Carbon Fluxes in a Young, Naturally Regenerating, Jack Pine Ecosystem

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Abstract

Within the network of tower-stations for performing long-term measurements of CO_2 exchange between forest ecosystems and the atmosphere, most research has focused on mature forests that are strong carbon sinks. Nevertheless, it is just as valuable to quantify fluxes from recently disturbed forests so that we can recognize and predict the impact of disturbance on carbon fluxes. We measured carbon fluxes and microclimatic variables within a naturally regenerating, young (12-14 years of age) jack pine ecosystem in northern Michigan. During the snow-free months (June-October), this ecosystem exhibited a low net uptake of approximately 18.6 g C m^{-2} in 2001, 19.7 g C m^{-2} in 2002, and 21.9 g C m^{-2} in 2003. Although 2002 was warmer than 2003, less CO_2 was taken up compared to that in 2003, the coolest year. This was in part due to enhanced respiration and a hard frost in early October of 2002 that effectively terminated photosynthesis for that year. However, this enhanced net C uptake over time may have also been an age-related increase in the productivity of this young forest. On a seasonal basis, daytime net ecosystem exchange (NEE) was accurately predicted by the empirically derived Landsberg model incorporating photosynthetically active radiation ($R^2 = 0.32 – 0.77$). An analysis of the model residuals showed a clear and significant correlation with both vapor pressure deficit and sensible heat. Soil respiration was independently measured and then modeled based on soil temperature. Model estimates were 627, 583, and 681 g C m^{-2} over the June-October months in 2001, 2002, and 2003, respectively. NEE and soil respiration were inversely correlated in mid-summer ($r = -0.6$, $p = 0.001$) during the period of lowest NEE (greatest uptake) and highest soil respiration rates. Our results indicate that 12-14 years following disturbance this ecosystem displays a small net uptake during the June – October months, but respiratory losses during the snow season (mid-October to April) could possibly counter-balance this carbon gain.

Keywords: net ecosystem exchange, soil respiration, carbon flux, eddy covariance, jack pine (*Pinus banksiana)*, disturbance, Great Lakes region, USA

1. Introduction

In recent years, much research has focused on long-term tower-based measurements of CO_2 exchange between forests and the atmosphere. In this effort to determine the role of terrestrial ecosystems in the global carbon budget, most studies that utilize the eddy covariance technique have focused on mature forests that are demonstrable carbon sinks (e.g., see the reviews of Law et al., 2002; Baldocchi et al., 2001). Equally valuable, and as a basis for comparison, are measurements within young, recently disturbed ecosystems.

Generally, net ecosystem productivity (NEP, or equivalently, net ecosystem exchange of carbon, NEE = -NEP) changes over the course of succession. This carbon flux is believed to exhibit negative to slightly positive values in young ecosystems, increase to a maximum value as the ecosystem reaches maturity, and then decline slightly as the ecosystem ages (Odum, 1969; Ryan et al., 1997; Pregitzer & Euskirchen, in press). Consequently, modifications in land use can play a dominant role in carbon cycling (Houghton et al., 1999, 2003; Schimel et al., 2000). In order to better understand carbon cycling in complex landscapes, it is important to consider ecosystems over a diverse array of developmental stages, site conditions, and disturbance regimes (Litvak et al., 2003; Thornton et al., 2002; Chen et al., 2002).

The disturbance history of the tree species jack pine (*Pinus banksiana* Lamb.) includes timber harvesting at 50-year intervals and frequent fires, resulting in numerous young (e.g., < 20 years) jack pine ecosystems within the landscapes of the northern Great Lakes region of the United States. Jack pine is one of nine tree species that are widespread and dominant in the North American boreal forest (Payette, 1992), and it is also prevalent within the northern limit of the temperate biome (Barnes & Wagner, 1996). It commonly grows on drier, less fertile soils than other native tree species in the Great Lakes region. The species is of both ecological and commercial importance in the United States, serving as habitat for unique plant assemblages and threatened bird species (Houseman & Anderson, 2002), and a source of timber production (Vasievich & Webster, 1997). The pervasiveness of this species combined with its commercial and ecological roles suggest that quantification of its ability to sequester carbon over a range of successional stages, and how this relates to biophysical constraints, is important both in terms of global climate change and international science treaties such as the Kyoto Protocol (IGBP Terrestrial Carbon Working Group 1998).

Although other researchers have examined NEE within jack pine ecosystems using the eddy covariance technique, these studies have taken place in mature and old jack pine forests (Baldocchi et al., 1997; Joiner et al., 1999; Griffis et al., 2003). On a daily, seasonal, and interannual basis, one would expect the carbon fluxes (including both NEE and soil respiration) within a young (12-14 years of age) jack pine ecosystem to vary due to fluctuations in air temperature, soil temperature, solar radiation, precipitation, soil moisture, vapor pressure deficit, phenology of the understory, and photosynthetic capacity. At the beginning of the growing season, the onset of net carbon uptake is likely related to timing of the spring snowmelt, leaf-out in the understory, and increases in air temperature while in the fall, declines in net carbon gain are correlated with decreases in the photoperiod and the first frosts (Havranek & Tranquillini, 1995; Lamontagne et al., 1998; Striegl & Wickland, 2001; Tanja et al., 2003). Both C gains through photosynthesis and C losses through respiration would likely be higher in mid-summer due to a long photoperiod and high temperatures. All the same, we do not know exactly how and why the fluxes in this type of ecosystem vary. Therefore, the study described in this paper focuses on the carbon fluxes over a young jack pine ecosystem located in northern Michigan. Over three snow-free seasons in 2001-2003, the specific objectives of this study were to: (i) define the daily, seasonal, and interannual patterns of NEE, (ii) investigate possible biophysical controls of daytime NEE, (iii) examine soil surface CO_2 efflux (or soil respiration) within this ecosystem, while relating this flux back to NEE, and (iv) compare our measured NEE estimates with those from published estimates of jack pine forests in different age classes.

2. Methods

2.1. Site description

The experimental site is located in the upper peninsula of Michigan, about 10 miles southeast of Lake Superior near the town of Alberta (46º N, 88º W). The naturally regenerated jack pine (*Pinus banksiana* Lamb., averaging 2.5 m in height) are growing on a site that was clearcut and left with large piles of slash in 1988. Also growing at the site are the occasional black cherry (*Prunus serotina*; averaging 1.5 m in height) and red oak (*Quercus rubra*; averaging 1.5 m in height). The stand density is 1,158 stems ha^{-1}, and the average diameter at breast height is 13.4±2.2 cm. The leaf area index is 0.93 ± 0.30 m^2 m^{-2}. The understory is extensive and dominated by blueberry (*Vaccinium* spp.), bracken fern (*Pteridium aquilinum*) and assorted graminoids.

The terrain is level with virtually unlimited fetch. The soils are excessively well-drained, drought-prone sands of the Rubicon series located on glacial outwash. They consist of 1.5% C and 0.07% N in the A/E horizon to a depth of 10 cm. The climate is strongly influenced by Lake Superior, with an average annual snowfall of 400-500 cm and average annual precipitation of 75-90 cm (Albert, 1995).

2.2. Instrumentation and measurements

2.2.1. Eddy covariance and microclimatic measurements

Due to the remote location of the site and the absence of line power, the eddy covariance equipment was driven by 12 volt deep-cycle marine batteries connected to three 100-watt solar panels. This set-up hindered measurements during winter periods when the snowpack was deep and cloud cover obscured solar radiation. Consequently, depending on the climatic conditions for a given year, all eddy covariance and meteorological data were typically collected from April or May to October or November, with the precise measurement periods for each set of variables noted in more detail below.

The eddy covariance measurement system for computing fluxes of carbon, water, and energy (Baldocchi et al., 1988) was placed on a triangular communication tower in the center of the site. This instrumentation consisted of a 3-D sonic anemometer (CSAT3; Campbell Scientific Instruments, Logan, UT, USA) and an open-path infrared gas analyzer (LI-7500 IRGA; LI-COR, Inc., Lincoln, NE, USA) mounted at a height of 3 m. These were connected to a digital system to log data at 10 Hz intervals with the on-line computation of 30-minute averages (CR23X; Campbell Scientific Instruments, Logan, UT, USA). Raw data and the 30-minute averaged data were collected once a week from a laptop computer that was linked to the data logger. The "WPL" corrections were applied off-line to the flux measurements to account for changes in mass flow caused by changes in air density (Webb et al., 1980; Leuning & Moncrieff, 1991). In 2001, the collection of the eddy covariance data began in May and ended in mid-November, while in 2002, the measurements began in April and ended in late October. During 2003, measurements began in April and ended in early November.

Basic microclimatic information was also collected, including: photosynthetically active radiation (PAR; 3 m above the ground; LI 190SB, LI-COR, Inc., Lincoln, NE, USA), air temperature (T_a) and relative humidity (Rh; at 1 and 3 m above the ground; HMP45C, Vaisala, Helsinki, Finland), soil moisture (M_s; Watermark #257 Campbell Scientific Instruments, Logan, UT, USA), soil heat flux (G; three replicates at the mineral soil surface, HFT3, Radiation Energy Balance Systems, Seattle, WA, USA), net radiation (Rn; Q*7.1, Radiation Energy Balance Systems, Seattle, WA, USA), precipitation (P; TE525, Texas Electronics, Dallas, TX, USA), and barometric pressure (Bp; PB105, Vaisala, Helsinki, Finland). This meteorological data was collected at 15-second intervals with the computation of 30-minute averages and stored on two data loggers (CR10X; Campbell Scientific Instruments, Logan, UT, USA). In 2001, collection of this suite of meteorological data began in late May and ended in early November. In 2002, meteorological measurements began in early February and ended in late October, and in 2003, measurements began in April and ended in early November.

Soil temperature ($T_{s;}$ at depths of 0, 5, and 20 cm) data was recorded at hourly to half-hourly intervals continuously from late May 2001 to early November of 2003 (HOBO four channel external data loggers; Onset Corp., Pocasset, MA, USA). During each measurement year, the dates by when 100% of the snowpack had melted and of leaf-out in the understory were recorded.

2.2.2. Soil respiration measurements

Beginning in June 2001, soil respiration (SR) measurements were taken using an infrared gas analysis system attached to a cylindrical chamber of known volume (EGM3 and SRC1; PP Systems, Haverhill, MA) at least once every two weeks during the snow free season. Prior to taking measurements in the spring, soil respiration collars constructed from polyvinylchloride tubing 10 cm in diameter were installed to create a tight seal between the soil respiration chamber and the ground. Simultaneous measurements of T_s (5 cm depth) were taken alongside each collar at the time of each soil respiration measurement using a digital thermometer (Checktemp; Hanna Instruments, Bedfordshire, U.K.). Soil samples were obtained to a 10 cm depth in the A horizon from four randomly selected points within the ecosystem at the time of each SR measurement. These samples were then oven-dried for 48 hr at 105°C to determine gravimetric moisture contents (M_{sg}, % dry weight).

2.3. Data treatment

2.3.1. Assessment of data quality

To determine the overall quality of the eddy covariance data, two analyses we employed were: (1) the determination of the energy budget closure, and (2) an assessment of a critical friction velocity (u*, a meteorological scaling quantity that represents the influence of surface friction) threshold. It is often assumed that the reliability of an eddy-covariance system is determined by the level of energy balance closure at a site. The energy budget closure was computed by summing the daytime sensible and latent heat fluxes (H + L) and plotting them against net radiation minus soil heat flux (Rn – G; Aubinet et al., 2000). In terms of the u* threshold, the flux community generally recognizes that the eddy covariance technique may underestimate fluxes under calm conditions at night due to weak vertical exchange. Therefore, the data was screened to determine a critical u* threshold, below which the respiratory fluxes would most likely be underestimated.

2.3.2. Gap-filling

Data gaps occurred due to either instrument malfunction or power outages. Gaps in meteorological data were filled using values from a nearby (approximately 4 km from the site) weather station. As a pre-treatment measure prior to filling large data gaps in the NEE data, small, 2-3 half-hourly data gaps, were filled via linear interpolation of the adjacent missing values (Falge et al., 2001). These short gaps in the eddy covariance data were usually caused by instrumental errors during times of precipitation.

For larger data gaps in NEE, typically1-6 days and due to power failure or instrument malfunction, our gap-filling methods consisted of calculations of mean diurnal variation (MDV). We followed the methodology of Falge et al. (2001) who found that the mean diurnal method of gap-filling provided stable approximations of missing data using 7-day independent windows during the nighttime hours (2200 – 500), and 14-day windows for the daytime hours (530 – 2130). Since the method of gap-filling can have a large impact on the calculated values for annual NEE, we also attempted to fill larger

NEE data gaps via semi-empirical methods (e.g., "look-up" tables and nonlinear regression; Falge et al., 2001). However, we found that this approach was not adequate because dividing the dataset into temperature and PAR classes on a bimonthly basis resulted in a relatively large number of empty bins, thereby making some of the regressions unstable. An equipment failure during July 2003 resulted in a near complete loss of eddy covariance data for the month. To determine the monthly value of NEE during this time, we used the average of NEE from July of 2001 and 2002. All gap-filling procedures and statistical analyses were performed using the SAS software (SAS Institute, Version 8.01).

2.4. Empirical modeling

2.4.1 Modeling NEE

We examined the relationship of daytime NEE to PAR with the Landsberg model,

$$NEE_{day} = P_{max}(1- \exp^{-\alpha(PAR - Icomp)}) \qquad \text{[Equation 1]}$$

P_{max} is the maximum rate of photosynthesis, α is a shape parameter representing apparent quantum yield (e.g., the slope of the curve), and I_{comp} is the light compensation point (e.g., the point at which photosynthesis is zero). NEE_{day} are the daytime values of NEE * (-1), such that the estimated Landsberg model coefficients are positive. Although this model was originally developed for leaf-level photosynthesis, other studies have successfully applied this model to examine ecosystem-level trends (e.g., Hollinger, 1994; Chen et al., 2002). We implemented this model to examine the NEE_{day} -PAR relationship on a seasonal basis and for all seasons combined.

After fitting this model to the NEE_{day} and PAR data, we investigated the residuals of the model, a technique that is useful in assessing the direct effect of each forcing variable. In particular, we looked for significant relationships between the residuals of the fitted Landsberg models and other biophysical variables such as vapor pressure deficit (VPD), air temperature, soil temperature, soil moisture, relative humidity, precipitation, latent heat, and sensible heat. To find the best-fit between the residuals and the biophysical variables, we analyzed a number of statistical regression models, including linear, power, polynomial, and logarithmic power functions.

2.4.2 Modeling soil respiration

Soil respiration (SR) was modeled based on two exponential models. One model examined the relationship with soil temperature (at a 5 cm depth) as the single predictor variable:

$$SR = \beta_0 * e^{\beta 1 * Ts} \qquad \text{[Equation 2]}$$

The other model incorporated both soil temperature and gravimetrically measured soil moisture:

$$SR = \beta_0 * e^{\beta 1 * Ts} * e^{\beta 2 * Msg} * \beta_3 * T_s * M_{sg} \qquad \text{[Equation 3]}$$

The models were fit to the data using a Gauss-Newton estimation method with the SAS software (SAS Version 8.02). The estimated regression coefficients from the simple exponential SR-T_s model were used in conjunction with the continually collected soil temperature data (see Section 2.2.1) to calculate total amounts of soil respiration over the measurement period, and to estimate SR during the winter months.

3. Results

3.1. Energy budget closure and u thresholds*

The energy budget closure was acceptable as indicated by the R^2 value (0.98) and slope (0.84) for the no-intercept model (Figure 1). Based on this closure, we did not correct the carbon flux data for deficiencies in carbon gain. Furthermore, we did not notice a trend of low NEE (e.g., more negative) during times of low u*, and consequently did not make any corrections in the data to this end (Figure 2).

3.2. Local weather and climatic anomalies

Over the three-year measurement period, 2002 was the warmest and wettest while 2003 was the coolest and driest. For example, monthly air temperatures averaged over the June-October months varied by 1.1°C, with 2002 having the warmest average of 15.2°C, 2003 being the coolest with an average of 14.1°C, and 2001 falling in the middle with an average of 14.6°C. On a daily basis, air temperature was most variable during April 2002, ranging from –18.0°C on April 4 (the lowest air temperature recorded during the measurements of NEE) to an anomalous 30.0°C that occurred 13 days later, on April 17 (Figure 3b). The highest air temperature recorded over the measurement period (35.4°C) occurred on July 1, 2002.

The day by which all the snow had melted in the spring varied by nine days over the three years. In 2002, all the snow had melted by April 18 while in 2003, all the snow had melted by April 15. Although we did not collect flux data in April 2001, we did note that all the snow had melted by April 23. On a year-to-year basis, there was a large degree of variability as to when the air temperature first fell below 0°C in the early fall:

this occurred on the 25th of September in 2001, the 5th October in 2002, and the 4th of September in 2003. From April – October, total precipitation in 2002 (143.6 cm) was nearly twice that of total precipitation in 2003 (78.7 cm), and about 40 cm greater than that in 2001 (98.0 cm; Figure 3c). One rainy period in May of 2003 contributed over 170 mm of rain in a day, equating to about 22% of the total precipitation received in 2003 (Figure 3c). Soil moisture varied from about 0.5-1.0 bar, with the greatest amounts occurring directly after the heavy rains (Figure 3c). As evidence of the sandy, excessively drained soils, the soil moisture remained high for a short period of time following a rain event and then declined rapidly in the absence of rain (Figure 3c). Averages of soil temperature (5 cm depth) for the June-October time frame mirrored that of air temperature, with the coolest soil temperatures occurring in 2003 (14.5°C), the warmest in 2002 (15.4°C), and 2001 falling in between (15.2°C; Figure 3b).

3.3. Net Ecosystem Exchanges of Carbon

3.3.1 Daily fluxes

On a day-to-day basis, the ecosystem usually behaved as a weak C sink (e.g., negative values of NEE), but there were some days when the ecosystem acted as a C source: most of these days occurred in spring and fall (e.g., positive values of NEE; Figure 3a). From May 21- October 21, the ecosystem was a C source for 10 days in 2001, 16 days in 2002, and 9 days in 2003 (Figure 3a). In the spring, during the period from April 1 to May 20, the ecosystem acted as a C source for 8 days in 2002 and 2 days in 2003. During the fall, from late October to early November, the ecosystem behaved as a source of C for 10 days in 2001, while during this same time period in 2003, the ecosystem was a C source for only 2 of these days (Figure 3a). The ecosystem reached a minimum value of daily NEE (-0.6 g C m^{-2} day^{-1}; Figure 3a) in April 2002 during a period of anonymously high temperatures and well before bud break in the understory (Figure 3a,b). Also during 2002, the ecosystem reached the maximum measured daily NEE (+0.2 g C m^{-2} day^{-1}), an event that occurred directly following warm temperatures in late September (Figure 3b).

3.3.2 Monthly and seasonal C fluxes

On a monthly time-step, the ecosystem was a net carbon sink with strongest uptake occurring between May and August, reaching a maximum fixation of 8.0 g C m^{-2} in July 2002. During early spring (April) and early fall (September-October), the ecosystem accumulated about half as much carbon as it did during the peak months, with a minimum of –0.6 g C m^{-2} taken up in October of 2002. There was less C uptake in June 2002 than either June 2001 or 2003 because of enhanced respiration caused by warm temperatures. Across the comparable measurement period during the growing season (June-October), the ecosystem accumulated the most carbon in 2003 (21.9 g C m^{-2}), and the least in 2001 (18.6 g C m^{-2}; Table 1).

3.3.3 Empirical modeling of daytime CO_2 uptake and PAR

On a seasonal basis, the Landsberg model was a significant predictor of NEE_{day} during the mid- to late summer periods (R^2 = 0.72-0.77, p< 0.001). In the early to late spring and fall, the model was also significant, but not as reliable a predictor (R^2 = 0.32-0.55, p < 0.0001; Table 2). Over the entire measurement period (all seasons, all years combined), the Landsberg model provided a decent fit to the data (R^2 = 0.54, p<0.0001). The saturation coefficients (P_{max}) ranged from 0.68 in fall to 1.34 in early spring. The light compensation point (I_{comp}) was lowest in early spring (15.62), and highest in late summer (82.57). The shape factor (α, an indication of the rate of change of daytime NEE per unit of PAR) varied from 1.59 x 10^{-3} in summer to 6.86 x 10^{-3} in early spring (Table 2; Figure 4a-c).

Analysis of the fitted Landsberg model revealed that on a seasonal basis the residuals were weakly, albeit consistently and significantly, correlated to VPD and H, illustrating that multiple environmental variables control NEE (Figure 4). In each case, the linear regression model provided the best fit to the residuals and the biophysical variables ($p < 0.0001$; Figure 4). As an indication that NEE was not consistently biased towards over- or underestimation at any hour, the time of day did not show a strong correlation with the residuals. Moreover, neither soil moisture nor precipitation was significantly correlated with the residuals. When all the daytime NEE data was combined across the seasons, the residuals did not show a clear correlation with any other single variable.

3.4. Soil respiration

Measured rates of soil respiration reached a maximum in August during all three years of measurements (Figure 5). These maximums were associated with the highest soil temperatures (Figure 3b). Measured soil respiration rates were around 0.1 g CO_2 m^{-2} hr^{-1} in early December of 2001, and were also low in April and early May of 2002 (~0.2 g

CO_2 m^{-2} hr^{-1}; Figure 5). However, by late May, soil respiration sharply increased to around 0.8-1.0 g CO_2 m^{-2} hr^{-1} during all three years (Figure 5).

The exponential model provided a statistically significant ($p < 0.0001$) fit to the SR-T_s relationship, explaining between 68% and 77% of the variability in the SR rates (Figure 5, Table 3). The intercepts for this exponential model ranged from 0.1202 (±0.0407) for the 2001 data to 0.2463 (±0.0493) in 2003 (Table 3). Based on this model, our estimates of soil respiration were 627, 583, and 681 g C m^{-2} over the June-October months of 2001, 2002, and 2003, respectively.

The model with an inclusion of M_{sg} and T_s x M_{sg} interaction terms explained between 75% and 88% of the variability in the SR rates, and was also statistically significant ($p < 0.0001$). In particular, in comparing the empirical soil respiration models with and without the inclusion of the soil moisture term, the data collected in the wet year of 2002 showed the most improvement when the moisture term was added (Table 3). The intercepts were typically lower in the models with the soil moisture term than those with just T_s, ranging from 0.0022 (±0.0018) in 2002 to 0.0523 (±0.3226) in 2001 (Table 3).

3.5. Coupling between NEE and soil respiration

The association between soil respiration and NEE fluctuated over the April – November time period (Figure 6). The inverse relationship between the two fluxes was generally most significant during the period of lowest NEE (e.g., greatest uptake) and highest rates of soil respiration in the summer months from June –August, when the average Pearson correlation coefficient was an average of –0.6 ($p = 0.001$) over the three years. In the spring months of April and May this correlation coefficient was not as significant, but was positive, at around an average of 0.4 ($p = 0.01$) over the three years. In an apparent decoupling of the soil fluxes and NEE, the Pearson correlation coefficient declined to an average -0.25 ($p = 0.2$) during September to early November over the three years. This apparent decoupling is probably due to the patterns of air temperatures (which were linked to the rates of NEE) and soil temperatures (which drove soil respiration rates) in early spring and late fall. While soil temperatures remained fairly steady during these times of the year, air temperatures showed greater variation (Figure 3b).

4. Discussion

4.1. Energy balance closure and the u threshold*

Given that we did not find perfect closure in the energy budget, it would have been possible to use the Bowen ratio of the eddy-covariance measurements to correct the CO_2 flux. However, we believe that this may not be an accurate method since this was a technique originally suggested for agricultural and grassland systems (e.g., Twine et al., 2000), and may not be applicable at our site. Furthermore, our lack of closure is more likely due to: (1) instrumental error of the closed-path system during extremely wet periods, and (2) the use of a single net radiometer when discrete measurements of the radiation components give a more precise assessment of the net available energy, and (3) the omission of a heat storage term in our measurements. Sampling errors associated with instrument biases in the energy measurements (G, Rn) do not affect the quality of the CO_2 measurements (Wilson et al., 2002).

Although numerous researchers have found a critical u* threshold at a given site (e.g., Barford et al., 2001; Goulden et al., 1996), we did not observe any apparent trends that would preclude regular nocturnal drainage flows (Figure 2). The reasons for this are likely related to the effectively unobstructed fetch and a study area that is level.

4.2. Seasonal and interannual behavior of NEE and soil respiration

The NEE data indicate that during the growing season there is moderate seasonal and interannual variability in this jack pine forest (Table 1), although any inferences drawn from these NEE estimates must include the stipulation that the gap-filled values were likely sensitive to the post-processing scheme (Falge et al., 2001). Nevertheless, some of this interannual variation may be an age-related increase of net C uptake of this aggrading forest (Pregitzer & Euskirchen, in press). Other sources of interannual variation might be attributed to the behavior of the ecosystem during the spring recovery of jack pine photosynthesis at the onset of the growing season and during the entrance into winter dormancy at the end of the growing season. In mid-summer, when the forest is a net C sink, there is less day-to-day variation in the carbon fluxes (Figure 3a), although high rates of mid-summer soil respiration could easily dominate NEE, as further discussed below.

We had originally anticipated that during the early spring in April and May, bud-break and full leaf-out in the dense understory of ferns, blueberry bushes, and grasses would contribute to a steep rise in photosynthetic capacity and a greater net CO_2 uptake in this ecosystem. Other investigators have previously reported that over the course of the growing season, photosynthesis of ground-cover plants in a 20-year old jack pine ecosystem accounted for 14% of total ecosystem CO_2 uptake, while ground cover assimilation of an 8-year-old ecosystem was substantially higher, at around 29% (Striegl & Wickland 1998). Furthermore, the values of P_{max} from the Landsberg equations were highest in the early spring (1.34 μmol CO_2 m^{-2} s^{-1}), declined in the late spring (0.75 μmol CO_2 m^{-2} s^{-1}), and then rose again in summer (0.90 μmol CO_2 m^{-2} s^{-1}; Table 2). Full leaf-out of the understory occurred earliest in the warm year of 2002 (May 15), and latest in 2003 (May 23), with first bud-break occurring about three weeks before full leaf-out during each year. The cumulative net C uptake from May 1 to May 15 was 1.3 g C m^{-2} in 2002 and 1.4 g C m^{-2} in 2003, with cumulative net C uptake from April – May being 7.8 g C m^{-2} in 2002 and 8.1 g C m^{-2} in 2003. That is, understory leaf-out occurred approximately one week earlier in 2002 than in 2003, but NEE during the early spring of 2002 was similar to that of 2003. It is also likely that respiratory losses did not offset any gain in NEE during leaf-out in the understory. This idea is substantiated by the low values of I_{comp} (15.6; Table 2) and soil respiration (Figure 6) during the early spring, suggesting a smaller contribution of respiration to NEE than during other periods of the year. Consequently, the relatively high rates of early season C uptake may be due to jack pine assimilation before bud break, with little overall influence from understory plant photosynthesis.

Lower values of P_{max} in late spring compared to early spring (Table 2) may have been caused by either nutrient or water limitations. Soil moisture was generally low (0.4-0.6 bar) during the later spring months, particularly in 2002 when most of the heavier rains occurred in mid-summer (Figure 3c). This decreased soil moisture may have contributed to water stress and a reduction in photosynthesis during the late-spring in this ecosystem. It is also possible that while the trees have considerable photosynthetic capacity in the early spring, before bud break and the development of new shoots, they retranslocate nitrogen to the developing needles during the late spring, resulting in nutrient limitations for a period of time. We did observe appreciable needle yellowing in the late spring, a characteristic of water-stressed and/or nutrient limited trees.

The effect of subzero air temperatures in the spring and early fall had a much different impact on net C uptake than they did in the late fall. The last day of frost in the spring occurred on May 30, May 25, and June 1 in 2001, 2002, and 2003, respectively. Nevertheless, these frosts seemingly did not decrease the net C uptake during this time (Figure 3a,b; Table 2), probably due to the increased photoperiod and overall greater frost hardiness than during the late fall (Havranek & Tranquillini, 1995). While the first frost occurred earlier in 2003 (September 4; daily minimum of –0.6 ºC) than in 2001 (September 25; daily minimum of –2.9ºC) or 2002 (October 5; daily minimum of – 8.2ºC), this early fall frost did not strongly decrease C uptake in the following weeks (Figure 3a). In fact, net C uptake was higher in September and October of 2003 than in September and October of 2001 and 2002 (Table 1), indicating that the plants easily recovered from this frost, perhaps due to the fact that temperatures were not substantially below 0ºC and the frost occurred relatively early in the fall. Lamontagne et al. (1998) induced artificial frosts during the growing season on jack pine and found that when the trees were treated to temperatures of -5.5ºC they recovered fully within 10 days, but when treated at -8.5ºC they exhibited a limited recovery. When the first frost occurred in 2002, temperatures did fall to near -8.5ºC, and accordingly the plants, which at this late point in the year may have already been approaching a stage of winter dormancy (Monson et al., 2002; Havranek & Tranquillini, 1995), ostensibly did not recover. NEE for this month of 2002 was near zero (-0.6 g C m^{-2}), while that of October 2001 was -1.1 g C m^{-2} and that of October 2003 was -1.4 g C m^{-2} (Table 1). Although temperature per se did not show a correlation to the residuals of the Landsberg model, sensible heat did (Figure 4g-i), and it is closely linked to leaf temperature. This connection substantiates the importance of temperature on rates of photosynthesis in this ecosystem. During the late fall there appear to be temperature thresholds that initiate a decline in stomatal conductance and gas exchange rates, effectively ending the growing season. These thresholds may also be related to the decreases in light intensity and photoperiod at this time of year (Havranek & Tranquillini, 1995).

The overall cool temperatures during September and October of 2002 that resulted in little net carbon uptake also resulted in generally low values of soil respiration, except for a brief period in late September 2002 when soil temperatures and soil respiration increased, and net carbon uptake decreased substantially (Figure 3a,b; Figure 5). In 2001, the warmest of the three measurement years, C losses from soil respiration were high from June-August (Figure 6a), and consequently, total net carbon uptake was reduced below that observed during 2002 and 2003 (Table 1). Thus, it appears that soil respiratory losses had a large impact on net carbon uptake in this ecosystem. However, to gain a more complete understanding of the influence of soil respiration in this system, it would be useful to obtain predictions of total soil respiration based not just on temperature, but also on moisture since moisture did have an influence on soil respiration rates in this ecosystem (Table 3).

The soil respiration rates we measured were comparable to those of others taken in coniferous ecosystems that were close in age to the one in this study. For example, estimates of soil respiration in jack pine forests during one growing season were 415.2 g C m^{-2} at an 8-year-old ecosystem and 378 g C m^{-2} at a 20-year forest in Saskatchewan, Canada (Striegl & Wickland, 1998). A decline in soil respiration between the 8- and 20-year forests may be caused by a decrease in the rate of decomposition as the large amounts of microbial substrate due to the previous disturbance are exhausted. In particular, the forest in this study contained large piles of slash left behind from logging practices that were probably a major source of substrate for heterotrophs (who tend to favor the less resilient organic mater fractions; Alexander, 1977), and a reason for relatively high soil respiration rates. Older jack pine forests have been shown to exhibit less soil respiration (e.g., 300 g C m^{-2} over the growing season at a 60-75 year-old jack pine ecosystem; Striegl & Wickland, 2001) than younger forests, a finding that is generally attributable to an absence of large pools of labile litter that are associated with disturbance events.

Nevertheless, the day-to-day activities of the soil microorganisms are highly temperature dependent and even with large amounts of labile substrate, their activities decline during cool temperatures. This occurrence helps to explain the perceptible decoupling in SR and NEE during the cool temperatures in the spring (Figure 6). When the soils remained cool, close to 1-3°C, soil respiration stabilized at around 1.0 g C m^{-2} day^{-1}, but the overall carbon balance of the ecosystem still fluctuated between -0.12 to 0.1 g C m^{-2} day^{-1} in concert with fluctuations in air temperatures (Figure 3 a, b; Figure 6). From roughly mid-October to November, there was also decoupling between soil respiration and NEE. At this point, the soils were still warm and the microbes still responsive, but the trees began to enter winter dormancy (Figure 6).

4.3. Annual NEE & non-growing season C losses

At the annual time-step, it is possible that the 12-14 year-old ecosystem in this study has recently switched from a source to slight sink of CO_2. All the same, the weak growing season sink strength measured in this young jack pine forest is undeniably an overestimation of the annual carbon uptake of this ecosystem. For instance, Griffis et al. (2003) found that non-growing season C losses accounted for 46% of the summertime NEE in an old jack pine ecosystem in Saskatchewan, Canada.

Moreover, although we did not consistently measure soil respiration in the winter, we did find that even during periods of near freezing soil temperatures some carbon efflux was occurring, the sum of which could amount to significant carbon losses at the site. For example, using the exponential models presented in Table 3 and the continually collected soil temperature data (Figure 3b), we estimated that the soils respired 109.8 g C m^{-2} between December 2001 and March 2002, and 174.8 g C m^{-2} between December 2002 and March 2003. Empirically-based studies of winter soil respiration have measured highly temperature dependent rates between 40 – 132 g C m^{-2}, with soil moisture having little to no effect (McDowell et al., 2000; Winston et al., 1997). Projections of climate change forecast warmer winters within the latitude of this forest. Such warming could elicit greater respiratory losses from the soil during the non-growing season, and consequently affect the C balance of these young jack pine ecosystems.

4.4. Comparison with other direct measurements of ecosystem C flux

Given the slight C gain this forest achieved over the growing season, it would be interesting to compare our estimates of growing-season NEE to direct net carbon flux measurements made within a younger (e.g., 0-5 years old) jack pine ecosystem. Although we know of no studies of this nature, Amiro (2001) used tower measurements to measure NEE in a one-year-old burned jack pine ecosystem for nine days in July 1998, during the height of the growing season. This ecosystem was a consistent source of C at roughly 0.8 g C m^{-2} day^{-1}. Furthermore, Pypker & Fredeen (2002) measured growing season fluxes in a 5-6 year-old sub-boreal clearcut comprised of white spruce and lodgepole pine. They estimated that the ecosystem was a source of carbon in amounts of 1.0 to 1.4 Mg C ha^{-1} during the growing season (Figure 7).

Mature jack pine ecosystems are likely to sequester greater amounts of carbon than the young ecosystem described in the current study. Joiner et al. (1999) reported a sink of –2.1 and –2.7 Mg C ha^{-1} over the growing season measurement for a 30-32 year-old jack pine ecosystem in Manitoba, Canada. These estimates and those from this study suggest that jack pine ecosystems switch from acting as a source to sink of CO_2 at around 20 years (Figure 7). In Pacific Northwest Douglas-fir forests, the source-sink transition age is also estimated at around 20 years (Janish & Harmon, 2000; Chen et al, in press). Meanwhile, older (e.g., > 50 year) jack pine ecosystems may sequester less carbon than mature jack pine ecosystems. For example, a jack pine forest measured during two growing seasons at 65 and 71years took up –0.47 and –0.36 Mg C ha^{-1}, respectively (Baldocchi et al., 1997; Griffis et al., 2003; Figure 7).

5. Conclusions

In all probability, due to the overall low net C uptake of this forest, young jack pine ecosystems are not substantial carbon sinks. On the contrary, when considering the full calendar year, they are potential C sources, and may not switch to acting as sinks until about age 20. Moreover, these forests may be vulnerable to climate warming given the sizeable amounts of soil respiration and its positive relationship with soil temperature. All the same, the factors that control NEE in this jack pine ecosystem on daily, seasonal, and interannual time scales are complex and still warrant future investigation. To more fully understand these patterns and processes, additional research evaluating the carbon, water, and nutrient dynamics over the full calendar year and more comprehensive partitionings of total ecosystem NEE into its component fluxes (e.g., autotrophic respiration, understory plant NEE) are needed.

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Table 1. Monthly and cumulative values of net ecosystem exchange (NEE; g C m^{-2}) and total estimated soil respiration (SR; g C m^{-2}) from June – October (bottom row) for the 2001-2003 measurement periods. These periods were May 20-November 11, 2001, April 1 – October 31, 2002, and April 11-November 4, 2003.

Month	2001	2002	2003
April	-	-2.7	-2.3
May	-1.4	-5.1	-5.8
June	-5.4	-4.0	-5.8
July	-5.4	-8.0	-6.6
August	-4.5	-5.5	-4.8
September	-2.2	-1.6	-3.3
October	-1.1	-0.6	-1.4
November	-0.2	-	-0.1
Cumulatives:			
[a] NEE Total	-20.2	-27.5	-27.0
NEE June – Oct.	-18.6	-19.7	-21.9
SR June – Oct.	627	583	681

[a] The cumulative values refer to the total summed NEE over the various measurement periods for each year, and for the comparable measurement period of June-October.

Table 2. Parameters (± standard errors) and R^2 values of the Landsberg model fitted to the daytime NEE (NEE_{day}; µmol CO_2 m^{-2} s^{-1}) data based on PAR (µmol m^{-2} s^{-1}). Models were formulated separately for five subsets of the seasons based on all three years and for all measurement periods combined (2001-2003). For all models, P > F is < 0.0001.

		Parameter (± standard error)[a]			
Season	Julian days	P_{max}	α	I_{comp}	R^2
Early spring	91-151	1.340 (0.4359)	6.86×10^{-3} (2.84×10^{-3})	15.618 (14.355)	0.32
Late spring	152-181	0.7546 (0.0495)	1.91×10^{-3} (2.41×10^{-3})	53.0857 (7.1857)	0.43
Summer	182-230	0.9033 (0.0507)	1.59×10^{-3} (1.60×10^{-3})	40.0704 (5.4664)	0.72
Late summer	231-273	0.7829 (0.0623)	1.99×10^{-3} (2.64×10^{-3})	82.5748 (5.9412)	0.77
Fall	274-315	0.6753 (0.1683)	2.00×10^{-3} (7.05×10^{-3})	63.0199 (8.2095)	0.55
All[b]	91-315	0.9000 (0.4359)	1.45×10^{-3} (1.14×10^{-3})	49.4515 (3.0951)	0.54

[a]The parameters of the Landsberg model, $NEE_{day} = P_{max}(1- \exp^{-\alpha(PAR - Icomp)})$, are P_{max} = the maximum rate of photosynthesis, α = a shape parameter, and I_{comp} = the light compensation point.

[b]All refers to the early spring – fall seasons combined across all years of data.

Table 3. Parameters and R^2 values of the exponential models fitted to the soil respiration (SR) data based on soil temperature (Ts, °C to 5 cm depth) and soil moisture (Ms, %). Models were formulated separately for each of the three years and for all years combined (2001-2003). For all models, P > F is < 0.0001.

		Parameter (± standard error)				
Year(s)	Model[a]	β_0	β_1	β_2	β_3	R^2
2001	Ts	0.1202 (0.0407)	0.1015 (0.0168)	-	-	0.76
2001	Ts * Ms	0.0523 (0.3226)	0.0884 (0.0569)	-0.6829 (5.8849)	0.1657 (0.8407)	0.78
2002	Ts	0.1375 (0.0556)	0.0846 (0.0198)	-	-	0.68
2002	Ts * Ms	0.0022 (0.0018)	0.0977 (0.0178)	-0.0371 (0.0879)	0.7279 (0.2839)	0.87
2003	Ts	0.2463 (0.0493)	0.0659 (0.0103)	-	-	0.77
2003	Ts * Ms	0.0144 (0.0198)	0.0448 (0.0129)	-0.5035 (3.0951)	0.6134 (0.2703)	0.88
All	Ts	0.1765 (0.0313)	0.0792 (0.0089)	-	-	0.69
All	Ts * Ms	0.0286 (0.0181)	0.0749 (0.0297)	-0.0745 (0.5930)	0.2098 (0.4311)	0.75

[a] Ts refers to the simple exponential model based on soil temperature, $SR = \beta_0 * e^{\beta 1 * Ts}$, and Ts * Ms refers to the exponential model with both soil temperature and soil moisture, $SR = \beta_0 * e^{\beta 1 * Ts} * e^{\beta 2 * Ms} * \beta_3 * Ts * Ms$.

Figure captions

Figure 1. Latent plus sensible heat flux (Le + H) versus net radiation minus soil heat flux (Rn – G, or available energy) over the measurement periods using half-hourly averages. The solid lines represent the 1:1 line (thick line) and the fitted line (thin line). The linear no-intercept model yielded a slope of 0.85 and R^2 of 0.95.

Figure 2. Half-hourly net ecosystem exchange (NEE) of CO_2 plotted as a function of friction velocity (u*) for nocturnal periods (2200 – 0500) during the sample period. The solid line depicts a fourth order polynomial fitted to the data: $NEE = -0.5628u^{*(4)} + 2.2970u^{*(3)} - 3.1002u^{*(2)} + 1.4904u^{*} - 0.0161$ ($p < 0.001$).

Figure 3. Time series of daily total NEE (a), average daily air and soil (5 cm depth) temperatures (b), and daily total precipitation (thin vertical lines) and soil moisture (thick lines) with the precipitation amounts summed over each measurement period (c) during the 2001, 2002, and 2003 measurement periods. Negative NEE values indicate a C sink while positive NEE values indicate a C loss.

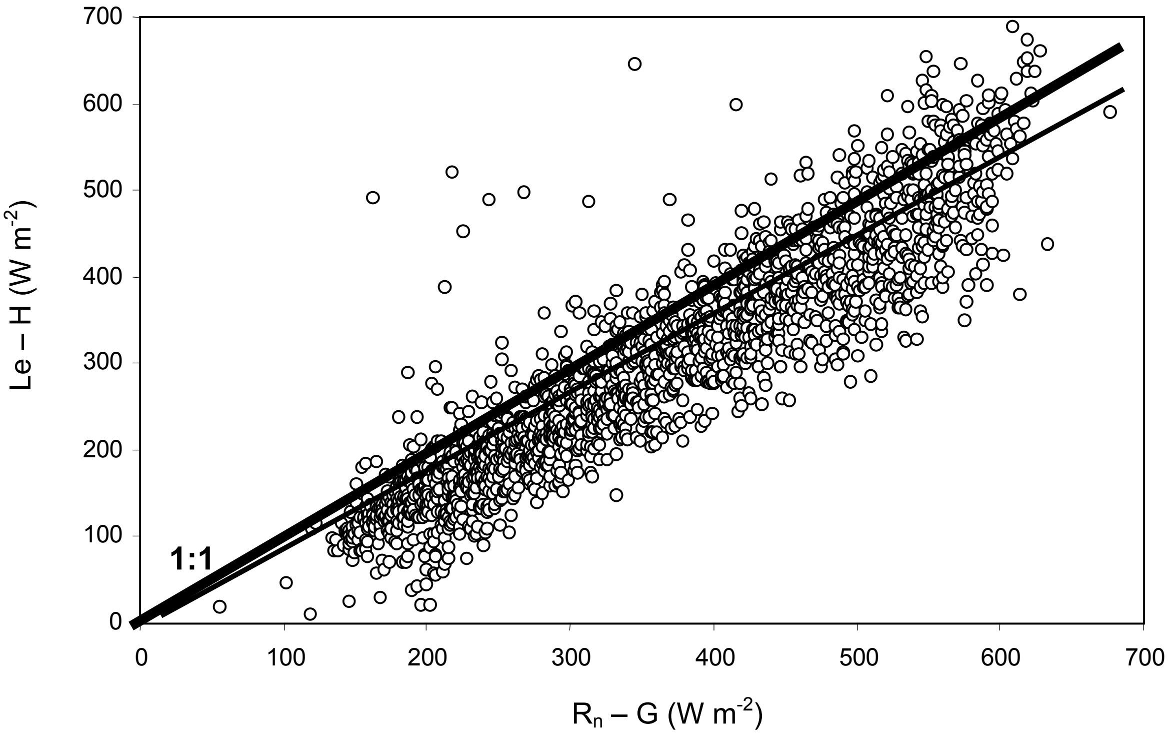
Figure 4. Relationship between daytime carbon flux (NEE_{day}) and photosynthetically active radiation (PAR) as modeled with the Landsberg equation (a-c), and the relationship between residual NEE_{day} (after the Landsberg equations) for vapor pressure deficit (VPD; d-f), and sensible heat (H; g-i) during the early spring, summer, and fall months. The parameters of the fitted models for the Landsberg equation are given in

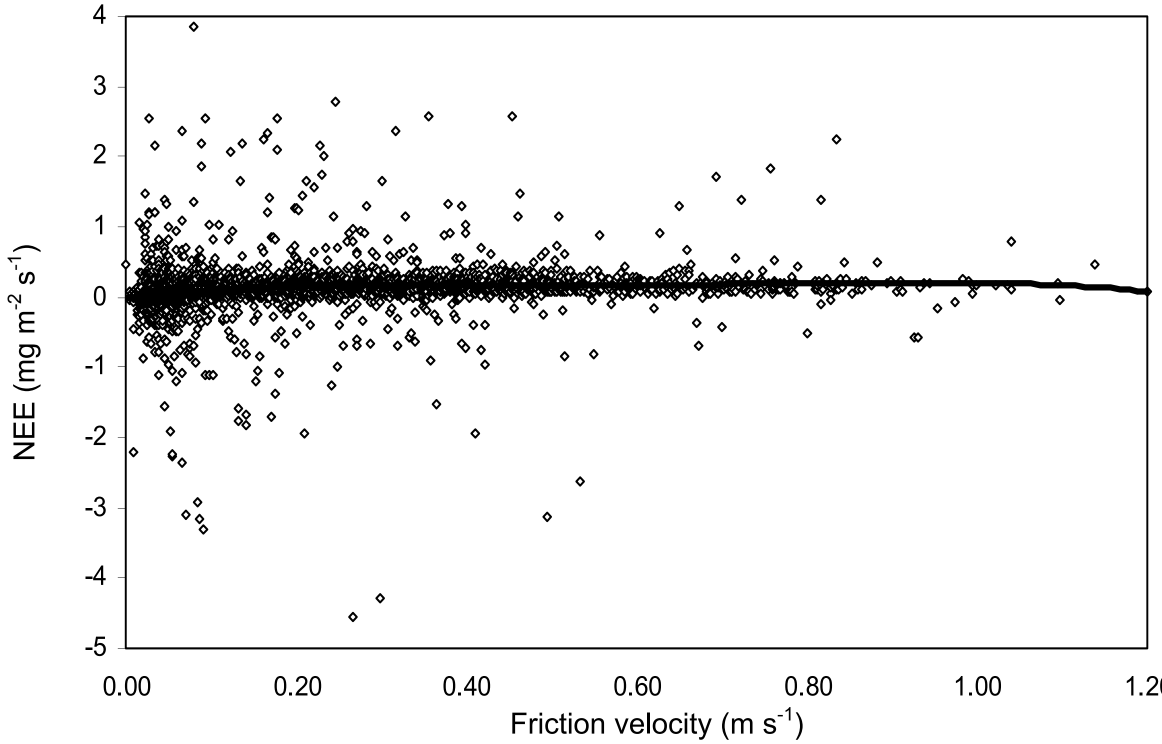
Table 2. The solid lines in graphs (d-i) represent best-fit linear regression models with a coefficient (*b*), and its significant deviation from zero based on a t-test ($p = 0.05$). Although the models were fit to the full range of data, in order to more clearly depict the trends in carbon flux, the y-axes in graphs (a-c) were truncated at -6 and 6 μmol m^{-2} s^{-1} and those in graphs (d-i) were truncated at -3 and 3 μmol m^{-2} s^{-1}.

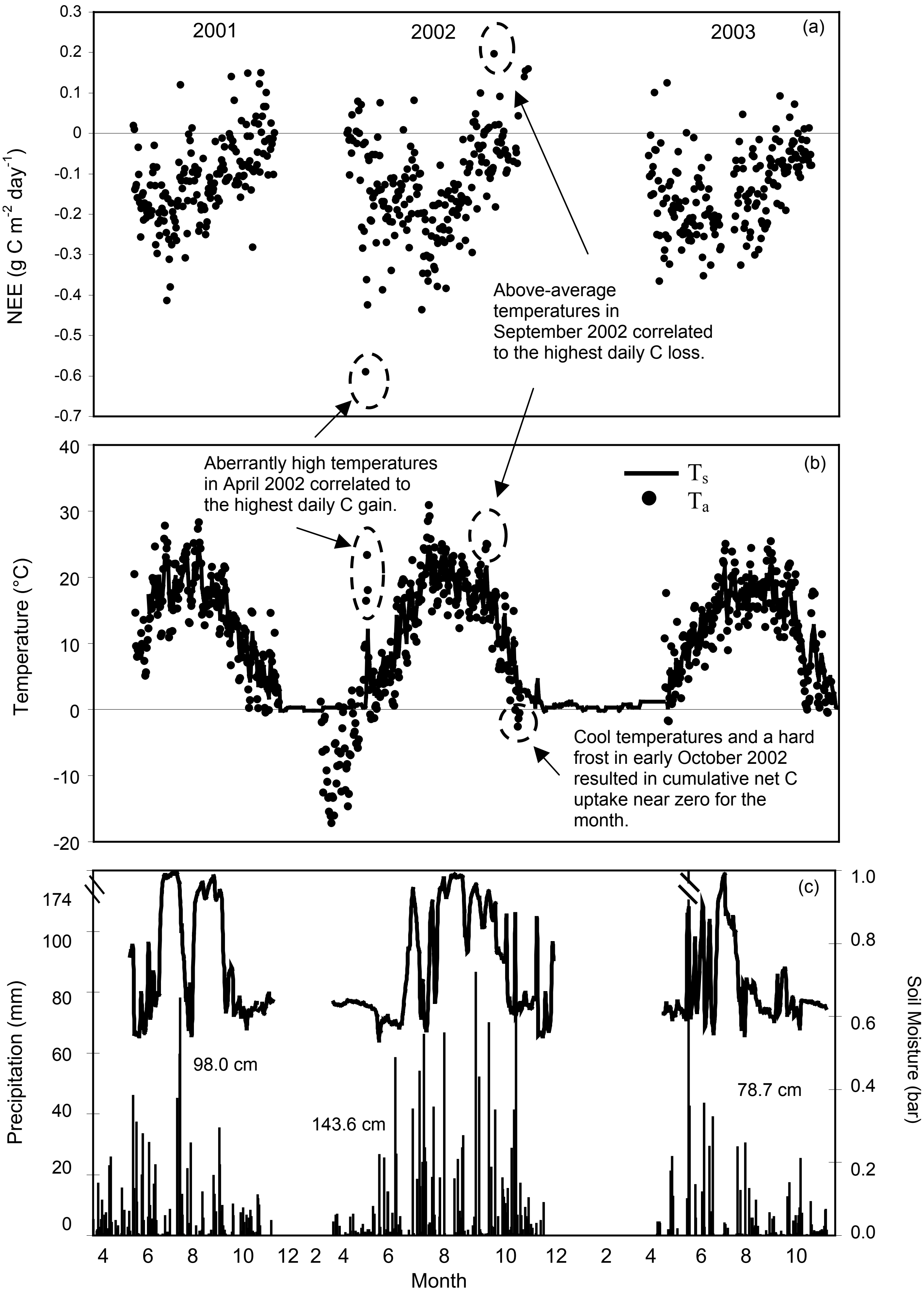
Figure 5. Comparison between actual soil respiration (SR) measurements and modeled SR estimates for the years 2001 –2003. The modeled SR estimates are based on the exponential model containing both soil temperature and soil moisture, as presented in Table 2. The breaks in the lines represent measurement gaps between the years.

Figure 6. Time series comparison (using five day backwards moving averages) for years 2001-2003 of daily net ecosystem exchange (NEE) and daily soil respiration (SR) rates computed from the exponential soil temperature model presented in Table 2.

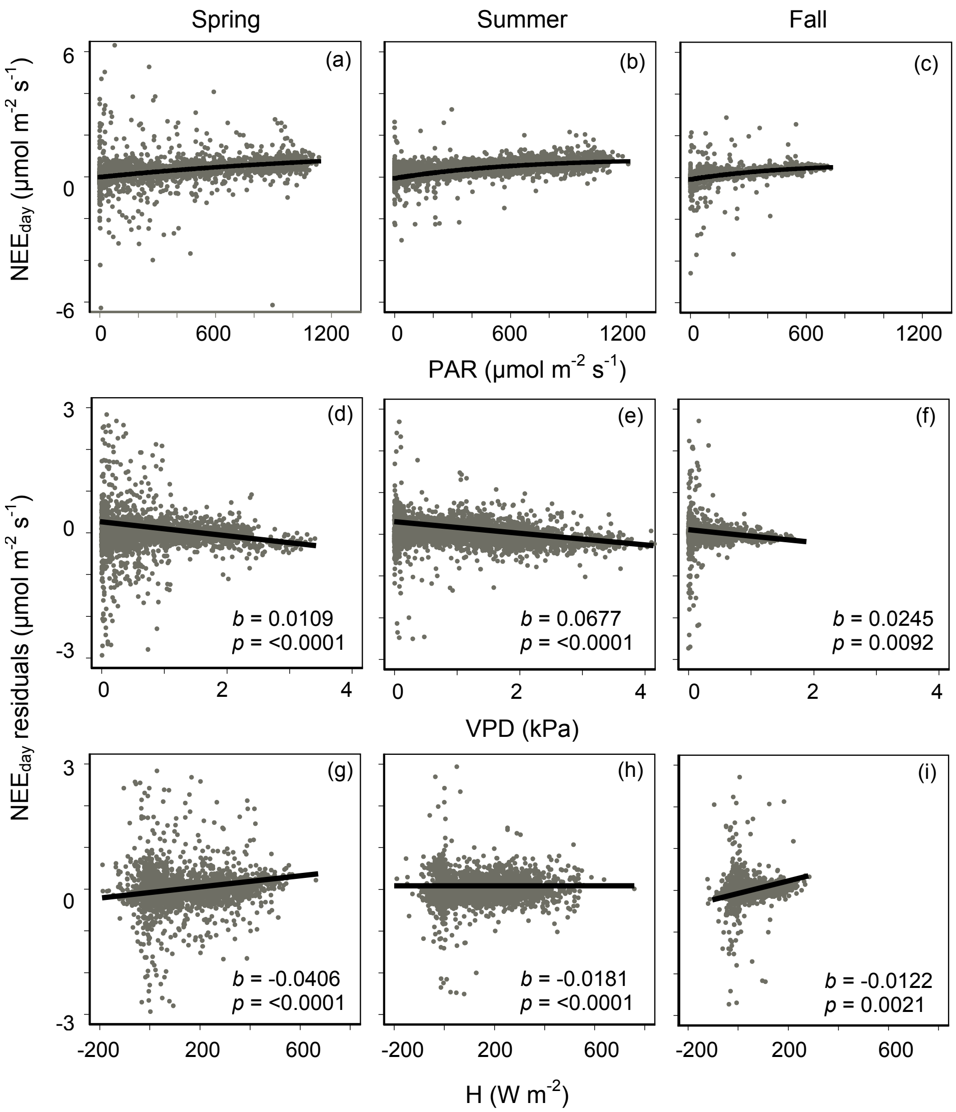
Figure 7. Summary of NEE during the growing season (Mg C ha^{-1}) for three comparable pine ecosystems of various age classes. Data is from Baldocchi et al., 1997; Joiner et al., 1999; Pypker & Fredeen, 2002; Griffis et al., 2003, and this manuscript. The solid line is drawn by hand to indicate a general trend in ecosystem carbon flux across the age classes.

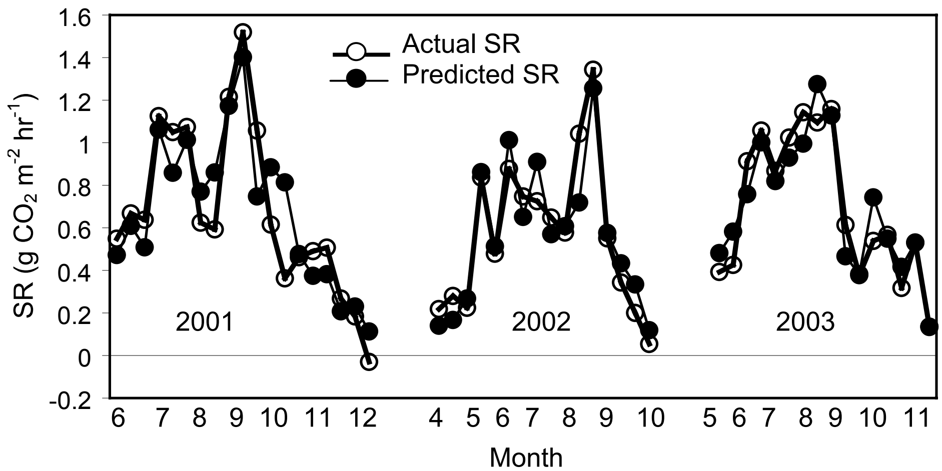

700
600
500
400
300
200
100
0
Le – H (W m-2)
1:1
0
100
200
300
400
500
600
700
Rn – G (W m-2)

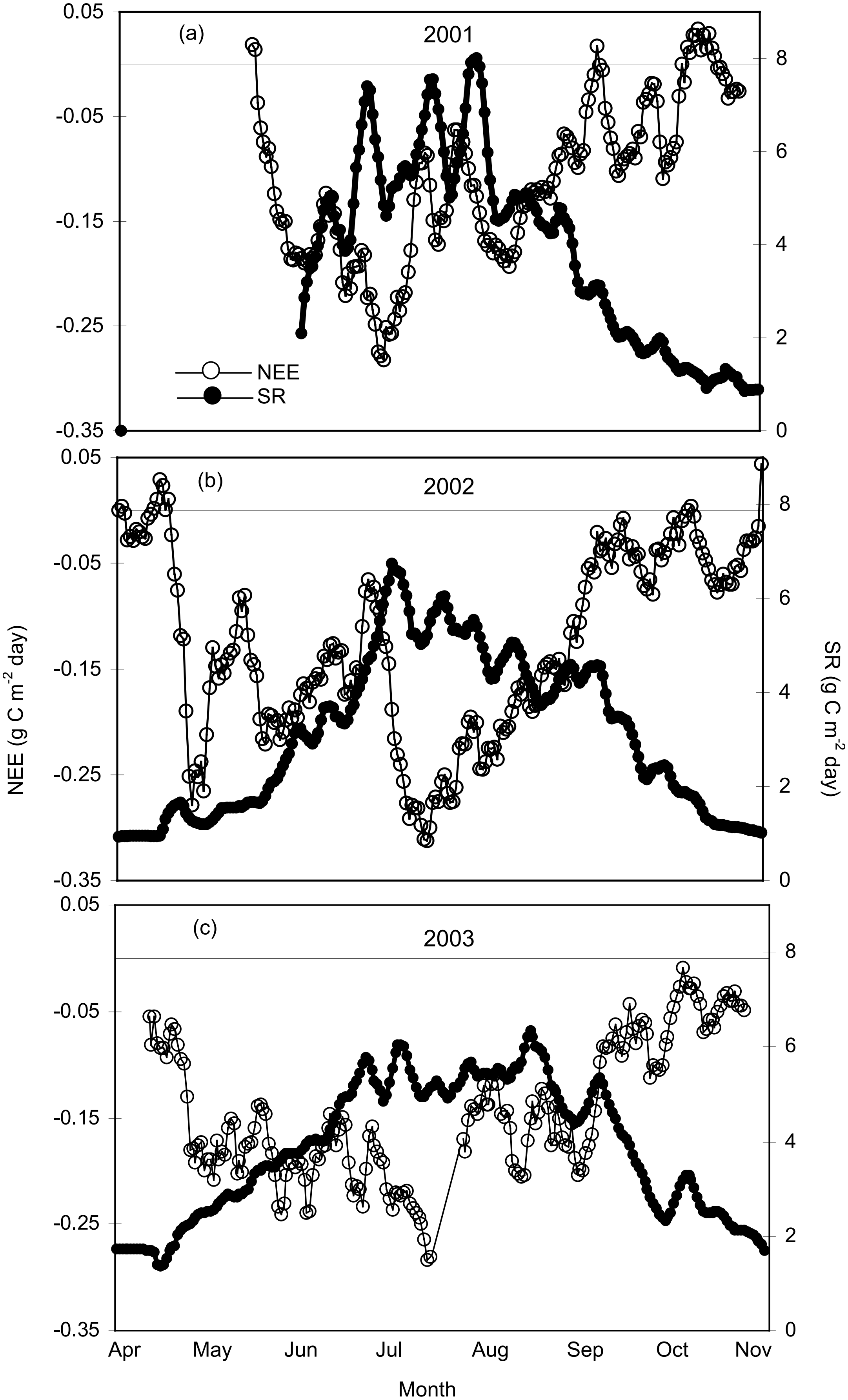

NEE (mg m-2 s-1)
4
3
2
1
0
-1
-2
-3
-4
-5
0.00
0.20
0.40
0.60
0.80
1.00
1.20
Friction velocity (m s-1)



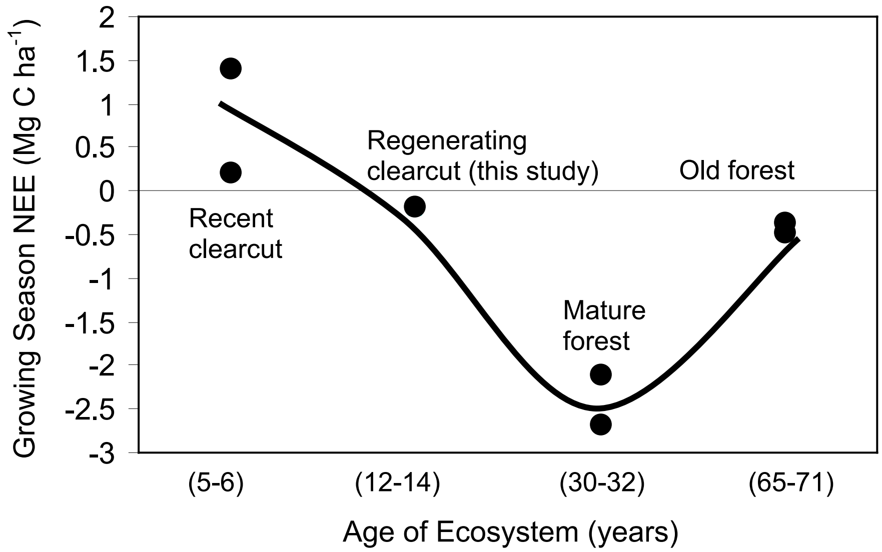
2001
2002
2003
(a)
NEE (g C m-2 day-1)
Above-average temperatures in September 2002 correlated to the highest daily C loss.
Aberrantly high temperatures in April 2002 correlated to the highest daily C gain.
(b)
Ts
Ta
Temperature (°C)
Cool temperatures and a hard frost in early October 2002 resulted in cumulative net C uptake near zero for the month.
(c)
Precipitation (mm)
Soil Moisture (bar)
98.0 cm
143.6 cm
78.7 cm
Month


Spring
Summer
Fall
(a)
(b)
(c)
NEEday (µmol m-2 s-1)
6
0
-6
0
600
1200
PAR (µmol m-2 s-1)
(d)
(e)
(f)
b = 0.0109
p = <0.0001
b = 0.0677
p = <0.0001
b = 0.0245
p = 0.0092
3
0
-3
0
2
4
VPD (kPa)
NEEday residuals (µmol m-2 s-1)
(g)
(h)
(i)
b = -0.0406
p = <0.0001
b = -0.0181
p = <0.0001
b = -0.0122
p = 0.0021
-200
200
600
H (W m-2)


Actual SR
Predicted SR
SR (g CO_2 m^{-2} hr^{-1})
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
2001
2002
2003
6 7 8 9 10 11 12
4 5 6 7 8 9 10
5 6 7 8 9 10 11
Month



(a)
2001
NEE
SR
(b)
2002
(c)
2003
0.05
-0.05
-0.15
-0.25
-0.35
0
2
4
6
8
NEE (g C m-2 day)
SR (g C m-2 day)
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Month


Growing Season NEE (Mg C ha-1)
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
Regenerating clearcut (this study)
Old forest
Recent clearcut
Mature forest
(5-6)
(12-14)
(30-32)
(65-71)
Age of Ecosystem (years)