Five years of carbon fluxes and inherent water-use efficiency at two semi-arid pine forests with different disturbance histories

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ABSTRACT

Five years of eddy-covariance and other measurements at a mature ponderosa pine forest and a nearby young plantation are used to contrast the carbon fluxes for long-term averages, seasonal patterns, diel patterns and interannual variability, and to examine the differing responses to water-stress. The mature forest with larger leaf area and wetter and cooler soils has a net uptake of carbon 3.3 times that of the young plantation. In the spring, photosynthesis is larger at the mature site as expected based on the difference in leaf area, however, another important factor is the reduction in springtime respiration at the mature site due to lower soil temperatures because of more shade from the canopy. Patterns of photosynthesis, inherent water-use efficiency (IWUE) and tree transpiration indicate that the young plantation responds to the seasonal drought sooner and to a more severe degree. Lower sensitivity to seasonal drought at the mature site is likely due to higher soil moisture reserves year round and a deeper root system that can access more water. Outside the seasonal drought period, the IWUE is the same at both sites, suggesting a species-specific value. Larger interannual variability at the plantation is associated with water-year drought and aggrading.

Keywords: carbon fluxes, net ecosystem exchange of carbon, eddy-covariance, water-stress, net ecosystem production, water-use efficiency

1. Introduction

To better understand the role of terrestrial ecosystems in global climate change, considerable research has been focused on measuring the net ecosystem exchange of carbon (NEE) between forests and the atmosphere for a wide variety of forest types. These observational studies are important for developing improved models for the underlying processes of photosynthesis and ecosystem respiration (ER). Within forest types and climate zones, long-term average NEE is thought to be primarily influenced by time since stand replacing disturbance (Kurz and Apps, 1999; Law et al., 2001a; 2001b), while interannual variations are likely driven by year-to-year changes in climate variables and their influence on short-term carbon pools (e.g. Barr et al., 2007; Pereira et al., 2007; Urbanski et al., 2007). Land use changes associated with disturbance may affect

vegetation cover, microclimate and soil processes, inducing for example, warmer and dryer soils after harvest (Amiro et al., 2006).

The current study expands on previous work studying carbon fluxes at different ponderosa pine forests in Central Oregon. Anthoni et al. (2002) compared 9 months of eddy-covariance carbon fluxes over a young (15–23 years old) natural regeneration site and an old site (mixture of 50- and 250-year-old) and found that water stress during summer at the young site led to a reduction in assimilation of carbon. By comparison, the fluxes at the old growth site were not significantly influenced by seasonal drought due to access to deep soil moisture. Irvine et al. (2004) found that during periods where soil moisture was not limiting, the sensitivity of mid-day canopy stomatal conductance to the logarithm of the vapour pressure deficit at a natural regeneration young pine site was 3.5 times larger compared to a nearby mature forest. Schwarz et al. (2004) presented eddy-covariance carbon fluxes for 2 yr of data (2001–2002) from a young pine stand (same young site

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studied by Anthoni et al., 2002) and 1 yr of data (2002) from a mature forest (same mature forest as this study) and simulations with the Soil-Plant-Atmosphere (SPA) model to show that older forests with well-established root systems appear to be better buffered from the effects of seasonal drought compared to younger stands. Based on 1 yr of coincident eddy-covariance measurements in 2002, they reported about three times larger net carbon fixation at the mature forest (371 g C m^{-2} yr^{-1}) compared to the natural regeneration young site (113 g C m^{-2} yr^{-1}).

In this study, a much longer 5-year dataset (2004–2008) of coincident eddy-covariance flux measurements are used to contrast the carbon and water fluxes and their sensitivities to water-stress for a mature (94-year-old in 2006) ponderosa pine forest and a nearby young (19-year-old) ponderosa pine plantation. A long-term record of fluxes allows one to examine the effects of interannual variation in climate on ecosystem processes and identify carry-over effects, vulnerabilities and resilience to climate, such as multiple years of drought. It also allows examination of trajectories of change in carbon uptake associated with ecological succession following disturbance (e.g. Stoy et al., 2008). Semi-arid regions have been recently identified as hot spots of interannual variability in carbon fluxes (Jung et al., 2011).

The young plantation is a different young site than that studied by Anthoni et al. (2002) and Schwarz et al. (2004), and the carbon fluxes presented here are the first reported for the young pine plantation. The mature forest here is the same one studied by Thomas et al. (2009). We hypothesize that: (a) the mature forest sequesters significantly more carbon than the young plantation, confirming previous studies based on 1 or 2 yr of biometric and/or eddy-covariance measurements or modelling; and (b) the young plantation is more sensitive to seasonal and water-year drought stress.

2. Materials and methods

2.1. Mature pine forest

The first dataset analyzed is from a 16-m tall 94-year-old mature ponderosa pine forest (Table 1) in Central Oregon, USA (Schwarz et al., 2004; Irvine et al., 2008; Thomas et al., 2009). Although the site is located on a relatively flat saddle region about 500 m across, it is surrounded by complex terrain. Imagery and surveys indicate that this age class of ponderosa pine is prevalent for several kilometres in all directions except to the north where there is a recently harvested area beginning approximately 500 m from the tower. Data from periods with northerly winds were discarded. The dominate wind direction is from the southwest throughout the year. The peak leaf area index

Table 1. Ponderosa pine stands in central Oregon, USA referred to in the text. The CWD (coarse woody debris) is >10 cm dia and >1 m length. FWD (fine woody debris) is >6 mm and <10 cm. LF (litterfall) includes foliage and wood <1 cm dia. The 5-year average (2004–2008) LAI is 1.5 at the young plantation and 3.3 at the mature forest

	Young plantation	Mature forest
Year of measurement	2003	2001
Latitude (deg N)	44.315	44.451
Longitude (deg E)	−121.608	−121.558
Elevation (m)	1005	1255
Mean age (years)	16	56
Oldest 10%	16	89
Mean height (m)	3.3	14.0
Tallest 10%	4.1	19.8
Density (trees ha^{-1})	260	325
Soil depth (m)	0.5	1.5
Rooting depth (m)	0.5	1.5
CWD (g C m^{-2})	27	1519
FWD (g C m^{-2})	200	382
LF (g C m^{-2} yr^{-1})	17	67

(LAI) was constant (3.3) within measurement error over the 5-year period. The understory accounts for about 17% of the total LAI. The understory LAI and biomass estimates are based on one sample, and therefore are considered constant in time. Tree height increased from 14.9 m in 2004 to 16.3 m in 2008. Rooting depth was measured on wind thrown trees of different sizes at and near the site and averaged approximately 1.5 m.

Eddy-covariance measurements were collected using a three-dimensional sonic anemometer (model CSAT3, Campbell Scientific Inc., Logan, UT) and an open-path infrared gas analyzer (model LI-7500, LI-COR Inc., Lincoln, NE) at 33 m above ground level (or about twice the canopy height). Additional measurements include profiles of the mean CO_2 concentration for computing the storage term using a closed-path infrared gas analyzer (model LI-6262, LI-COR Inc.) with inlets at 1, 3, 6, 15 and 33 m above ground, atmospheric temperature and relative humidity (model HMP45, Vaisala, Oyj, Helsinki, Finland), automated soil chamber measurements of respiration, sap flux measurements of transpiration and periodic biological measurements. The soil chamber, sap flux and biological measurements are described below. Soil moisture content in the top 30 cm was measured using a model CS615 from Campbell Scientific Inc., and soil temperature was measured at multiple depths using thermocouples. Precipitation was measured using a rain gauge (model TE525WS, Texas Electronics, Dallas, TX) located near the top of the tower. The CO_2 profile system was replaced by a new system with a LI-820 gas analyzer with inlets

at 0.3, 1, 3, 6, 10, 18 and 33 m above ground in August of 2006. Tree height was measured using a laser ranging scope (models MapStar and Impulse 200, Laser Tech, Inc., Englewood, CO). LAI was measured using a LAI-2000 (LI-COR Inc.) and is hemi-surface area basis corrected for clumping and includes understory. The data analyzed here were collected during 2004 through 2008 to coincide with the measurements at the young pine plantation.

2.2. Young pine plantation

The second dataset is from a 4-m tall, even-aged 19-year-old ponderosa pine plantation with seasonal grass understory and nitrogen-fixing bitterbrush in Central Oregon, USA with continuous measurements since late 2003 (Table 1). The site was clear cut, stripped of debris, tilled and replanted by the U.S. Forest Service in 1987. The replanting was done at a density lower than normally found in naturally regenerated stands. The dimensions of the area with the uniform young pines is 300×375 m, and the flux tower is located approximately in the centre. Compared to the mature pine site, the young plantation is more heterogeneous in terms of the vegetation when the flux footprint is outside the plantation (see discussion below). The terrain slopes upward at about 2% to the

west and southwest, and slopes weakly downward (<1%) or is flat in other directions. The peak LAI increased 64% (from 1.1 to 1.8) over the 5-year measurement period. Approximately 22% of the peak LAI is due to understory (bitterbrush and grasses). The mean tree height increased 40% (from 3.7 to 5.2 m). Rooting depth is approximately 0.5 m, depending on cracks or obstruction by rock.

The instrumentation at the young plantation follows that deployed at the mature site. Differences include: (a) the eddy-covariance data was collected at 12 m above ground (or about three times the canopy height); and (b) the vertical profile system inlets were at 1, 5 and 12 m above ground. The data analyzed here were collected during 2004 through 2008.

2.3. Climate and soils

The climate is semi-arid (or Mediterranean) with cool, wet winters and hot, dry summers. The air temperature is generally slightly higher at the younger stand (Fig. 1) likely due to the 250-m lower elevation. A 26-year precipitation record for 1981–2007 from the PRISM Group at Oregon State University indicates the average annual precipitation in the immediate region of the mature site is 535 ± 41 mm yr^{-1}, mostly occurring in the winter as rain and snow. Only 5% of the annual precipitation
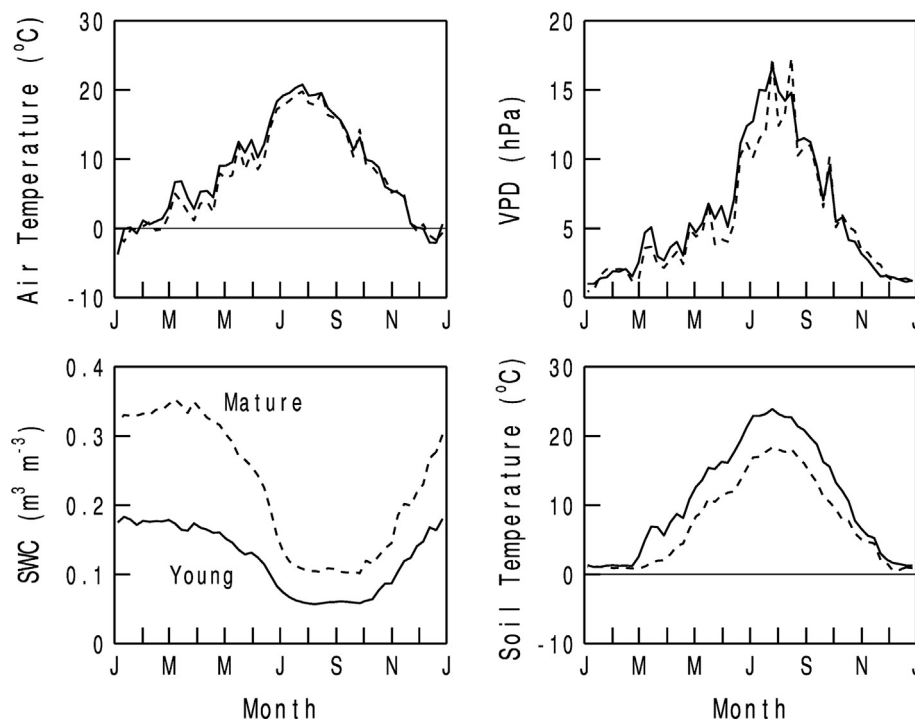

Fig. 1. The 5-year average weekly means of air temperature, vapour pressure deficit (VPD), soil water content (SWC) in the top 30 cm, and the 16-cm soil temperature for the mature pine (dashed) and the young plantation (solid). The sharp peaks in VPD are from extreme hot and dry events that survive the 5-year averaging.

occurs during July–August–September. Onsite rain gauges estimated the 5-year annual average precipitation to be 480 ± 160 mm at the mature site and 360 ± 90 mm at the plantation. Although precipitation patterns are highly variable from year to year, they are generally synchronous between the two sites. Precipitation and temperature are out of phase, leading to soil water recharge in the cool winter season (Fig. 1) (Waring and Running, 2007).

The soil water content (SWC) in the top 30 cm is significantly higher at the mature forest compared to the young plantation throughout the year (Fig. 1). The 5-year annual average SWC is about 85% larger at the mature site (0.227 m^3 m^{-3} at the mature forest and 0.122 at the young plantation). Larger soil moisture reserves at the mature forest can be attributed to more precipitation according to the onsite rain gauge measurements, which indicate about 30% more precipitation at the mature forest. The soil water difference may also be related to the less settled soil at the young plantation, due to tilling that occurred prior to planting by the Forest Service. The warmer soil temperature at the plantation (Fig. 1) is presumably due to less shade afforded by the smaller LAI of the younger stand (5-year average peak LAI of 1.5 compared to 3.3 at the mature site). The soils at both sites are volcanic, with the percentages of sand, silt and clay at 69, 24 and 7% in the top 50 cm, and 54, 35 and 11% from 50 to 100 cm (Irvine et al., 2008).

2.4. Calculating fluxes

A description of the initial quality control and eddy-covariance flux calculations used to arrive at the 30-minute averaged carbon and water fluxes for the mature forest and the young plantation is given in Thomas et al. (2009). Thirty-minute block averaging was used to define the local mean for computing the perturbations. Raw 10/20 HZ eddy-covariance data and 30-minute fluxes and variances were subjected to quality control based on a combination of tests for plausibility and stationarity. However, unlike Thomas et al. (2009), who applied a filter based on (σ_w/u_*) to test for similarity (Thomas and Foken, 2002), we applied a u_*-filter (see below) to identify weak mixing conditions (Goulden et al., 1996; Falge et al., 2001), where σ_w is the standard deviation of the vertical velocity and u_* is the friction velocity.

2.5. Filtering nighttime fluxes

A u_*-filter was applied to discard nocturnal eddy-covariance fluxes in the weakest mixing conditions because they are not representative of the NEE, most likely due to neglected advection terms (Vickers et al., 2011). An exponential temperature-dependent model of respira-

tion (Arrhenius-type) with time-dependent coefficients is used to replace the fluxes. The critical u_* value is found using the 95% rule: the critical value is the smallest class value of u_* with a flux class mean that is greater than or equal to 95% of the average fluxes for all larger u_* classes. The constant critical u_* value used in the filter for the mature site is 0.5 m s^{-1}. Application of the filter at the mature site reduces the 5-year average annual $-$NEE from 534 to 415 g C m^{-2} yr^{-1}. At the plantation we apply a u_*-filter with a critical value of 0.1 m s^{-1}, and the 5-year average annual $-$NEE at the young plantation is reduced from 183 to 126 g C m^{-2} yr^{-1}.

2.6. Flux footprint

At the young plantation, an additional complication for the eddy-covariance method at night is the short fetch of the plantation. Predictions of the flux footprint were made based on a three-dimensional forward Lagrangian stochastic trajectory model (Göckede et al., 2006). A brief description of the model is available in Vickers et al. (2010). The footprint model was run for 10 meteorological scenarios ranging from unstable to stable atmospheric stability. The model predicts that the fraction of the eddy-covariance flux footprint inside the plantation decreases approximately linearly with increasing atmospheric stability z/L, where L is the Obukhov length scale, from 95% for $z/L < -1$ (unstable), to 85% for near-neutral, to 70% or less for stable conditions with z/L near unity. We note that the assumptions required by the footprint model are not always met, and the footprint results should only be used as a guide. For example, the footprint model assumes horizontal homogeneity of the turbulence while in reality the situation may be considerably more complex. The flux footprint is further away from the tower in stable conditions because of weaker vertical mixing associated with weaker nocturnal winds (less shear-generation of turbulence) and stronger temperature stratification (more buoyancy destruction of turbulence). Using the u_*-filter with a critical value of 0.1 m s^{-1} (see previous discussion) effectively removed the strongest stability periods where more than approximately 25% of the footprint was predicted to be outside the plantation. At this particular site, filtering with a critical friction velocity of 0.1 m s^{-1} is approximately equivalent to filtering with a critical z/L of 1.

2.7. Gap-filling

Approximately 70% of the 30-minute average carbon dioxide and water vapour eddy-covariance flux data passed the quality control testing and u_*-filtering at each site for the 5-year period of record. The bulk of the missing

data is associated with winter precipitation, snow and ice on the sensors and nocturnal periods identified by the u_*-filter. For nighttime periods, short gaps in the NEE time series were filled using an exponential temperature response model with time-dependent coefficients. Each year was partitioned into eight 45-day periods as a compromise between capturing seasonal changes in soil moisture and radiation, and having a sufficient number of data samples in each window. Short gaps in the daytime NEE were filled using the mean diurnal variation method (Falge et al., 2001), which was found to be the most stable method for data sets with a large percentage of missing data. Two passes were made using window widths of first 5 and then 9 d. Any gaps remaining after the two passes of the mean diurnal variation method were filled using the multi-year average NEE for that specific 30-minute period. The daytime NEE estimates were partitioned into assimilation and respiration components by extrapolating the nighttime approach (exponential temperature dependence with time-dependent coefficients) into daytime conditions. The time-dependent coefficients are required to capture the seasonal variability in soil moisture. NEE was calculated as the sum of the eddy-covariance vertical flux and the storage term, and the gross ecosystem production (GEP) was calculated as a residual to balance the carbon budget.

2.8. Uncertainty

The relative uncertainty (corresponding to one standard deviation) in an individual estimate of annual NEE was estimated as 16% using the maximum relative variability resulting from three different gap-filling and flux partitioning approaches as described in Thomas et al. (2009). The absolute uncertainty scales with the magnitude of the flux such that the relative uncertainty is more nearly constant from year to year at a given site and between sites. Note that while random flux sampling errors can be very large for individual 30-minute flux estimates, especially in stable conditions (Vickers et al., 2010), random errors mostly cancel as the number of samples increases, as when computing longer time-averages. At both sites, the uncertainty in the monthly average and annual average NEE due to random flux sampling errors is small compared to the uncertainty associated with gap-filling and flux partitioning.

2.9. Sapflow measurements

Tree transpiration was measured using heat dissipation sapflow sensors (Granier, 1987) between April and November at both the young plantation and the mature site. At the mature site, 12 trees covering the range of tree diameters were instrumented with a combination of sap flux sensors in the outer conductive xylem and variable-length heat dissipation sensors (Jassal et al., 2007) to measure the radial sap velocity profile as a function of sapwood depth. Ten trees were instrumented with heat dissipation probes only in the external 2 cm conductive xylem at the young plantation. The data were scaled to equivalent transpiration (mm day^{-1}) using surveys of tree diameter distributions (Irvine et al., 2004). Problems with sensor degradation (Moore et al., 2010) eliminated the 2005 sapflow data at the mature site (new sensors were installed in 2001 and 2006) and the 2007–2008 data at the plantation, leaving good quality data for between-site comparisons in 2004 and 2006. Due to potentially large spatial scaling errors involved with sapflow sensors, we normalise the time series of transpiration using the maxima for individual years to contrast the seasonal patterns (but not the absolute values) at the two sites.

2.10. Soil chamber measurements

Chamber-based estimates of ER were made by combining high temporal resolution (1-hour average) data from an automated soil chamber system (Irvine and Law, 2002) with estimates of foliage and live wood respiration derived from temperature response functions specific to ponderosa pine (Law et al., 1999). The efflux of CO_2 from the soil comprises a majority (70–80%) of the total ER (Law et al., 1999). The spatial average 1-hour average ER was constructed from an array of 10 automated soil chambers at the mature site and four chambers at the plantation, where each chamber has a surface area of 0.21 m^2. Foliage respiration from bitterbrush and grasses at the plantation was computed using LAI and measurements and equations developed at a nearby young pine natural regeneration site (Law et al., 2001c). The soil chamber estimates include the respiration from fine woody debris.

Extensive periodic manual soil respiration measurements using a LI-6400 with a LI-6000-9 soil chamber (LI-COR, Inc.) were used to correct the automated chamber measurements for spatial heterogeneity as described in Irvine et al. (2008). Approximately 150 d of data were obtained from each automated chamber each year. The chambers were not deployed in winter. The chamber-based estimates of ER were gap-filled by fitting the air temperature, soil temperature, soil moisture and incident radiation dependences using the method described in Thomas et al. (2009).

2.11. Biological measurements

Each site had a 1-ha plot where we measured tree and shrub dimensions, age and growth increment from

wood cores, LAI, herbaceous plant biomass, coarse and fine woody detritus, and annual litterfall. On four 12 m radius subplots within each 100×100 m plot, structure measurements were made of incremental annual tree height with a laser ranging scope (models MapStar and Impulse 200, Laser Tech, Inc., Englewood, CO), and diameter at breast height (DBH, 1.37 m) on all trees. Dendrometer bands were used on all trees to calculate annual incremental diameter change.

Annual above and belowground wood productivity (ANPP, BNPP) were estimated from the increment diameter growth and tree dimensions, and local allometric equations (Table 3 in Law et al., 2001b). BNPP was estimated as the sum of coarse root increment and the product of fine root mass and fine root turnover. Coarse root increment was assumed to be 0.25 of wood production. Fine root mass was measured once in 2001 (see Irvine et al., 2007 for methodology) and coarsely scaled proportionally to soil respiration for the subsequent years, and site specific fine root turnover was taken from Andersen et al. (2008). Net primary productivity (NPP) was then defined as NPP = ANPP + BNPP, where ANPP is aboveground net primary production (trees, shrubs, forbs and grasses), and BNPP is below ground net primary production (fine and coarse root growth). Heterotrophic respiration (Rh) was estimated from gap filled automated soil respiration data (from Irvine et al., 2008; Thomas et al., 2009) combined with monthly estimates of Rh fraction (from Law et al., 2001c). Net ecosystem production (NEP) was calculated as NEP = ANPP + BNPP–Rh.

3. Results and discussion

3.1. Long-term average carbon fluxes

Net carbon uptake ($-$NEE) by the mature forest is 3.3 times larger than by the young pine plantation (Table 2). The difference in the 5-year average annual $-$NEE between the mature forest and the young plantation (415–126 = 289 g C m^{-2} yr^{-1}) is larger than can be explained by the interannual variability or the uncertainty in each annual estimate. The relative difference in annual NEE found here is similar to the difference reported by Schwarz et al. (2004) using 2002 eddy-covariance data at a nearby natural regeneration young site and the mature forest and the SPA process-model to estimate fluxes for multiple years. We note that the net carbon uptake at the young plantation would probably be smaller than observed here if all the woody debris had not been removed from the site prior to planting.

Gross ecosystem production ($-$GEP), ER and net ecosystem exchange are all larger at the mature forest than

Table 2. Estimates of mean annual gross ecosystem production ($-$GEP), ecosystem respiration (ER) and net ecosystem exchange ($-$NEE) (g C m^{-2} yr^{-1}) based on eddy-covariance measurements. The uncertainty (one standard deviation) in an individual estimate of annual NEE due to gap-filling and flux partitioning is shown in parenthesis

	Young plantation			Mature forest		
	$-$GEP	ER	$-$NEE	$-$GEP	ER	$-$NEE
2004	810	708	102 (16)	1444	1042	402 (64)
2005	669	620	49 (8)	1398	999	399 (63)
2006	839	710	129 (21)	1331	983	348 (56)
2007	767	617	150 (24)	1517	1054	463 (74)
2008	818	619	199 (32)	1490	1029	461 (73)
Mean	781	655	126	1436	1021	415
SD	68	49	56	74	30	48
Range	170	93	150	186	71	115

the young plantation (Table 2). Over the 5-year study period, the mature forest took up 3275 g C m^{-2} more than the young plantation through photosynthesis, and released 1832 g C m^{-2} more than the young plantation through respiration. Integrating over the 5 yr, the mature forest sequestered 2075 g C m^{-2} and the young plantation sequestered 630 g C m^{-2}, with the mature forest total net uptake 1445 g C m^{-2} more than the young plantation. The 5-year average $-$GEP:ER ratios (1.2 at the plantation and 1.4 at the mature forest) are well within the range reported for other evergreen forests in North America (0.87– 2.1; Falge et al., 2002).

3.2. Chamber-based estimates of respiration

At the mature pine forest, estimates of total ER based on eddy-covariance and storage measurements and those based on chamber measurements are correlated with $r = 0.92$ for 10-day block averages, and the 5-year averages differ by only 5%. The correlation increases with increasing averaging time due to random sampling errors. At the young plantation, the two methods of estimating ER are correlated with $r = 0.86$ for 10-day block averages, and the 5-year average ER based on chambers is 15% smaller than the 5-year average from eddy-covariance. The cumulative estimates of ER from both methods over the 5-year period are shown in Fig. 2.

The larger percentage disagreement between eddy-covariance and chambers at the young plantation may be because there are fewer soil chambers and more data gaps compared to the mature site. The lack of agreement may also be related to an over-estimation by the eddy-covariance method associated with nocturnal flux footprints partially outside the plantation that may include older pines or wetter areas, even though the weakest
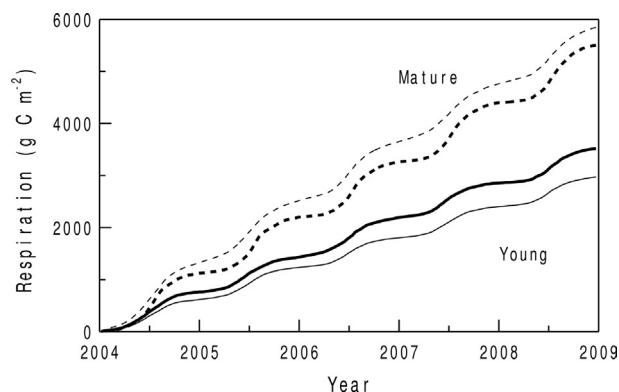
Fig. 2. Cumulative estimates of total ecosystem respiration (ER) for the mature pine (dashed) and the young plantation (solid) for the eddy-covariance method (heavy curves) and the chamber-based method (light curves).

vertical mixing nocturnal periods with the largest modelled flux footprints were removed through use of the u_*-filter. Another factor is that over estimates of daytime ER from eddy-covariance data and flux partitioning can result when daytime temperatures are outside the nighttime temperature range used to calibrate the model of ER. Errors associated with both methods of estimating ER are large (Thomas et al., 2009), and therefore it should not be assumed that the differences between methods found here (Fig. 2) are significant. The difference in ER between sites is considerably larger than the difference between methods at either site.

3.3. Biological NEP estimates

Estimates of NEP based on biological measurements are considerably lower than $-$NEE (Fig. 3, top two panels), which is common for these comparisons. For example, at eastern North American deciduous forests, Curtis et al. (2002) found that the ratio of $-$NEE to NEP exceeded 2 for three out of the five sites studied, and exceeded unity for four out of five sites. Good agreement between estimates of NEP and NEE has also been reported (e.g. Barford et al., 2001), where biometric NEP was simply computed from the difference between change in live aboveground biomass and change in coarse wood debris over a year, a method that assumes soil carbon storage is near steady-state.

At the mature site, the 5-year average NEP is 168 g C m^{-2} yr^{-1} compared to a 5-year average $-$NEE of 415 g C m^{-2} yr^{-1}, or a difference of 247 g C m^{-2} yr^{-1} (Table 3). At the plantation, where the 2008 biological data is not available due to deterioration of growth bands, the 4-year average NEP is $-$35 g C m^{-2} yr^{-1} (net carbon source) compared to the 4-year average $-$NEE of 108 g C m^{-2} yr^{-1} (net carbon sink), or a difference of 143 g C m^{-2} yr^{-1}.
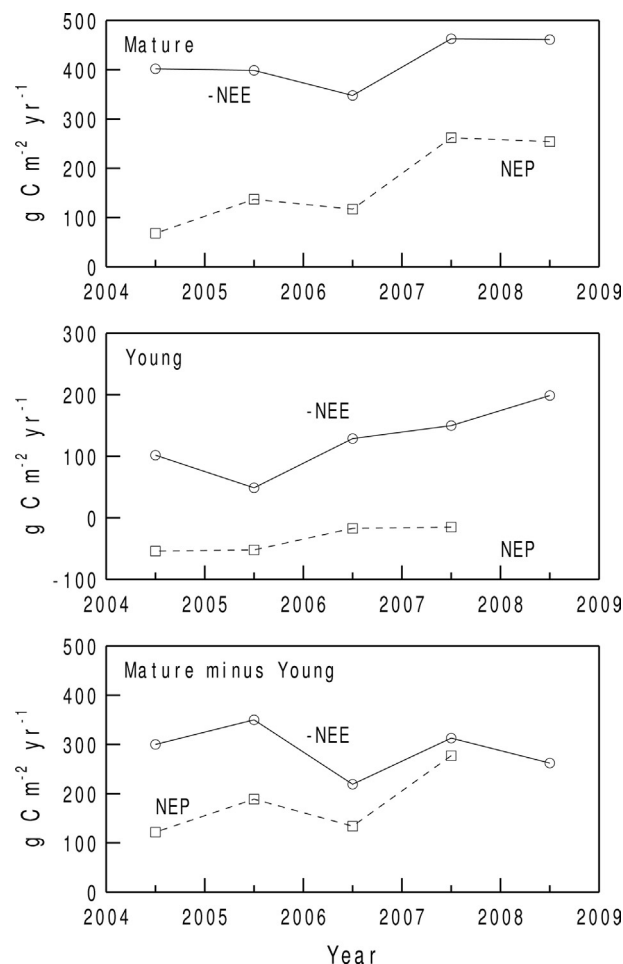

Fig. 3. Annual $-$NEE based on eddy-covariance and storage measurements and NEP based on biometric measurements for the mature pine (top) and the young plantation (middle). The bottom panel is the difference (mature minus young) between sites using NEE (solid) and NEP (dashed).

The 4-year average NEP estimates indicate 181 g C m^{-2} yr^{-1} more sequestration at the mature site compared to the plantation, while the NEE estimates for the same time period indicate 295 g C m^{-2} yr^{-1} more sequestration. Considering only 2006 and 2007, NEE indicates 266 g C m^{-2} yr^{-1} more sequestration at the mature site, while NEP indicates 207 g C m^{-2} yr^{-1} more sequestration. Thus, while the absolute estimates of NEP and $-$NEE are considerably different at each site, the biometric and eddy-covariance methods tend to agree on the relative difference between sites (Fig. 3, bottom panel).

The increasing trend in NEP at the mature site (Fig. 3, top panel) is not consistent with the eddy-covariance flux measurements (NEE). NEP relies on static assumptions about heterotrophic respiration and below-ground allocation so temporal trends may not represent

Table 3. Five-year average (2004–2008) quantities described in the text, except for the biological estimates at the young plantation which are 4-year averages (2004–2007)

	Young plantation	Mature forest
LAI	1.5	3.3
$-$GEP (g C m^{-2} yr^{-1})	781	1436
ER (g C m^{-2} yr^{-1})	655	1021
$-$NEE (g C m^{-2} yr^{-1})	126	415
ET (mm)	365	515
PPT (mm)	360	480
IWUE (g C hPa)/(kg H2O)	20	15
ANPP (g C m^{-2} yr^{-1})	65	299
BNPP (g C m^{-2} yr^{-1})	67	233
NPP (g C m^{-2} yr^{-1})	132	532
Rh (g C m^{-2} yr^{-1})	167	364
NEP (g C m^{-2} yr^{-1})	-35	168

real conditions. It is difficult to determine which values of carbon sequestration (NEP versus NEE) truly represent these sites; however, we feel that each measure has distinct merit. Unknown systematic errors may influence NEE estimates; however, NEE is capable of resolving short- and long-term temporal trends that NEP cannot because any measurement bias with the NEE technique changes little through time. Curtis et al. (2002) pointed out that small errors in the measurements of large trees can lead to large errors in NEP because the allometric equations are highly nonlinear, and that simplistic partitioning of total respiration into heterotrophic respiration is a major source of uncertainty in NEP estimates. Rh fraction may be the largest source of uncertainty in NEP.

3.4. Seasonal patterns

The seasonal patterns of the carbon fluxes are shown in Fig. 4. The $-$NEE peaks around the beginning of June, when both sites normally begin to experience water-stress (explored further below) that triggers a decrease in $-$NEE associated with $-$GEP levelling off while ER continues to increase in response to the warming soil. The young plantation is influenced by the seasonal water-stress about 1 month sooner than the mature forest based on the time when $-$GEP reaches a maximum. The 5-year average date of the onset of decline in $-$GEP is 16 June at the young plantation and 15 July at the mature site. The average onset of decline in $-$GEP precedes the onset of decline in ER by 15 d at the young plantation and 9 d at the mature site. The average time lag between the peak in $-$GEP and the peak in ER is 11 d at both sites when using the independent chamber measurements for ER instead of the estimate based on eddy-covariance and daytime flux partitioning. From August to the end

of the year, GEP and ER remain in approximate balance at the young plantation (NEE near zero), while small net uptake occurs at the mature site (Fig. 4), which may reflect the higher soil moisture near the surface and an ability to draw water from deeper soil layers compared to the young plantation (Anthoni et al., 2002). The larger $-$GEP at the mature site during the strong growth season (April–June), when neither stand is thought to be water-stressed, is likely due to the larger LAI (5-year average of 3.3 at the mature forest compared to 1.5 at the young plantation). GEP and ER do not go to zero during the winter due to the moderate winter temperatures compared to colder, more continental sites at similar latitudes.

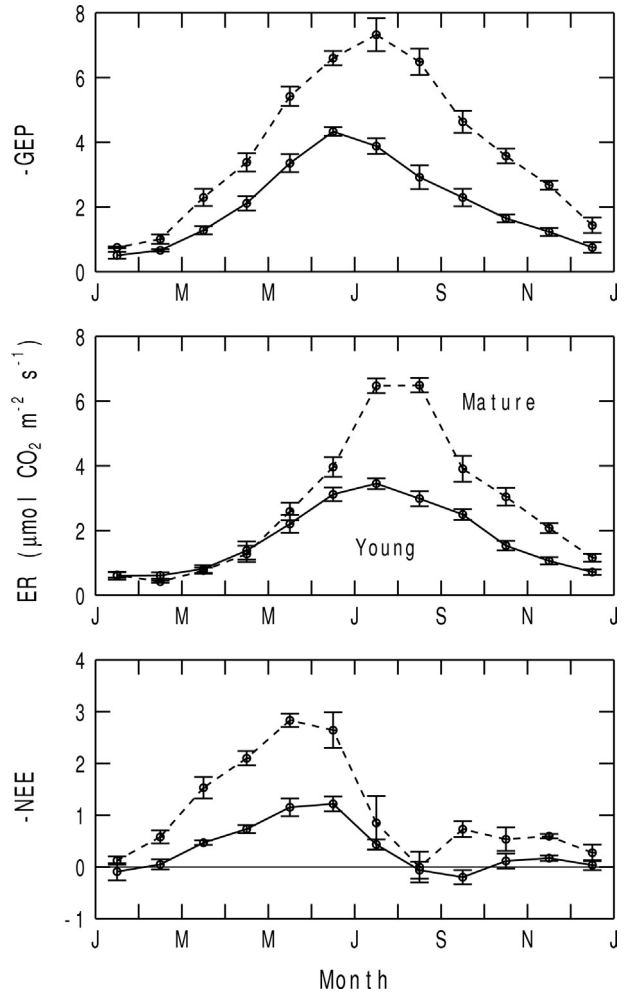The ratio of GEP at the mature site to GEP at the young plantation is relatively constant throughout the

Fig. 4. The 5-year average monthly mean carbon fluxes for the mature pine (dashed) and young plantation (solid). Error bars denote ± 1 standard error based on the interannual variability.

year and averages 1.9 (Fig. 5). A GEP ratio significantly greater than unity and relatively constant throughout the year is consistent with a difference in LAI. The 5-year average LAI ratio of 2.2 is about 15% larger than the GEP ratio of 1.9. The slight increase in the GEP ratio during the seasonal drought transition, and the generally larger values in the dry autumn compared to the wet spring, are consistent with relatively less water-stress on photosynthesis at the mature site compared to the young plantation.

The seasonal pattern of the ER ratio (ER at the mature site divided by ER at the plantation) is more variable, where the ratio is near unity in the spring and two in the fall (Fig. 5). The explanation for the lower ER ratio in spring appears to be higher soil temperatures at the plantation because of less snow accumulation and less shading by the canopy leading to an earlier snowmelt. We attribute the sharp increase in soil temperature at the plantation in March (but not at the mature site, Fig. 1) to snowmelt lowering the surface albedo, although we do not have automated measurements of fractional snow cover data. As a result of the cooler soil temperatures at the mature forest, the ER difference in spring is smaller than would be anticipated based on the differences in LAI and GEP. The warmer soil temperature throughout the year at the plantation, excluding November through February, is presumably due to less shade from the younger stand with lower LAI (Amiro et al., 2006).

The seasonal patterns of precipitation (PPT, from rain gauges) and evapotranspiration (ET, from eddy-covariance) are shown in Fig. 6. The 5-year annual average ET is 515 mm at the mature site and 365 mm at the plantation. The peak monthly mean ET is found in June at the plantation and in July at the mature site, corresponding to the timing of maximum $-$GEP. A strong

correlation is found between monthly mean photosynthesis ($-$GEP) and water vapour exchange (ET, evaporation plus transpiration) at the ecosystem scale, consistent with leaf-level physiological control. The correlation ranges from a low of $r = 0.84$ in 2006 to a high of $r = 0.98$ in 2004 at the young plantation, with a 5-year average of 0.92. At the mature site, the correlation ranges from $r = 0.57$ in 2006 to $r = 0.90$ in 2005, with a 5-year average of 0.80. The correlations are lowest in 2006 perhaps due to a larger fraction of missing data in 2006.

Precipitation minus evapotranspiration (PPT$-$ET) is positive in November–February (soil water recharge), negative in May–September (soil dry down), and near zero in the transition months of March, April and October (Fig. 6). The 5-year annual average PPT$-$ET is -35 mm

Fig. 6. The 5-year average monthly mean water fluxes (PPT from rain gauges and ET from eddy-covariance) for the mature pine (dashed) and young plantation (solid). Error bars denote ± 1 standard error based on the interannual variability. The bottom panel is the difference (PPT–ET).
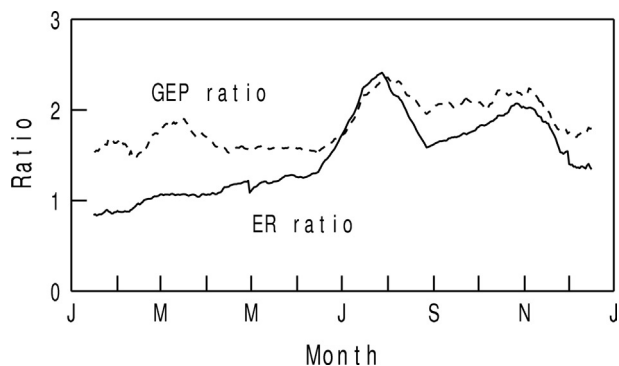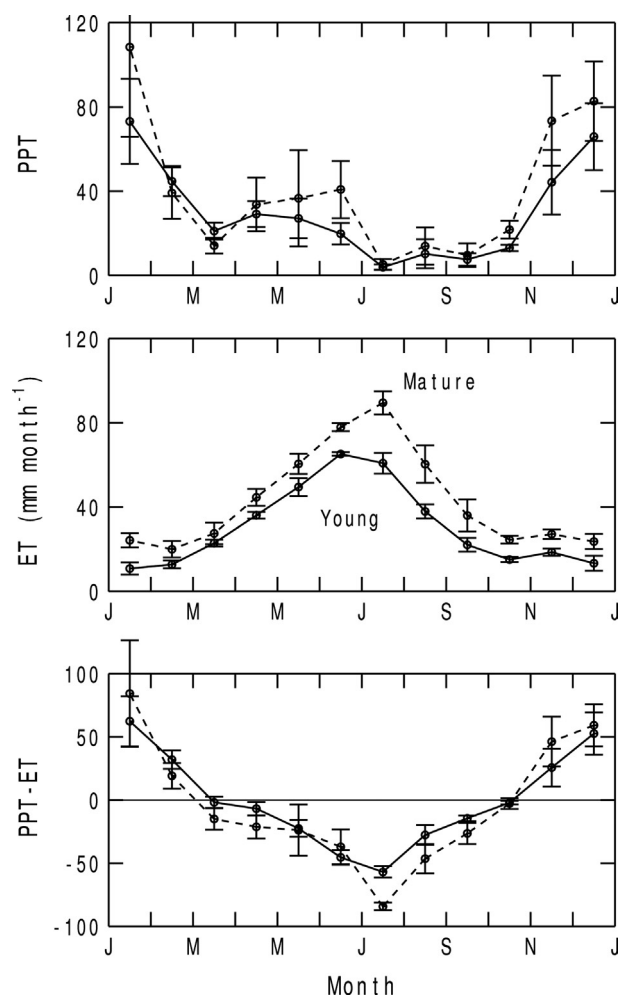

Fig. 5. The 5-year average of the 30-day running mean GEP ratio (GEP at mature site divided by GEP at young plantation, dashed) and the ER ratio (solid).

at the mature site and −5 mm at the plantation, corresponding to a relative imbalance in annual PPT–ET of 7% of total precipitation at the mature site and only 1% at the plantation (Table 3). The 5-year average monthly means of PPT–ET and dSWC are correlated at $r = 0.86$ at the mature site and $r = 0.88$ at the plantation, where dSWC is the change in SWC across the month (time derivative). This suggests that about 75% of the variance in SWC can be explained by PPT–ET. Additional variance in SWC is related to interannual variability in the timing of the soil dry down and to penetration of moisture through the 30-cm thick soil layer.

3.5. Diel patterns

Here we examine the diel cycle of the −GEP averaged over two 30-day periods: (a) prior to the onset of seasonal drought (May 15–June 15); and (b) subsequent to the onset of seasonal drought (July 15–August 15). In the first period, the temperature is increasing and soil moisture is decreasing, and in the second period, temperature is near its annual maximum and soil moisture and precipitation are at their annual minimum. The solar radiation is similar for these two periods. Here we focus on 2007.

In the first period, the maximum gross carbon uptake occurs near local noon (11 am at the mature site and 2 pm at the plantation), suggesting that photosynthesis is primarily limited by radiation, and that water availability is not limiting (Fig. 7). However, in the second period, the maximum uptake occurs well before the time of maximum radiation (9 am at the mature site and 8 am at the young plantation), strongly suggesting that photosynthesis is moisture-limited at both sites. The 6-hour shift in the time of peak photosynthesis at the young plantation, compared to 2 h at the mature site, is consistent with higher sensitivity to water-stress at the plantation. The water-stress is associated with a lack of precipitation, decreased SWC and increased vapour pressure deficit (Fig. 1).

In addition to the shift in timing of the hourly peak in photosynthesis, the magnitude of the peak 1-hour average −GEP is reduced in the second period compared to the first. The maximum 1-hour average −GEP at the mature site decreases from 16.2 μmol CO_2 m^{-2} s^{-1} in the first period to 12.6 μmol CO_2 m^{-2} s^{-1} in the second, while at the plantation the maximum 1-hour average decreases from 10.3 μmol CO_2 m^{-2} s^{-1} to 5.3 μmol CO_2 m^{-2} s^{-1} (Fig. 7). The relative reduction in the peak 1-hour average −GEP from the first period to the second period is 25% at the mature site and 64% at the plantation.
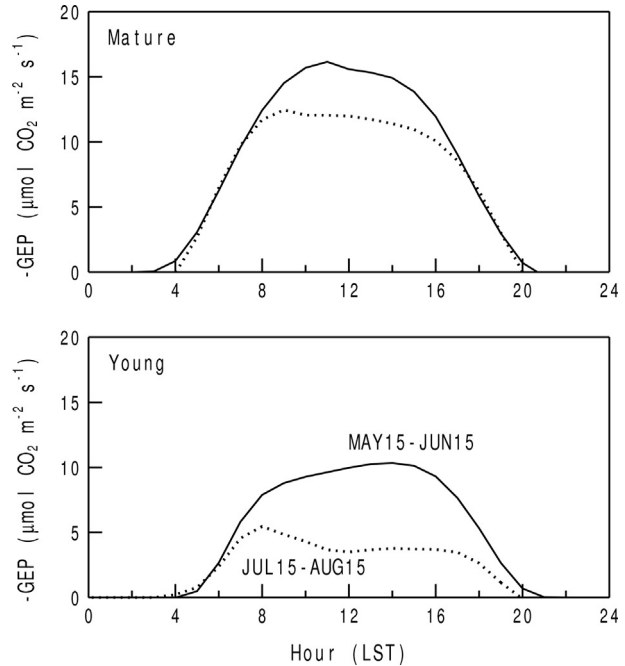

Fig. 7. The average diel cycle of −GEP at the mature site (top) and the young plantation for 15 May to 15 June (solid) and 15 July to 15 August (dotted).

3.6. Interannual variability

At the mature site, no single year is significantly different than any other year in terms of annual NEE based on the 90 or 80% confidence intervals for the 5-year record considered here (Fig. 8). The standard deviation here is based on the estimate of uncertainty in an individual estimate of annual NEE due to different gap-filling methods as described above. However, at the young plantation, the annual −NEE for 2005 is significantly different (lower at 90% confidence) than every other year. Lowering the significance level from 90% to 80%, the annual NEE difference at the plantation is significant between 2004 and 2007, 2004 and 2008, and 2006 and 2008. We note that the confidence levels here are crude estimates because of the small sample size.

An important component of the interannual variability of −NEE at the plantation is an increasing trend associated with a 64% increase in peak LAI over the 5-year record (aggrading, an increase in peak LAI from 1.1 to 1.8). The annual −NEE increased 97 g C m^{-2} yr^{-1} over the 5 years (Table 2). Removing the linear trend in −NEE with year, reduces the standard deviation of annual NEE by about a factor of two (from 56 to 30 g C m^{-2} yr^{-1}), suggesting that much of the variance in annual NEE at the plantation can be attributed to the aggrading young forest, as LAI has not yet reached the
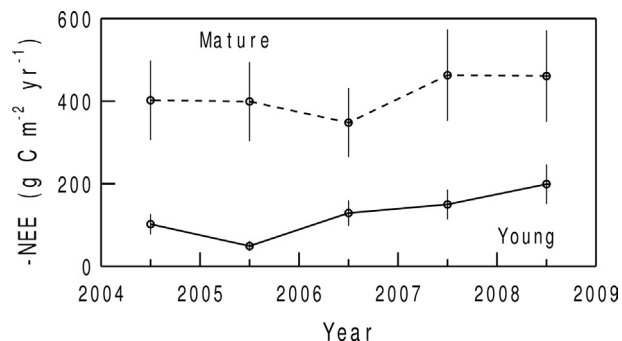
Fig. 8. Interannual variability of −NEE at the mature site (dashed) and the young plantation (solid). Error bars denote the 90% confidence interval based on the uncertainty in the annual average due to gap-filling and flux partitioning.

potential for the site (potential LAI = 2.5; Coops et al., 2005).

During the 2004–2008 study period, only 2005 is classified as a moderate drought year based on PRISM analysis and the on-site rain gauges. The 2005 water-year precipitation (October 1, 2004 to September 30, 2005) at the mature site was 330 mm, or about 70% of the 5-year average. Water-years 2004, 2007 and 2008 were near-normal, and 2006 was slightly above the 5-year average. The drought year (2005) clearly coincides with the smallest annual −GEP and −NEE observed at the plantation, however, 2005 does not stand out as a low annual −NEE year at the mature site (Table 2 and Fig. 8). A higher sensitivity to water-year drought at the plantation contributes to a larger interannual variability of NEE.

3.7. Inherent water-use efficiency (IWUE)

Plants control their stomata in an attempt to maximise the amount of carbon assimilated per amount of water transpired. The water-use efficiency, or the amount of carbon gained per unit of water loss, is used to quantify this process. The inherent water-use efficiency (IWUE), introduced by Beer et al. (2009) as a proxy for the intrinsic water-use efficiency, is shown in Fig. 9, top panel. The ecosystem-level IWUE is calculated here as the daily −GEP times the mean daylight vapour pressure deficit divided by the daily evapotranspiration (IWUE = −GEP × VPD/ET), where GEP and ET are determined from eddy-covariance flux measurements and VPD from temperature and relative humidity measurements at the top of the tower. The actual ecosystem water use efficiency (WUE = −GEP/ET, Fig. 9, bottom panel) is obscured by variations in VPD across the seasons, and therefore IWUE is more reflective of real water limitations at these two sites.

Beer et al. (2009) found that the IWUE increases in response to short-term drought conditions. The current data support this, where WUE and especially IWUE increase during the seasonal drought (Fig. 9). Both sites become more efficient at water-use when they are water-stressed. The increase in IWUE occurs first at the young plantation, probably because the younger stand has a lower baseline soil moisture and a shallower root system that cannot access deeper soil moisture. Irvine et al. (2004) reported that 80% of water used during the summer months of 2002 at a nearby naturally regenerating young pine site was extracted from a depth of 80 cm or less, whereas almost half of the water extracted at an old growth pine site during the same months came from below 80 cm depth. During the summer drought, the IWUE is larger at the young plantation, suggesting that in addition to suffering seasonal drought stress sooner, the young plantation also experiences more severe stress.

The 5-year annual average IWUE is 15 (g C hPa)/(kg H_2O) at the mature site and 20 (g C hPa)/(kg H_2O) at the plantation (Table 3). During the seasonal drought (June–September), the 5-year average IWUE is 26 (g C hPa)/(kg H_2O) at the mature forest and 40 (g C hPa)/(kg H_2O) at the plantation. For the other 8 months of the year, the 5-year average IWUE is 9 (g C hPa)/
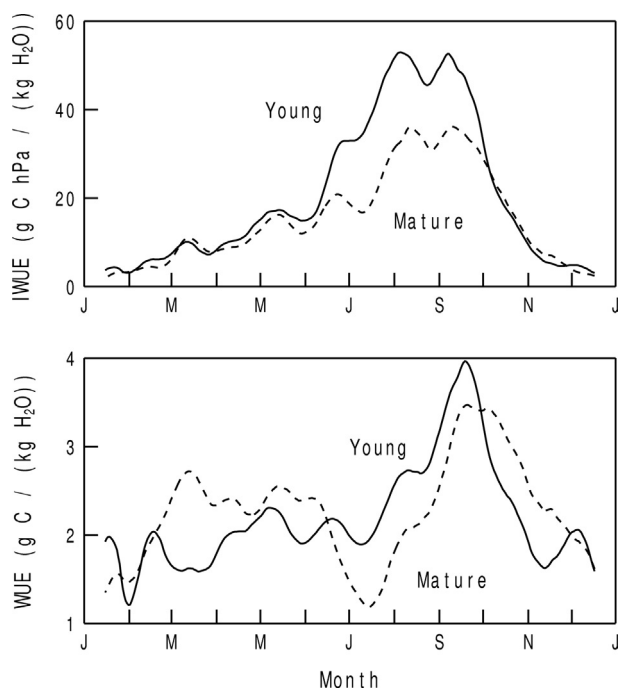

Fig. 9. The 5-year average seasonal pattern of daily inherent water-use efficiency (IWUE = −GEP × VPD/ET) for the mature pine (dashed) and young plantation (solid). The bottom panel is the actual water-use efficiency (WUE = −GEP/ET). Daily values have been smoothed with a 15-day running average for display.

(kg H_2O) at the mature forest and 10 (g C hPa)/(kg H_2O) at the plantation. The close agreement in IWUE values outside the seasonal drought period (Fig. 9, top panel), when neither forest is thought to be primarily water-stressed, raises the possibility of a species-specific value of IWUE independent of stand age. By contrast, differences in WUE between stands outside the drought period are substantial; however, the increases of both IWUE and WUE at both sites in late summer tend to confirm that the two ages of forest are responding to drought conditions similarly.

Summer maximum IWUE is 1.5 times higher at the young plantation than the mature forest, yet summer maximum LAI and GEP at the young plantation are approximately 50% of that of the mature site during severe drought. Normalizing the IWUE for LAI suggests that the young plantation is three times as sensitive to soil water deficit as the mature site (Table 3). In addition, the ratio of evaporation to transpiration is probably higher at the young plantation due to the lower LAI and higher amount of solar radiation reaching the soil, and the effect of drought likely reduced evaporation more than GEP at the young plantation (yielding a higher IWUE).

3.8. Transpiration

The seasonal pattern of the normalised transpiration rates estimated from sapflow measurements averaged over 2004 and 2006 are shown in Fig. 10. The peak in transpiration occurs on 24 June at the young plantation and 6 July at the mature site. These dates are within 1 week of the corresponding peaks in the $-$GEP estimated from eddy-covariance for the corresponding years, indicating a strong link between GEP and tree transpiration through the inherent dependence of stomatal conductance on photosynthesis rates. The dates of peak transpiration from sapflow measurements and peak ET from eddy-covariance measurements are within days of each other. By the end of August, the young plantation is transpiring at a rate equal to 25% of its annual maxima, compared to 50% for the mature site, again suggesting more seasonal drought water-stress at the young plantation (Fig. 10). The decrease in the rate of decline in transpiration beginning in the last half of August corresponds with unusual dry season precipitation that occurred in August 2004.

4. Conclusions

The net carbon uptake (annual $-$NEE) at the mature site is 3.3 times larger than at the young plantation based on 5 yr of coincident eddy-covariance measurements.
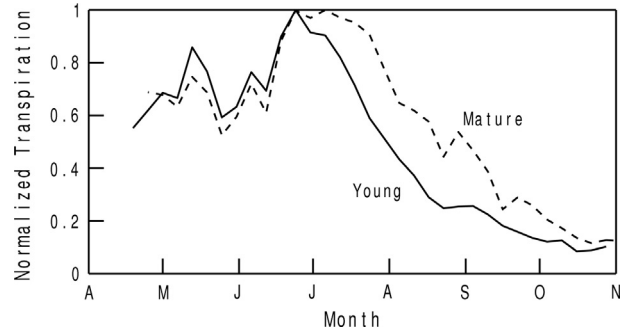

Fig. 10. The 2-year average (2004 and 2006) seasonal pattern of the normalised tree transpiration from sapflow measurements for the mature pine (dashed) and the young plantation (solid) for April–November.

The difference in the 5-year average annual $-$NEE between sites (415–126 = 289 g C m^{-2} yr^{-1}) is larger than can be explained by the observed interannual variability or by the uncertainty in the individual annual estimates. The annual NEE difference between sites is supported by the biometric-based estimates of NEP. Chamber-based estimates of ER compare well to the estimates based on the eddy-covariance method. We attribute the significantly higher annual net carbon uptake at the mature forest to larger springtime gross uptake (photosynthesis) associated with larger LAI, and to reduced springtime ER due to lower soil temperatures.

Both sites experience seasonal water-stress beginning in June/July that triggers a decrease in $-$NEE associated with $-$GEP levelling off while ER and soil temperature continue to increase. That is, GEP responds to the onset of seasonal drought sooner than ER. Based on seasonal and diel patterns of GEP, and seasonal patterns of the IWUE and the normalised transpiration, a consistent pattern develops indicating that the young plantation responds to the seasonal drought sooner and to a more severe degree. The increased sensitivity to seasonal drought at the plantation is also seen in the cumulative $-$NEE curves, where 75–80% of the calendar year net uptake of carbon is achieved by the onset of seasonal drought at the mature site, while 90–95% of the annual carbon uptake is achieved by the onset of seasonal drought at the plantation. Lower sensitivity to seasonal drought at the mature site is likely due to higher soil moisture reserves year round, a deeper root system that can access more water, and a larger storage capacity in the stems that provides a buffer against water-stress.

The 5-year average seasonal patterns of the IWUE at both sites show close agreement outside the seasonal drought period, when neither forest is thought to be primarily water-stressed. This result raises the possibility of a species-specific value of the IWUE that may be

independent of stand age. During the summer drought, the IWUE increases sharply at both sites and becomes larger at the young plantation, suggesting that both sites become water-limited and that the plantation experiences more severe water-stress.

The lowest annual $-$GEP and $-$NEE observed at the young plantation occurred during the only water-year classified as moderate drought. By contrast, the same drought year did not stand out as a low annual $-$NEE year at the mature site, suggesting that the younger stand is more susceptible to reduced carbon uptake associated with water-year drought, in addition to seasonal drought. The aggrading (steady increase in LAI) and the increased sensitivity to drought accounts for the larger interannual variability at the young plantation.

With expected increases in climate-related disturbances from precipitation regime shifts and mortality from insects and fire, forests may become more vulnerable to prolonged or sequences of disturbances (e.g. Bond-Lamberty et al., 2007; Kurz et al., 2008), and this could be compounded by changes in land-use. More research is needed to provide useful information on forest vulnerability and resilience to aid management and mitigation, and to better understand the feedbacks of forest disturbances to climate. Long-term data from multiple sources such as eddy covariance, biological and microclimate measurements can play a major role in addressing these research needs.

5. Acknowledgements

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