temperature at the 2-cm depth (T_s), (d) mean daytime ($Q > 0$) above-canopy atmospheric saturation deficit (D), (e) total rainfall (mm), and (f) mean soil water content (θ) in the 0–30 cm layer for 2002–2006 at DF49, HDF88, and HDF00. The dotted curve represents the 1971–2000 precipitation (snowfall plus rainfall) normals for Campbell River Airport, elevation 105 m, 10 km NE of DF49. Average monthly snowfall totals (mm liquid-water equivalent) for 2002–2006 were January, 24.3; February, 8.6; March, 27.7; April, 1.0; November, 22.1; December, 19.7.

growing seasons with the lowest θ values occurring during July to September and August being the driest month at all three sites. R at HDF88 was higher than other sites especially during winter–spring months, but not during growing season. However, θ at HDF88 was generally higher than at the other two sites due to finer textured soil (Table 1).

[13] Interannual variations in annual total Q (Q_{Annual}), annual mean above-canopy air temperature (T_{Annual}), spring (March to May) mean above-canopy air temperature (T_{Spring}), annual total rainfall (R_{Annual}) and total May–September rainfall ($R_{\text{May–Sept}}$) at DF49, HDF88 and HDF00 are shown in Figure 2. All three sites showed similar interannual variation with HDF88 being somewhat warmer. Based on climate data from the Environment Canada meteorological station at the Campbell River Airport (49° 57'N, 125° 16.2' W, elevation 105 m), 10 km NE of DF49, the 1971–2000 mean annual temperature was 8.4°C and the mean R_{Annual} was 1452 mm (snowfall 109 mm liquid-water equivalent). ENSO has been identified as a key source of interannual climatic variations for the PNW and has a periodicity of 2–7 years [Rasmussen and Wallace, 1983] whereas PDO fluctuations influence climate on a decadal scale. In the PNW, El Niño events typically occur from October through March or April, and induce mild winters followed by unusually warm springs and dry summers, while La Niña years are generally characterized by wet winters and relatively cool and cloudy conditions in the following spring and summer [Shabbar *et al.*, 1997; Shabbar and Khandekar, 1996]. During the study period from 1998 to 2006, El Niño events occurred in the winters of 1997–1998 (strong), 2002–2003 (medium) and 2006–2007 (weak) while La Niña events occurred during the winters of 1998–1999 (moderate) and 1999–2000 (strong)

(http://www.msc-smc.ec.gc.ca/education/el_nino/comparing/enso1950_2002_e.html).

[14] The impact of El Niño and La Niña events were pronounced in 1998 and 1999 as evident from temperature and $R_{\text{May–Sept}}$. The highest T_{Annual} (9.1°C) and second highest spring, summer and autumn temperatures at DF49 occurred in 1998 with dry summer periods as a result of below-normal $R_{\text{May–Sept}}$. The highest R_{Annual} occurred in 1998. The coldest spring and summer temperatures of the measurement period occurred in 1999 following the La Niña event in the previous winter (1998–1999). The 1999–2000 La Niña event did not significantly influenced temperatures and precipitation at the study sites and 2000 was a normal year in terms of T_{Spring} and $R_{\text{May–Sept}}$. So was the case with 2001. 2002 experienced the second coldest spring, which resulted from two weeks of cold weather in March. A moderate El Niño event in 2002–2003 had no impact on T_{Spring} but $R_{\text{May–Sept}}$ was below normal. Of the other neutral years, 2004 and 2005 had warm springs and wetter than normal May–September periods. Summer and April–June temperatures (not shown) at DF49 were highest in 2004, even higher than that in 1998. Even though 2005 was the year with highest T_{Spring} (8.7°C), annually, it was a cool year with the third (to 1999 and 2001) coolest summer (June–August) and the lowest Q of the 9 growing seasons. Figure 2 also suggests an increase in T_{Annual} during the study period excluding 1998, the strong El Niño year. All three sites, especially HDF00, had low $R_{\text{May–Sept}}$ in 2003, a relatively warm year following the moderate El Niño event in 2002. Even though, 2005 had slightly higher $R_{\text{May–Sept}}$, Q_{Annual} and T_{Annual} were lower than those in 2004. 2006 had a normal T_{Spring} with a below-normal $R_{\text{May–Sept}}$, especially at HDF00. Even though annual rainfall was slightly higher at

Figure 2. Interannual variations in (a) annual total of PAR (Q_{Annual}), (b) annual mean above-canopy temperature (T_{Annual}), (c) spring (March–May) mean above-canopy air temperature (T_{spring}), (d) annual total rainfall (R_{Annual}), and (e) May–September total rainfall ($R_{\text{May–Sept}}$) at DF49, HDF88, and HDF00. The dotted lines represent 1971–2000 climate normals for Campbell River Airport, elevation 105 m, 10 km NE of DF49. At the airport, annual rainfall was 89–97% of annual precipitation for 1998–2006. Snowfall (liquid-water equivalent) at HDF00 (measured using the Geonor precipitation gauge) and at the airport in 2004 were 43 and 86 mm and in 2005 were 63 and 52 mm, respectively.

HDF88 during most of the years, $R_{\text{May–Sept}}$ was quite similar in magnitude to values for the other two sites. The results suggest that the main interannual variations in climate at these sites result from variation in T_{Spring} and summer rainfall rather than annual means of the environmental variables.

3.2. Interannual Variation in Annual C Fluxes

3.2.1. Annual C Fluxes

[15] The patterns of the interannual variation of F_{NEP} at the three sites were similar during 2002–2006. This was also true for P_g and R_e (Figure 3). DF49 was a moderate C sink (mean $\pm$ SD = 328 ± 52 g C m⁻² yr⁻¹ during 2002–2006 and 357 ± 51 during 1998–2006) while HDF88 and HDF00, during 2002–2006, were a weak C source (-64 ± 75 g C m⁻² yr⁻¹) and a large C source (-515 ± 88 g C m⁻² yr⁻¹), respectively. The interannual variation of R_e at DF49 (1830 ± 173 during 2002–2006 and 1767 ± 147 g C m⁻² yr⁻¹ during 1998–2006) was greater than that of P_g (2158 ± 163 during 2002–2006 and 2124 ± 125 g C m⁻² yr⁻¹ during 1998–2006). For HDF88 and HDF00 during 2002–2006, the interannual variation of P_g (1423 ± 193 and 781 ± 226 g C m⁻² yr⁻¹, respectively) was greater than that in R_e (1487 ± 147 and 1297 ± 185 g C m⁻² yr⁻¹, respectively), while P_g for HDF88 was 642 g C m⁻² yr⁻¹ greater than that for HDF00 and R_e was only 190 g C m⁻² yr⁻¹ greater (Table 2). HDF88 changed from a weak C source (-105 ± 10 g C m⁻² yr⁻¹) during 2002–2004 to a weak sink (21 ± 30 g C m⁻² yr⁻¹) during 2005–2006. As shown in Table 2, intersite differences were greater than interannual variation showing the dominating role of stand age [Humphreys et al., 2006] in determining the magnitude of F_{NEP} . Regardless of stand age,

Figure 3. Interannual variation in annual (a) net ecosystem productivity (F_{NEP}), (b) gross ecosystem photosynthesis (P_g), and (c) ecosystem respiration (R_e) at the three sites. The inset in each plot shows relationships of the F_{NEP} , P_g , and R_e to stand age. Uncertainty in annual F_{NEP} (see section 2.4) were ± 44 , ± 22 , and ± 24 g C m⁻² yr⁻¹ during 1998–2006 at DF49 and 2002–2006 at HDF88 and HDF00, respectively.

Table 2. Interannual and Intersite Variation of F_{NEP} , P_g , and R_e During 2002–2006

	Variable (g C m ⁻² yr ⁻¹)	Mean ± SD (g C m ⁻² yr ⁻¹)	Range (g C m ⁻² yr ⁻¹)	CV ^a
<i>Interannual Variation^b</i>				
Site				
DF49	F_{NEP}	328 ± 52	119	0.16
	P_g	2158 ± 163	386	0.08
	R_e	1830 ± 173	396	0.09
HDF88	F_{NEP}	-64 ± 75	153	1.18
	P_g	1423 ± 193	489	0.14
	R_e	1487 ± 148	368	0.10
HDF00	F_{NEP}	-516 ± 88	175	0.17
	P_g	781 ± 226	583	0.29
	R_e	1297 ± 185	435	0.14
<i>Intersite Variation</i>				
Year				
2002	F_{NEP}	-136 ± 421	842	3.09
2003		-109 ± 467	933	4.29
2004		-153 ± 430	860	2.82
2005		-15 ± 389	777	25.57
2006		-6 ± 402	804	68.18
2002	P_g	1250 ± 713	1425	0.57
2003		1302 ± 733	1456	0.56
2004		1551 ± 744	1479	0.48
2005		1705 ± 600	1199	0.35
2006		1462 ± 665	1329	0.45
2002	R_e	1389 ± 289	577	0.21
2003		1411 ± 277	523	0.19
2004		1704 ± 325	619	0.19
2005		1721 ± 215	422	0.13
2006		1468 ± 262	523	0.17

^aCoefficient of variation (CV) is calculated as the ratio of standard deviation (SD) to the mean.

^bAt DF49 1998–2006 mean ± SD, values of range and CV, were 357 ± 51, 143, and 0.14 for F_{NEP} , 2124 ± 125, 386, and 0.06 for P_g , and 1767 ± 146, 429, and 0.08 for R_e , respectively.

the general pattern of interannual variations in F_{NEP} , P_g and R_e were roughly similar suggesting similar responses to environmental variables with few exceptions due to stand age.

[16] In 1998, the warmest year of the record (Figure 2) with a warm spring and dry growing season, both P_g and R_e at DF49 were higher than for all years except for 2004 and 2005 (Figure 3). In 2002, the lowest P_g of the record, mainly due to the cold period in March, led to the second lowest value of annual F_{NEP} at DF49. The lowest F_{NEP} values at all three sites were recorded in 2004, the second warmest year for DF49 and the warmest year for HDF88 and HDF00 with a wet and warm growing season. At DF49, R_e and P_g in 2004 were higher than their 9-year mean by 17% and 10%, respectively, and were the highest of the record, while F_{NEP} was lower than its 9-year mean by 32%. 2005 had the second highest P_g and R_e of the record. At HDF88 and HDF00, P_g , R_e and F_{NEP} were highest in 2005. In 2006, a cool year with a dry growing season, R_e was suppressed more than P_g resulting in the third highest F_{NEP} of the record at DF49 and the second highest F_{NEP} at HDF88 and HDF00. F_{NEP} at DF49 was highest during the normal years, 2000 and 2001 (400 and 410 g C m⁻² yr⁻¹, respectively).

3.2.2. Climatic Controls of Interannual Variability of Annual C Fluxes

[17] To obtain better insight into the factors controlling the interannual variability of C fluxes, a linear regression

analysis of the relationship between C balance components and environmental variables was carried out on monthly and seasonal scales (Tables 3 and 4). The monthly regression analysis suggests that temperature had a positive effect on P_g and R_e at DF49 until July whereas it had a negative effect on F_{NEP} from May onward. In the latter part of the year, the negative impact of temperature on F_{NEP} was due to the relatively greater increase in R_e than in P_g with increasing temperature at all three sites. The impact of θ on F_{NEP} , P_g and R_e at all sites was most pronounced in August. The interannual variation of seasonal weather, and its control on C balance components was discernible only for spring (Table 4) and was mainly a result of the effect of T_a on P_g and R_e at all three sites although relationships between F_{NEP} and T_a were not significant. It appears that environmental variables exerted a strong effect on the C balance at half hourly to daily (data not shown) and even monthly timescales. Progressing to the seasonal scale, it was difficult to distinguish the effect except for temperature and to some extent θ .

[18] To examine the influence of T_a during the early part of the growing season on the annual C balance, we carried out linear regression analysis as shown in Figure 4. An increase in T_{Spring} had a positive effect on annual values of P_g and R_e at all three sites; however, its effect on annual F_{NEP} was not significant. At DF49, annual F_{NEP} showed a stronger correlation with April to June temperature ($r = -0.40$, not shown) than with T_{Spring} ($r = -0.09$). Annual F_{NEP} showed a nonsignificant decrease with an increase in summer and autumn temperature at all three sites; however, the correlation was much higher for HDF88 and HDF00 than DF49. As a result, F_{NEP} had a relatively better negative correlation to T_{Annual} for HDF88 and HDF00 than for DF49. Both P_g and R_e increased with the T_{Annual} , but the increase was not significant (not shown). The above analysis suggests that annual F_{NEP} at the younger sites was more sensitive to changes in temperature than at DF49.

[19] $R_{May-Sept}$ had a strong positive effect on P_g and R_e at all three sites (Figure 5), but its effect on F_{NEP} was negative although not significant. To analyze it further, we examined the response of annual F_{NEP} , P_g and R_e to θ of the 0–30 cm soil layer. At DF49, annual F_{NEP} , P_g and R_e were more dependent on θ in the latter part of the growing season, mainly August to October. At HDF00, P_g and R_e were better correlated with August–October θ (both positive) than $R_{May-Sept}$. At HDF88, P_g and R_e were only significantly correlated to August θ . The small range of θ at this site made it difficult to assess its effect, so we carried out an analysis comparing the effect of θ of the 0–30 cm soil layer with that of the 0–100 cm soil layer. At DF49, the P_g and R_e relationships were similar for both layers but for HDF88, both P_g and R_e were better correlated to θ of the 0–30 cm soil layer.

[20] As shown above, T_{Spring} and August–October θ explained most of the variation in P_g and R_e at DF49; and, F_{NEP} correlated better to April–June temperature. Therefore, we used the above environmental variables to develop a regression model to explain the effect of climate induced variability on the C balance at DF49, which is expected to have reached a nearly constant growth rates with little year-to-year change in LAI [Humphreys et al., 2006] and most of the interannual variability attributable to varia-

Table 3. Results of the Linear Regression Analysis ($y = bx + c$) of the Relationship of Monthly Total C Fluxes to Monthly Mean Environmental Variables^a

Site	y Variable	J	F	M	A	M	J	J	A	S	O	N	D
DF49	F_{NEP}	T_a, D	T_s	T_a, Q	$- \theta$	$-T_a, \theta$	$-T_a, -T_s, -D, -Q$	$-Q, -T_a, \theta, (D)$	θ, Q	$-T_s, -T_a$	$-T_s, (Q)$	$\theta, -T_a, Q$	$\theta, -T_a, -T_s$
DF49	P_g	$T_a, (D)$	T_a, T_s	T_a, T_s, D	$T_a, T_s, -\theta, (Q)$	$T_a, T_s, \theta, (D)$	T_a, T_s, Q	$T_a, T_s, \theta, (D)$	$\theta, -D, -Q$	$-T_s, -T_a$	$D, Q, T_s, (-\theta)$	$Q, -T_a, -\theta$	$\theta, -T_a, -T_s$
DF49	R_e	T_a	T_a, T_s	T_a, T_s	T_a, T_s	T_a, T_s	T_a, T_s	T_a, T_s	$\theta, -D, -Q$	$-T_s, -T_a$	$-T_a, Q, T_s, D$	$Q, -T_a, -\theta$	T_a, T_s
HDF88	F_{NEP}	θ	$-T_a, \theta$	D	$- \theta$	$-T_a, \theta$	$-T_a, -D, -Q$	$-T_a, -D, -Q$	$\theta, -D$	$-T_a, \theta$	Q, T_s, D	$Q, -T_a, -\theta$	$-T_a, D, -T_s, (\theta)$
HDF88	P_g	$T_s, (\theta)$	T_a	T_a, T_s	T_s	T_a, T_s	$-T_a, -D, -Q$	$-T_a, -D, -Q$	$\theta, -D$	$-T_a, \theta$	$-T_s, D$	$T_s, -\theta$	T_a, T_s
HDF88	R_e	T_s	T_a	T_a, T_s	T_s	T_a, T_s	$-T_a, -D, -Q$	$-T_a, -D, -Q$	$\theta, -D$	$-T_a, \theta$	$-T_s, D, Q$	$T_s, -\theta$	$D, -T_a, (-T_s)$
HDF00	F_{NEP}	$-D$	$-T_a, -T_s$	$-T_s, -T_a, \theta$	$-T_a, \theta, -D, -Q, (-T_s)$	T_a, T_s	$\theta, (-T_s)$	θ, T_s	$-T_a, -T_s, -Q$	$-T_s, -T_a$	$-T_s, D, Q$	$T_s, -\theta$	T_a, T_s
HDF00	P_g		T_a	T_a, T_s	T_s	T_a, T_s	θ, T_s	θ, T_s	$-D, \theta$	$-T_s, -T_a$	$-T_s, D, Q$	$T_s, -\theta$	T_a, T_s
HDF00	R_e		$T_a, (T_s)$	T_a, T_s		T_a, T_s	θ, T_s	θ, T_s	θ	$-T_s, -T_a$	$-T_s, D, Q$	$T_s, -\theta$	T_a, T_s

^aHere y is the independent variable (F_{NEP} , P_g , and R_e), and x is the dependent variable (T_a , T_s , θ , and D). The bold letters indicate the x variables with highly significant relations with the y variable ($p < 0.05$), nonbold letters indicate relationships with $0.1 < p > 0.05$, and letters given in parentheses are for relationships with $0.2 < p > 0.1$. Relationships with $p > 0.2$ are not shown here. Negative signs indicate negative correlations.

tions in climate [Schwalm *et al.*, 2007; Jassal *et al.*, 2008b]. We added March average temperature to account for the significant effect of frost events in late winter–early spring as in 2002 when it markedly reduced P_g .

[21] The empirical relations for DF49 (1998–2006) using air temperature and θ of the 0–30 cm layer are:

$$F_{NEP} = 1295.87 - 55.73 T_{Apr-Jun} - 5180.68 \theta_{Aug-Oct} + 35 T_{March},$$

$$r^2 = 0.88, p < 0.05$$

$$P_g = 224 + 82.6 T_{Apr-Jun} + 9791.48 \theta_{Aug-Oct} + 26.68 T_{March},$$

$$r^2 = 0.87, p < 0.05$$

$$R_e = -1071.62 + 138.35 T_{Apr-Jun} + 14969.94 \theta_{Aug-Oct}$$

$$- 8.45 T_{March}, r^2 = 0.92, p < 0.05$$

At the younger sites similar empirical relations using T_{Spring} and late growing season θ (Figure 5) were able to explain only ~40% of the variance in annual F_{NEP} , P_g and R_e . This was likely the effect of stand age on the annual totals of F_{NEP} , P_g and R_e at HDF00 and HDF88 (Figure 3 and Table 2). F_{NEP} at these sites showed a better correlation to T_{Annual} than at DF49.

3.3. Seasonal Variation in C Fluxes

[22] The above analysis shows that the annual C balance is influenced by stand age and variation in seasonal environmental variables. To better understand ecosystem C exchange dynamics at the three sites, a close inspection of the seasonal fluctuation of F_{NEP} , P_g and R_e in relation to environmental variables at the three sites is required.

3.3.1. Seasonal C Fluxes

[23] At DF49, where the annual courses of cumulative F_{NEP} showed a similar pattern for the 9 years, C gain started in February and continued to the end of July (Figure 6). The maximum rates achieved in March–April varied little among years with the exception of 2002, the year with the cold March. P_g generally exceeded 100 g C m^{-2} in March (Figure 7), except in 2002, in response to the increase in Q to values $>500 \text{ mol m}^{-2} \text{ mon}^{-1}$, while R_e in March (Figure 7) generally remained low due to low temperature (Figure 1). This resulted in a marked increase in cumulative F_{NEP} early in the growing season. The interannual differences in C sequestration became visible mainly from May onward (Figure 6). During May–June, R_e increased substantially with the increase in temperature (Figure 1) and served to offset the high values of P_g resulting in a decrease in monthly F_{NEP} from May to July. From August to October, F_{NEP} was close to zero resulting in almost no change in cumulative F_{NEP} . In 2004, a year with a warm spring and wet growing season, F_{NEP} was close to zero or slightly negative from August to October resulting in the lowest annual F_{NEP} of the record. Similar variations were observed at HDF88 in 2004.

[24] In contrast to the interannual variations in cumulative F_{NEP} for DF49, cumulative F_{NEP} at HDF88 early in the year increased each year as stand age increased. However, interannual differences in F_{NEP} observed early in the year changed in the latter part of the growing season (Figure 6). A remarkable increase in cumulative F_{NEP} began in early April of 2005 and 2006 compared with the previous years. This C gain eventually helped HDF88 to slightly exceed C neutrality (i.e., $F_{NEP} = 0$ annually) by the end of these two

Table 4. Results of the Linear Regression Analysis ($y = bx + c$) of Seasonal Total C Fluxes to Seasonal Mean Environmental Variables^a

y Variable	Site	Winter (DJF)	Spring (MAM)	Summer (JJA)	Autumn (SON)
F_{NEP}	DF49				
	HDF88	$-T_s, -\theta, (-T_a)$	$(-\theta)$	$-T_a, (\theta), (-D)$	$-T_s, -\theta, (Q)$
	HDF00	$-T_a$	$-\theta, D, (T_a)$	$(-T_a), (-T_s), (-D)$	
P_g	DF49		$T_a, T_s, D, (-\theta)$	(T_s)	$-T_s$
	HDF88	$-T_s, (-\theta)$	$T_a, (T_s)$	$-Q, -D, \theta, (-T_a)$	$-Q, -D, (-T_a)$
	HDF00		T_a, T_s	$\theta, -Q, (-D)$	(θ)
R_e	DF49		$T_a, T_s, (-\theta)$	(T_s)	(T_s)
	HDF88	T_a, T_s, θ	T_a, T_s		T_s
	HDF00	(T_a)	T_a, T_s	θ	(θ_s)

^aHere y is the independent variable (F_{NEP} , P_g , and R_e), and x is the dependent variable (T_a , T_s , θ , and D). The bold letters indicate the x variables with highly significant relations with the y variable ($p < 0.05$), nonbold letters indicate relationships with $0.1 < p > 0.05$, and letters given in parentheses are for relations with $0.2 < p > 0.1$. Relations with $p > 0.2$ are not shown here. Negative signs indicate negative correlations.

years. The relatively high loss of CO_2 during most of the year resulted in HDF00 being a strong C source. However, the positive changes in F_{NEP} during June to August 2005 and 2006 resulted in an increase in annual F_{NEP} of 150 g C m^{-2} , similar to those for HDF88 in these two years. While DF49 and HDF88 had significant photosynthesis throughout most

of the year, P_g at HDF00 was significant only during April to October (Figure 7). During the peak growing season, monthly total R_e at DF49 was $\sim 100 \text{ g C m}^{-2}$ higher than that at HDF88 or HDF00. During January to March and October to December, R_e values at HDF00 were similar to those at DF49 while at HDF88 they were higher than at

Figure 4. Annual gross ecosystem photosynthesis (P_g) and ecosystem respiration (R_e) at the three sites as a function of spring temperature, and net ecosystem productivity (F_{NEP}), as a function of spring, summer, autumn, and annual mean air temperature. The numbers in parenthesis are values of slope, intercept, r^2 , and p for the respective regression relations.

Figure 5. Annual gross ecosystem photosynthesis (P_g) and ecosystem respiration (R_e) at the three sites as a function of May–September rainfall and August–October 0–30 cm soil water content (θ), for DF49, HDF88, and HDF00, respectively. The relationships of annual net ecosystem productivity (F_{NEP}) to rainfall and θ were not significant. The numbers in parenthesis are values of slope, intercept, r^2 , and p for the respective regression relations.

the other two sites. Wintertime R_e was nearly equal to soil respiration [Jassal *et al.*, 2007, 2008a].

3.3.2. Effect of Seasonal Changes in Environmental Variables on the C Balance

[25] To examine the seasonal response of the C balance components to changes in T_a , θ , and to aid in our interpretation of annual F_{NEP} , the time series of 5-day running averages of T_a , θ , F_{NEP} , P_g , R_e and E during 1998 (for DF49 only), and 2004, 2005 and 2006 (for all 3 sites) are shown in Figure 8. These years were chosen because

2004 and 2005 were years with a warm spring and a wet growing season whereas 2006 was a year with a normal spring with a warm and dry growing season. 1998 is included to show the pattern during a year with a warm spring, like 2004 and 2005, but with a warm and dry growing season. The main difference between 2004 and 2005 was the precipitation distribution and the variation in θ during

Figure 6. Annual cycles of cumulative F_{NEP} at DF49, HDF88, and HDF00.

Figure 7. The 2002–2006 mean monthly F_{NEP} , P_g , and R_e at DF49, HDF88, and HDF00.

Figure 8. Five-day running mean of air temperature (T_a), soil water content (θ) in the 0–30 cm layer, F_{NEP} , P_g , and R_e during 2004–2006 at DF49, HDF88, and HDF00. The years 2004 and 2005 were years with a warm spring and a wet growing season whereas 2006 was a year with a normal spring with a dry growing season. The year 1998 is included to show the pattern during a year with a warm spring, like 2004 and 2005, but with a warm and dry growing season. Of the 4 years, 2005 had the coldest growing season. Values of annual E for 2004–2006 were 420, 429, and 398 mm at DF49 (418 mm for 1998), 387, 382, and 361 mm at HDF88, and 302, 316, and 253 mm at HDF00. Annual C fluxes (g C m^{-2}) at DF49 for 1998, 2004–2006 were 379, 267, 355, and 386 for F_{NEP} , 2131, 2338, 2310, and 2112 for P_g , and 1752, 2071, 1955, and 1726 for R_e , respectively. The annual C fluxes at HDF88 for 2004–2006 were -132 , 20 and 15 for F_{NEP} , 1457, 1694, and 1490 for P_g , and 1589, 1694, and 1475 for R_e , respectively, and at HDF00, annual values were -593 , -421 , and -418 for F_{NEP} , 859, 1111, and 784 for P_g , 1452, 1533, and 1204 for R_e , respectively.

the growing season. 2004 had a dry early growing season and a wet late growing season whereas 2005 had a wet early growing season while the rest of the growing season was relatively dry. E is shown here because of the close relationship between the CO_2 and water vapor exchange processes. This coupled dependence is further examined using parameters describing physiological responses of the ecosystem, namely, canopy level g_s and WUE as shown in Figure 9. At all the three sites, P_g was highly correlated to E ($P_g (\text{g C m}^{-2} \text{ mon}^{-1}) = 5.78E (\text{mm mon}^{-1}) + 9.6, r^2 = 0.97$, $P_g = 3.25E + 18, r^2 = 0.86$ and $P_g = 3.68E - 14, r^2 = 0.91$ for DF49 (1998–2006), HDF88 (2002–2006) and HDF00 (2002–2006), respectively). F_{NEP} , P_g and R_e values were highest at DF49. Even though peak F_{NEP} was lowest at HDF00, magnitudes of P_g and R_e at HDF00 were higher than those at HDF88 during some part of growing season in 2004, 2005 and 2006. Furthermore, the number of days when daily $F_{NEP} > 0$ (C sink) was higher at DF49 than at the other two sites (233 ± 15 , 167 ± 19 , 42 ± 14 days for

DF49, HDF88 and HDF00, respectively, during 2004, 2005 and 2006). Maximum daily E at all three sites reached a value of 2.5 mm d^{-1} indicating a relatively conservative response to stand age.

[26] In 1998, even though P_g , R_e and E increased in response to the relatively warmer than normal February to May temperature, the relatively dry conditions during the growing season, especially in August and September, suppressed P_g , R_e , E and g_s . The greater decrease in R_e than P_g in August and September resulted in an increase in F_{NEP} . In 2004, the year with second warmest spring and a warm growing season with the warmest August, the values of θ up to July at all the three sites were similar to those of 2006, which had low $R_{\text{May–Sept}}$ (Figure 8). The dry conditions in early summer had no effect on P_g and R_e at DF49, with both being higher than in other years. At HDF88 on the other hand, the dry conditions during May end to July resulted in low values of P_g , R_e , and g_s . In August of 2004, the increase in θ increased R_e more than P_g leading to the lowest values

Figure 9. Five-day running mean of dry-foliage surface conductance (g_s) and water use efficiency (WUE) at DF49, HDF88, and HDF00 during May–September for the years considered in Figure 8. Mean May–September WUE values at DF49 for 1998–2006 were 5.95, 5.95, 5.76, 6.43, 5.94, 6.48, 6.29, 6.01, and 6.33 g C kg⁻¹ H₂O, and at HDF88 for 2002–2006 values were 3.24, 3.21, 3.74, 4.37, and 4.13 g C kg⁻¹ H₂O, and at HDF00 for 2002–2006 values were 2.42, 3.00, 3.30, 3.89, and 3.40 g C kg⁻¹ H₂O, respectively.

of F_{NEP} for the four years at all the three sites. The warmer than normal spring in 2005 followed by a relatively cool summer, favored P_g and g_s at all three sites leading to an increase in F_{NEP} during the early part of the growing season with very discernible effects at the younger sites. Wetter growing conditions from June to September resulted in higher than normal P_g , R_e , E and g_s at all three sites, especially the younger sites. The cool and wet summer in 2005 suppressed annual R_e more than P_g resulting in an increase in annual F_{NEP} over that in 2004 (Figure 3). This effect on P_g was more pronounced at the younger sites resulting in the highest annual values of P_g and F_{NEP} of the record. The dry growing season in 2006, a year with normal T_{Spring} , led to an increase in F_{NEP} at DF49 due to the relatively larger decrease in R_e than P_g in response to the dry conditions. At the younger sites, the dry conditions in the latter part of the growing season decreased P_g more than R_e resulting in low F_{NEP} during September and October and slightly lower annual F_{NEP} values than those in 2005. However, in a comparison of C fluxes at HDF88 for the years 2005 and 2006, Jassal *et al.* [2008a] found that the late summer–early fall (August–October) drought in 2006 resulted a greater decrease in R_e than in P_g leading to an increase in F_{NEP} over the same period in 2005.

3.3.3. Response of Canopy Level Physiological Parameters

[27] Both WUE and g_s at these sites have been reported to decrease in response to increasing D at hourly timescales [Ponton *et al.*, 2006; Humphreys *et al.*, 2003]. As shown in Figure 1, D reached its highest values in August, the driest month at all three sites. Results indicated that high D and dry soil water conditions had a strong negative effect on P_g (Figure 8). The differences in the magnitude of g_s with high values at DF49 and low values at HDF00 were as expected considering the ages of the stands and low LAI at HDF00

[Kelliher *et al.*, 1993] (Figure 9). g_s values at all the three sites were lowest during July and August, the period with lowest θ and highest D . The lowest values of g_s occurred in 2006 due to its dry and warm weather. The changes in g_s at these sites closely followed the changes in θ shown in Figure 8. For example, the increase in θ in mid-August 2004 increased g_s , P_g and R_e at all three sites. Time series of WUE (Figure 9) show that during May to September, it was slightly higher at HDF88 than at HDF00. At HDF88, mean May–September WUE increased from 3.2 to 4.4 g C kg⁻¹ water and at HDF00 2.4 to 3.9 g C kg⁻¹ water from 2002 to 2005. At the two younger sites, WUE was lower in 2006. At DF49, WUE in July 2006 was slightly higher than that in 2005. The interannual (1998–2006) variability in mean May–September WUE at DF49 was less than 4% of the mean (6.12 ± 0.24 g C kg⁻¹ H₂O) whereas at the younger sites it was more than 15% of the mean (3.21 ± 0.54 and 3.74 ± 0.52 g C kg⁻¹ H₂O at HDF00 and HDF88, respectively) likely due to their young age and less developed root systems. The small variation in WUE at DF49 indicates that it is a relatively conservative quantity. In general, WUE at HDF00 was low in May and September and reached almost a steady value in July and August. Similar values of WUE during the peak growing season at all three sites irrespective of changes in θ between the years suggest strong coupling of CO₂ and water vapor exchange processes at these sites.

3.3.4. Response of P_g and R_e to Wet and Dry Conditions

[28] In order to examine the responses of P_g and R_e to wet and dry conditions, we examined the response of daytime P_g to Q and nighttime R_e to T_s at the 2-cm depth during May to September for wet and dry conditions as shown in Figure 10. The parameters of the equations obtained from the regression analysis (equation (1) for R_e and equation (2) for P_g) during dry and wet conditions are shown in Table 5.

Figure 10. Influence of wet (circles) and dry (triangles) conditions on the response of P_g to Q , and R_e to T_s at the 2-cm depth. Here wet conditions refer to $\theta_R > 0.40$ in the 0–30 cm soil layer, and dry conditions refer to $\theta_R < 0.20$ in the 0–30 cm soil layer. Symbols in Figure 10 (left) represent binned P_g using bin width of $50 \mu\text{mol m}^{-2} \text{s}^{-1}$, and symbols in Figure 10 (right) represent R_e using bin widths of 0.2°C . Vertical bars represent standard deviations in each bin. Parameters for the fitted curves (solid lines for $\theta_R > 0.40$ and dashed lines for $\theta_R < 0.20$) are in Table 5.

Here ‘wet conditions’ refers to periods when relative available water content (θ_R) in the 0–30 cm soil layer was >0.40 and ‘dry conditions’ refers to periods when it was <0.20 . θ_R is defined as $(\theta - \theta_{WP})/(\theta_{FC} - \theta_{WP})$, where θ_{FC} and θ_{WP} are θ at field capacity (soil water matric potential = -10 kPa) and the wilting point (matric potential = -1.5 MPa), respectively. θ_{FC} and θ_{WP} were 0.24 and $0.11 \text{ m}^3 \text{m}^{-3}$ at HDF88 [Jassal et al., 2008a], 0.21 and $0.06 \text{ m}^3 \text{m}^{-3}$ at DF49 and 0.24 and $0.11 \text{ m}^3 \text{m}^{-3}$ at HDF00 [Humphreys et al.,

2006], respectively. Periods with $\theta_R < 0.40$ have been reported to cause noticeable drought stress to plants [Campbell and Norman, 1998; Krishnan et al., 2006].

[29] During dry conditions both P_g and R_e at all the three sites showed a decreased sensitivity to Q and T_s , respectively. The impact of dry conditions on the response of P_g to Q was less pronounced at DF49 than HDF00 and HDF88. Photosynthetic capacity in dry conditions decreased by 18%, 59% and 44% from their values in wet conditions

Table 5. Parameters of Equations (1) and (2) Describing the May–September Relationships Between R_e and T_s at the 2-cm Depth, and P_g and Q for Dry and Moist Conditions^a

Site	Soil Condition	A	B (K^{-1})	Q_{10}	R_{10} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	r^2	α ($\text{mol CO}_2 \text{mol}^{-1} \text{photons}$)	P_{max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	r^2
DF49	moist	0.134	0.562	3.8	6.7	0.92	0.09	24.47	0.96
	dry	0.067	1.234	1.9	6.8	0.60	0.09	20.7	0.94
HDF88	moist	0.118	0.381	3.3	4.8	0.97	0.06	19.84	0.96
	dry	0.096	0.278	2.6	3.4	0.88	0.08	8.08	0.85
HDF00	moist	0.081	0.682	2.0	4.5	0.92	0.03	14.15	0.90
	dry	0.046	0.879	1.6	3.8	0.50	0.06	7.94	0.87

^aSee Figure 8. Temperature coefficient of ecosystem respiration, $Q_{10} = \exp(10B)$, and ecosystem respiration at a reference temperature of 10°C , $R_{10} = Q_{10} \exp A$. All relationships are significant at $p < 0.05$. Moist conditions refer to periods when $\theta_R > 0.4$, and dry conditions refer to periods when $\theta_R < 0.2$. θ_R is the relative available water content in the 0–30 cm layer (see text).

at DF49, HDF88 and HDF00, respectively. Changes in the response of R_e to T_s under dry conditions occurred for $T_s > 11^\circ\text{C}$ (Figure 10). Even though Q_{10} values decreased by 50% from those in wet conditions at DF49, R_{10} increased slightly. R_{10} at HDF88 and HDF00 decreased by 21% and 20%, respectively, whereas Q_{10} decreased by 29% and 16% at HDF88 and HDF00, respectively. For the same range of soil temperature ($12\text{--}14^\circ\text{C}$) during July–September, the driest part of the growing season, mean R_e during dry conditions (as shown in Figure 10) decreased by 15% (10.7 to $9.1\text{ g C m}^{-2}\text{ d}^{-1}$) at DF49, 29% (7.5 to $5.3\text{ g C m}^{-2}\text{ d}^{-1}$) at HDF88 and 26% (6.4 to $4.7\text{ g C m}^{-2}\text{ d}^{-1}$) at HDF00 from values in moist conditions. This analysis suggests that the availability of soil water has a strong influence on R_e and P_g at the younger sites, especially at HDF88, consistent with the findings of Jassal *et al.* [2008a].

4. Discussion

4.1. Effect of Stand Age

[30] Our study indicates that the intersite differences in F_{NEP} , P_g and R_e were much greater than the interannual variability. For the near-end-of rotation stand, there was greater control of the interannual variability in F_{NEP} by R_e whereas for the younger stands it was largely controlled by P_g (Table 2). The relatively greater control by P_g than R_e has mainly been reported for boreal ecosystems [Barr *et al.*, 2007; Krishnan *et al.*, 2006; Zha *et al.*, 2008] mainly because of the role of growing season length in those ecosystems in controlling the C balance. Based on long-term measurements of C exchange in a 75–110 year-old mixed-deciduous Harvard Forest in central Massachusetts, USA, Urbanski *et al.* [2007] reported that interannual variation in the annual C balance is mainly due to P_g . However, for a southern boreal black spruce forest, R_e in years with a warm spring was found to control interannual variation [Krishnan *et al.*, 2008]. Similar reports suggesting the dominant role of R_e in controlling the annual C balance were made by Valentini *et al.* [2000], Bubier *et al.* [2003], and Dunn *et al.* [2007] for European forests, peatland in Ontario and a northern boreal black spruce forest, respectively.

[31] The intersite and interannual differences in F_{NEP} , P_g and R_e for these three temperate Douglas-fir stands were higher than those reported for a boreal jack pine chronosequence (2–90 years) by Zha *et al.* [2008]. In our study, HDF88 became C neutral at about an age of 17 years whereas in the jack pine chronosequence, the ecosystems were reported to switch from a C source to sink of C at an age of about 10 years [Zha *et al.*, 2008] and about 11–19 years in a black spruce chronosequence [Bond-Lamberty *et al.*, 2004]. Annual C loss ($F_{NEP} = -515 \pm 88\text{ g C m}^{-2}\text{ yr}^{-1}$) following harvest at HDF00 (2–6 years) was higher than that reported for a 4-year-old Scots pine stand ($F_{NEP} = -386\text{ g C m}^{-2}\text{ yr}^{-1}$) [Kolari *et al.*, 2004], a 2-year-old boreal jack pine stand ($F_{NEP} = -137\text{ g C m}^{-2}\text{ yr}^{-1}$) [Zha *et al.*, 2008], a 3-year-old black spruce stand ($F_{NEP} = -124\text{ g C m}^{-2}\text{ yr}^{-1}$) [Bergeron *et al.*, 2008].

[32] Harvesting influences the forest C balance components in different ways: because of the changes in above-ground and belowground biomass, it can induce soil warming and enrich soil organic matter that together with dead roots and logging debris can stimulate decomposition and enhance

respiratory fluxes. Furthermore, harvesting can cause an increase in θ as a result of reduced E following harvest, thus preventing the occurrence of dry-soil conditions that can limit soil respiration. Furthermore, C uptake by young stands is limited by the low LAI [Humphreys *et al.*, 2005]. Grant *et al.* [2007] hypothesized that changes in F_{NEP} during the aging of coastal Douglas-fir stands can be explained by changing nutrient uptake caused by different timescales for decomposition of fine nonwoody and coarse woody litter left after harvesting, a drop in canopy water potential with lengthening of the water uptake pathway during bole and branch growth, and increases in the ratio of autotrophic respiration to P_g with phytomass accumulation.

4.2. Effect of Temperature

[33] In our study, the early growing season temperature had a significant positive effect on both annual P_g and R_e at all sites. Because of the greater response of R_e than P_g to temperature and an almost yearlong growing season, an increase in temperature during any part of the year could result in a decrease in F_{NEP} . A similar response of P_g and R_e to temperature and almost no dependence of F_{NEP} on temperature was reported by Reichstein *et al.* [2007] based on an analysis of the determinants of the C balance using 93 site years of EC data from the EUROFLUX and CARBOEUROPE networks. Chen *et al.* [2002] reported that temperature had no significant influence on CO_2 fluxes at the old-growth Douglas-fir–western hemlock forest stands in the Wind River Valley but it significantly affected CO_2 exchange in the younger stands. The variations in F_{NEP} , P_g and R_e in Figure 8 suggest that regardless of age, Douglas-fir stands responded similarly to the changes in T_{Spring} and growing season θ . A similar response was reported for the Douglas-fir stands at the Wind River site [Chen *et al.*, 2002, 2004], which has a climate similar to that on the east coast of Vancouver Island, with the majority of C uptake occurring during early spring, followed by C loss in summer and little net C exchange in winter. In southern boreal aspen and black spruce forests an increase in spring temperature was found to increase annual F_{NEP} , P_g and R_e [Black *et al.*, 2000, 2005; Krishnan *et al.*, 2006, 2008]. We found that the increase in summer or autumn temperature resulted in a decrease in F_{NEP} and this effect was more noticeable at the younger sites than at DF49. This agrees with the findings of Piao *et al.* [2008] who analyzed EC CO_2 flux measurements from 28 northern ecosystems. Since the magnitude of C loss at the younger sites during the latter part of the year was higher than the near-zero values at DF49, changes in temperature had more effect on annual F_{NEP} at the younger sites than that at DF49.

4.3. Effect of Changes in Water Availability

[34] Our analysis suggests that dry soil conditions during the growing season had a significant effect on the C balance. While R_e was controlled by temperature, soil moisture strongly influenced its response to temperature. Soil respiration (R_s) measurements during 2003–2006 at DF49 suggested that more than 60% of R_e is due to R_s [Jassal *et al.*, 2007]. Mean R_s during May 2002 to December 2002 was found to be higher at HDF88 than that at DF49 and HDF00 [Humphreys *et al.*, 2006]. The drying of the soil causes a large reduction in both hetero-

trophic respiration and autotrophic respiration [Jassal *et al.*, 2008a]. Because of the large contribution of R_s , the decrease in R_e could be largely due to the reduction in R_s . As shown in Figures 8, 9, and 10, HDF88 responded more to dry conditions than the other two sites. In a recent study using 2005–2006 soil chamber and EC measurement at HDF88, Jassal *et al.* [2008a] concluded that in extremely dry conditions, R_s is more influenced by θ than T_s . Figure 10 suggests that higher θ during the growing season has a strong effect on both P_g and R_e at all sites. The slightly higher response of R_e than P_g resulted in a decrease in annual F_{NEP} during the very wet year 2004 and an increase in annual F_{NEP} during the dry years 1998 and 2006 at DF49. This is similar to the earlier report by Krishnan *et al.* [2008] for the SOBS forest in Saskatchewan. Direct evidence of an increase in F_{NEP} with increasing rainfall during the growing season is reported mainly for grass ecosystems [Flanagan *et al.*, 2002; Ma *et al.*, 2007]. We found that the increase in θ during the growing season is more likely to decrease F_{NEP} at DF49 due to the greater response of R_e than P_g to θ , although it was found to be insignificant.

[35] Dry conditions reduce long-term photosynthetic rates as soil water becomes depleted in the root zone [Goulden *et al.*, 1996; Reichstein *et al.*, 2002; Griffis *et al.*, 2004]. The reduction in P_g could occur due to direct effects of soil water stress on carboxylation [Warren *et al.*, 2003] or the decrease in stomatal conductance associated with soil water stress and high values of D [Farquhar and Sharkey, 1982; Baldocchi, 1997; Anthoni *et al.*, 2002; Reichstein *et al.*, 2002; Krishnan *et al.*, 2006, 2008]. Because of the developed root system in mature stands, P_g can be maintained due to the available water deep in the root zone whereas it appears that the impact of a shallower root zone on P_g in the younger stands result in a greater reduction in F_{NEP} (Figure 8 for 2004).

[36] Future climate projections forecast greater variability in precipitation and higher frequency of drought events in the mid and high latitudes [IPCC, 2007]. Earlier reports on drought effects focused on localized short-term and moderate drought [Law *et al.*, 2001; Reichstein *et al.*, 2002; Rambal *et al.*, 2003; Ciais *et al.*, 2005; Goulden *et al.*, 1996; Baldocchi, 1997; Goldstein *et al.*, 2000; Barford *et al.*, 2001; Anthoni *et al.*, 2002; Gu *et al.*, 2006]. Recent reports are on regional-scale and long-term drought, e.g., the 2003 drought in Europe [Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007] and the drought in Western North America in 2001–2003, which affected the southern boreal forest [Barr *et al.*, 2007; Krishnan *et al.*, 2006; Kljun *et al.*, 2006]. All these studies suggested strong effects on the ecosystem C balance. Dry summers like those in 1998 and 2006, decreased R_e more than P_g resulting in an enhancement in F_{NEP} in mature sites similar to that observed in the first year of drought in 2001 at the SOA forest [Barr *et al.*, 2007; Krishnan *et al.*, 2006; Kljun *et al.*, 2006]. Drought early in the growing season or in spring or during canopy development can more strongly affect P_g than R_e resulting in a decreased annual F_{NEP} as reported by Noormets *et al.* [2007] for a 50-year-old mixed-oak woodland in northern Ohio, USA and by Krishnan *et al.* [2006] for the third year of drought at the SOA forest. This effect will likely be greater for younger stands than mature stands as seen here at HDF88 and HDF00 in 2004.

[37] The impact of changes in water availability on P_g and R_e likely depends on the water holding capacity of the soil, the vertical distribution of the amount of soil organic matter and roots in the soil and the general drought sensitivity of the vegetation [Heimann and Reichstein, 2008]. Warren *et al.* [2005], in a study of the vertical distribution of soil water in PNW old-growth ponderosa pine, young and old-growth Douglas fir stands, reported that the greater responsiveness of a young Douglas-fir stand to changes in θ was associated with the difference in the vertical distribution of root surface area in the young and old stands, which they attributed to developmental stage and stand density. They reported that total fine root biomass in the upper 1 m were higher for the young stand with 60% of the fine roots located in the upper 20 cm. Studies conducted on young and old-growth ponderosa pine stands [Irvine *et al.*, 2002; Anthoni *et al.*, 2002] also showed higher drought stress in young stands than in old-growth forest because soil moisture was being extracted from greater depths at the old-growth site [Irvine *et al.*, 2002]. In our study, high E in younger stands with less developed root systems, similar in magnitude to that at DF49 during the growing season, could result in greater water uptake leading to water stress earlier in these stands than at DF49 for similar environmental conditions (Figure 2). Furthermore, the greater response of the younger stands (Figure 10), especially HDF88, to changes in θ could be due to the differences in soil physical and chemical characteristics at that site (Table 1). The greater response of HDF88 to θ is in contrast to the finding of McMillan *et al.* [2008] that younger stands were more susceptible to water or heat stress during a warm dry year. Even with the differences in stand density, LAI, basal area, soil characteristics, elevation, and proximity to the ocean, all sites showed similar responses when exposed to similar climate.

4.4. Effect of ENSO and Climate Change on the Long-Term C Balance

[38] As mentioned above, ENSO plays an important role in year-to-year climate variability and hence potentially influences long-term trends in temperature and precipitation in the PNW [Mote *et al.*, 1999; Mote, 2003]. The globally averaged growth rate of atmospheric CO_2 is also tightly correlated to ENSO climate variations [Heimann and Reichstein, 2008] and with a warming planet the frequency of occurrence of stronger El Niño events is likely to increase. In a warmer climate, the change in precipitation distribution in the growing season is an important factor in controlling the C balance of ecosystems. The warmer conditions can extend the length of the effective growing season. As seen in our analysis, the extreme climatic conditions include a warm and mild winter followed by unusually warm spring months and a dry summer during El Niño (e.g., 1998), a wet winter and relatively cool and cloudy conditions in the following spring and summer during La Niña (e.g., 1999), and a warm winter and spring followed by a wet summer and autumn in neutral years (e.g., 2004 and 2005). As seen above, a warm spring and a wet growing season usually has a more positive effect on P_g than R_e at all the three sites. However, the increase in winter temperature can result in early enhancement of R_e and reduce the number of days with positive F_{NEP} in the early part of the growing season resulting in a reduction in annual F_{NEP} at the near-

end-of-rotation site. For the younger sites, this could increase the number of C uptake days in early part of the growing season and enhance annual F_{NEP} . The effect of dry versus wet conditions and their times of occurrence (early versus late in the growing season) are important in this ecosystem as shown in our analysis. While wet soil conditions early in the growing season can favor P_g , R_e and F_{NEP} (as in 2005), dry conditions in the latter part can reduce R_e more than P_g resulting in an enhancement of F_{NEP} (as in 2006) at near-end-of-rotation site. However, wetter conditions in latter part of the growing season can enhance R_e and decrease F_{NEP} (e.g., 2004) at all three sites. The question of how each component (P_g or R_e) responds to changes in soil water availability and the impact on F_{NEP} depends on the time of occurrence of dry and wet conditions. Almost parallel variations of P_g and R_e and the lack of a statistically significant relationship of F_{NEP} to environmental variables suggest that we need to consider the impact of environmental variables on the C balance components rather than on F_{NEP} when simulating the impact of a changing climate on the C balance. In addition, the increase in annual and autumn temperature had a negative effect on F_{NEP} , especially at the younger sites. The C balance of this ecosystem in the long-term will likely be determined by how the temperature-driven enhancement of C uptake in the early part of the growing season compares with the effect of changes in the soil water conditions or temperature during the latter part of the growing season.

5. Conclusions

[39] 1. Stand-age effects on F_{NEP} , P_g and R_e were much higher than that of interannual variability. The near-end of-rotation Douglas-fir stand, DF49, was a C sink ($357 \pm 51 \text{ g C m}^{-2} \text{ yr}^{-1}$) during 1998–2006 while the young plantation, HDF00, was a large C source ($-515 \pm 88 \text{ g C m}^{-2} \text{ yr}^{-1}$) during 2002–2006. The pole-sapling stand, HDF88, was initially (2002–2004) a weak C source ($-105 \pm 10 \text{ g C m}^{-2} \text{ yr}^{-1}$) and in the last 2 years (2005–2006) was a weak sink ($21 \pm 30 \text{ g C m}^{-2} \text{ yr}^{-1}$).

[40] 2. Interannual variability in annual F_{NEP} at DF49 was mainly due to interannual variability in annual R_e whereas at the younger sites interannual variability in annual P_g largely determined interannual variability in annual F_{NEP} .

[41] 3. Early growing season (spring) temperature and May–September (summer) soil water availability were the main factors determining the interannual variability in P_g and R_e of the three Douglas-fir stands. The linear relationship between annual F_{NEP} and the above variables was not significant because of the similar changes in P_g and R_e . Even though not statistically significant, the decrease of F_{NEP} with increasing spring, summer, autumn temperatures and growing season water content were due to a slightly greater response of R_e than P_g to the above climatic variables.

[42] 4. The impact of extremely dry conditions on P_g and R_e at the younger sites, especially at HDF88, was greater than at the near-end-of-rotation site, DF49. Drought conditions during the latter part of the growing season had a positive effect on F_{NEP} because of the greater reduction in R_e than P_g in response to the decrease in θ .

[43] 5. Empirical relationships using controlling environmental variables were effective in explaining more than 85% of the interannual variability in P_g , R_e and F_{NEP} at DF49; however, less than 40% could be explained using similar empirical relationships for the younger sites.

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