Phenology of Forest-Atmosphere Carbon Exchange for Deciduous and Coniferous Forests in Southern and Northern New England: Variation with Latitude and Landscape Position

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Abstract We used ecosystem carbon exchange measurements at five sites in New England to examine how interannual variation in leaf development and leaf abscission, as well as latitude and landscape position, affected the phenology of carbon exchange in recent years. We studied three deciduous forest sites, two in southern and one in northern New England, at latitudes of about 42.54 and 44.28°N with carbon exchange records of 3–15 years, and also two coniferous forests, one also at about 42.54°N and the other at 45.25°N, with records of 4 and 11 years, including 3 years of concurrent data. In the southern New England deciduous forest with 15 years of data, the time at which carbon uptake increased in spring was significantly correlated with observed leaf development, but the cessation of carbon uptake was not significantly correlated with observed leaf abscission, which does not quickly follow leaf senescence in the dominant species, red oak (*Quercus rubra*). A measure of canopy greenness appears necessary for accurately estimating or predicting cessation of carbon uptake by this species. Differences between two southern New England deciduous forests in landscape position, slope aspect (northwest vs. east), and the degree of dominance by red oak vs. other deciduous and coniferous

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trees had effects on the annual time course of carbon exchange which were similar in magnitude to the effects of the 1.75° difference in latitude between these two deciduous forests and one further north. We hypothesize that a change in dominant tree species from red oak, which has ring-porous wood and must form new xylem each year prior to leaf growth, to diffuse porous trees (*Acer*, *Betula* and *Fagus* spp.), which lack this requirement, further north could enable the timing of leaf development to remain relatively early in the more northerly location, despite a cooler climate. A coniferous forest in southern New England (latitude 42.54°) showed two annual peaks in carbon uptake: a large one in spring before maximum carbon uptake by deciduous forests, and a smaller peak in autumn. In contrast, in a more northerly coniferous forest (45.25°N), the autumn peak was not observed. Significant late-winter (March) carbon uptake also occurred only in the more southerly conifer forest when early soil thawing occurred in 2006.

1 Introduction

Recent papers (Barr et al. 2004, 2007; Urbanski et al. 2007) have shown that interannual climate variation can strongly affect annual carbon exchange of temperate and boreal forests, through climatic influences on the development and senescence of the forest canopy, which can also be termed canopy phenology. In this chapter we will examine variation in the phenology of carbon (C) assimilation by forests in relation to forest canopy phenology at a long-term C exchange measurement site in New England, USA. We will also examine differences in phenology of C exchange at five New England sites in relation to two geographic and topographic variables, latitude and slope aspect, that influence either forest macroclimate or microclimate. Three of the sites are in predominantly deciduous forests and two in coniferous forests, allowing us to look at differences between these two fundamentally different forest types. Two of the deciduous forest sites are very close to each other at the same latitude, but with differences in slope aspect and wind exposure. In addition, there are nearly continuous records of net carbon exchange for more than a decade at two of the sites, creating a data set that is useful to at least begin an analysis of carbon exchange phenology.

The questions we will address in this chapter include:

What are the relationships between observed spring leaf development and autumnal leaf abscission and the beginning and end of forest ecosystem carbon uptake each year?

How do the timing and rate of change of the annual transitions from forest carbon loss to forest carbon uptake and *vice-versa* differ between forests of differing latitude, wind exposure, and species composition within the northeast U.S.?

What climatic and microclimatic variables are linked to differences between forests in the timing and rate of these annual carbon exchange transitions?

Do differences between the dominant tree species in different forests also affect the annual time course of carbon uptake and carbon loss?

2 Methods

In our analysis we use data from two sites with carbon flux data covering 10 or more years: a predominantly deciduous portion of the Harvard Forest in southern New England, containing about 25% conifers (HF-EMS; see Wofsy et al. 1993; Goulden et al. 1996; Barford et al. 2001; Urbanski et al. 2007) and a coniferous northern New England forest near Howland, Maine (Hollinger et al. 1999, 2004). In addition we will present data from a second deciduous area of the Harvard Forest, first measured in 2002 (HF-LPH; see Hadley et al. 2008) that has fewer conifers, less water and eastern hemlock stand (HF-Hemlock) with measurements in 2000–2001 and 2004 onward (Hadley and Schedlbauer 2002; Hadley et al. 2008). Finally, we will use measurements from a deciduous forest about 175 km further north than the Harvard forest, at the Bartlett Experimental Forest (BEF) in northern New Hampshire, with data from 2004 onward. Relevant data for all of these forests is given in Table 1, and some details of the eddy flux measurement

Table 1 Characteristics of the five New England forests. *HF-EMS* Harvard Forest Environmental Measurement Site, *HF-LPH* Harvard Forest Little Prospect Hill, *HF-Hemlock* Harvard Forest hemlock stand. Abbreviations of genera: *A. Acer*, *B. Betula*, *F. Fraxinus, Q. Quercus*, *T. Tsuga*. Mean annual temperatures are for 2004–2006

Site	HF-EMS	HF-LPH	HF-Hemlock	Bartlett	Howland
Latitude	42.538°N	42.540°N	42.539°N	44.28°N	45.25°N
Longitude	72.171°W	72.180°W	72.175°W	71.05°W	68.73°W
Elevation (m)	340	390	360	210	60
Tree age range (years)	65–100	45–100	100–200	70–120	60–190
Forest type	Deciduous	Deciduous	Coniferous	Deciduous	Coniferous
Dominant species (in decreasing abundance)	*Q. rubra* *A. rubrum* *T. canadensis* *Pinus rubra*	*Q. rubra* *A. rubrum*	*T. canadensis* *Pinus strobus*	*A. rubrum* *F. americana* *B. papyrifera* *A. saccharum*	*Picea rubens* *T. canadensis* *A. rubrum* *B. papyrifera*
Canopy height (m)	25	17	22	24	20
Aboveground carbon (t ha^{-1})	95	40	105	105	120
Tree density (ha^{-1})	660	900	600	625	2000
Basal area (m^2 ha^{-1})	33	18	50	38	48
Mean air temperature (°C)	8.1	7.9	8.1	7.5	6.1
Annual precipitation (mm)	1100	1100	1100	1300	990

systems are given in Table 2. Approximate locations of the three New England carbon flux study sites are shown in Fig. 1, and the three Harvard Forest flux towers are shown in Fig. 2. Data for the Harvard Forest EMS tower used in this chapter

Table 2 Characteristics of the eddy covariance systems used at the five flux tower sites

Site	HF-EMS	HF-LPH	HF-Hemlock	Bartlett	Howland
Sonic anemometer	ATI[a] SAT 211/3K	Campbell[b] CSAT3	Campbell[a] CSAT3	ATI[a] SAT 211/3K	ATI[a] SAT 211/3K
Analyzer manufacturer and model (all closed-path)	Licor[c] LI6262	Licor[c] LI6262	Licor[c] LI6262 LI7000[d]	Licor[c] LI6262	Licor[c] LI6262
Sampling height above canopy (m)	5	4.5	5	3	9
Minimum night turbulence (u*) to accept data (m/s)	0.2	0.35	0.4	0.35	0.25

[a] Applied Technologies Inc. (Boulder, Colorado, USA).
[b] Campbell Scientific, Inc. (Logan, Utah, USA).
[c] Licor Biosciences Inc. (Lincoln, Nebraska, USA).
[d] LI-6262 was used until October 2001, LI7000 was used in 2004 and after.

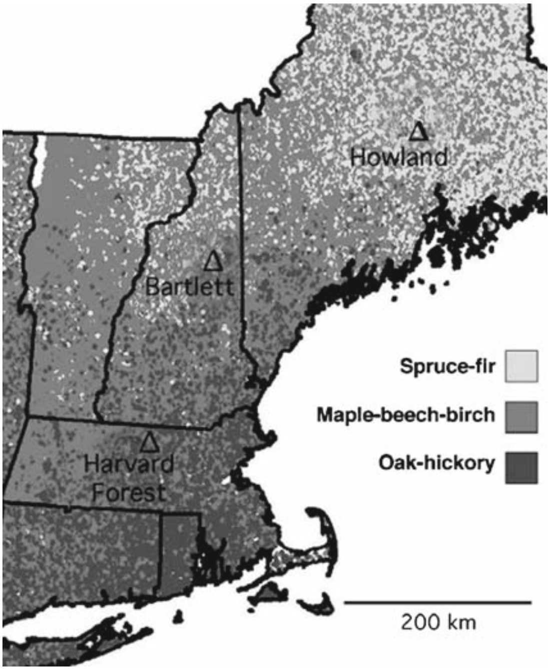

Fig. 1 Locations of study sites, indicated by *black triangles*: Harvard Forest, Massachusetts; Bartlett Experimental Forest (BEF), New Hampshire; and Howland Forest, Maine. Forest type classifications are based on county-level Forest Inventory and Analysis (FIA) data from the USDA Forest Service.

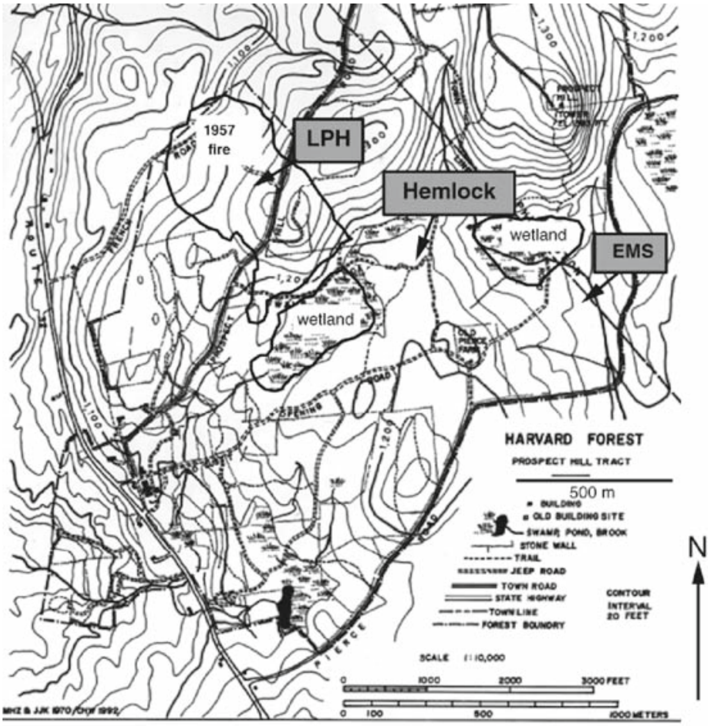

Fig. 2 Locations of Harvard Forest (HF) carbon flux measurement towers: Little Prospect Hill (LPH), Hemlock and Environmental Measurement Site (EMS).

are calculated from data at ftp://ftp.as.harvard.edu/pub/nigec/HU_Wofsy/hf_data in the "Final" folder. Data for the Harvard Forest Hemlock and LPH towers can be found at http://harvardforest.fas.harvard.edu/data/atm.html in data sets HF103 and HF072. Data for the Bartlett Experimental Forest is summarized in Jenkins et al. (2007) and is accessible through the Ameriflux network web site at: http://public.ornl.gov/ameriflux/data-access.shtml, while Howland data is at ftp://epg-ftp.umaine.edu/CDIAC. Throughout this chapter, we use the convention that negative values of net ecosystem exchange (NEE) indicate net carbon uptake by the forest, and positive values indicate carbon flux to the atmosphere. To better portray seasonal changes, in our analyses we use 10-day running means to remove large day-to-day variations in carbon exchange due to synoptic weather events.

In this chapter we use data from this suite of eddy flux towers, along with microclimatic data (Table 3) to show the relationships between detailed observations of canopy phenology, microclimate, and the beginning and end of gross and net carbon uptake at the deciduous Harvard Forest flux tower that presently has a 15-year record. We will also examine effects that differences in slope aspect and wind exposure may

Table 3 Microclimate data used in analysis of phenological change in ecosystem carbon uptake

Microclimate parameter	Measurement location
Air temperature	4–5 m above canopy
Soil temperature	10 cm depth, except where other depths are specified in text and figure captions
Photosynthetically active radiation (PAR)	2–5 m above canopy
Wind direction and speed	At flux measurement height, 4–9 m above canopy

have on seasonal carbon exchange patterns, and differences in the seasonality of net carbon exchange between coniferous, deciduous and mixed forests in New England.

3 Results

3.1 Harvard Forest Leaf Phenology and Net Carbon Exchange of a Predominantly Deciduous Forest

Because most photosynthesis in forests occurs in the leaf canopy, the timing of leaf development in spring and leaf abscission in autumn should show a strong relationship with carbon uptake by the forest. Leaf development and leaf abscission have been observed on 20 species of trees and shrubs at the Harvard Forest since 1991 (Richardson and O'Keefe, in current volume). In Fig. 3a we show average dates of budbreak and the midpoint between budbreak and 75% leaf enlargement for red oak and red maple, which are the two dominant species in the deciduous portions of Harvard Forest. Dates of the first daily net carbon uptake by the forest each year (STARTNCU) and dates at which 20% of maximum daily carbon uptake was reached (20%maxCU) are also plotted. Figure 3b shows the average dates of 50% leaf fall for red oak and red maple in each year, along with dates of the last net carbon uptake (ENDNCU).

Both STARTNCU and 20% maxCU show positive correlations with the average date of budbreak for red oak and red maple (Fig. 4a). There was no statistically significant correlation between the average date for 50% leaf abscission for red oak and red maple and ENDNCU (Fig. 4b), although there is a positive relationship ($r^2 = 0.40$, $p = 0.04$) if the two outliers near the bottom and right-hand end of the graph are removed if the two outliers were removed. The slopes of all regression lines are less than 1, so the time difference between the observed phenological event and the beginning or cessation of net carbon uptake is smaller later in the season. The relatively weak relationship between leaf loss in the fall and ENDNCU is very likely due to the fact that carbon uptake by leaves may stop substantially before leaf fall, and leaves of red oak sometimes do not abscise for weeks or months after they turn brown and are no longer photosynthetically active. An indicator of leaf physiological activity, such as leaf greenness, is likely to correlate better with the end of photosynthetic activity in autumn than leaf abscission.

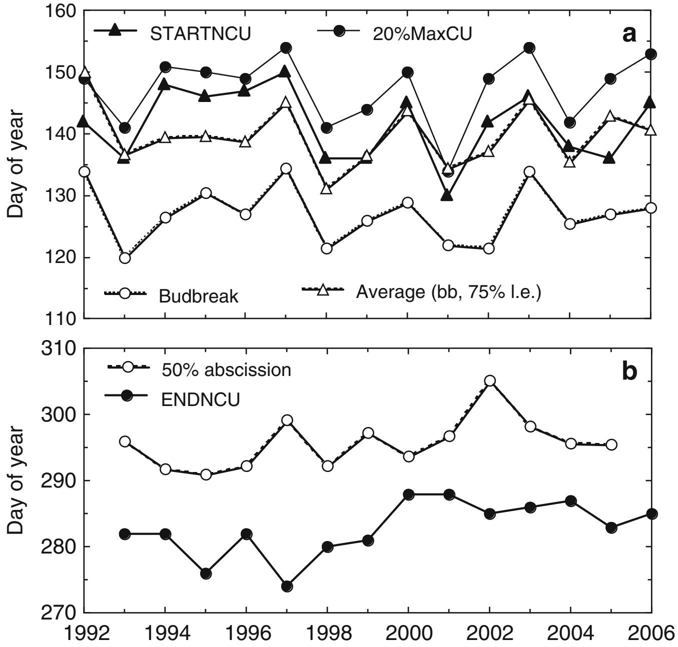

Fig. 3 (**a**) Average dates of bud break and the midpoint between budbreak and 75% leaf expansion for red oak and red maple at Harvard Forest, plus the dates of first 10-day average daily NEE less than zero (start of net ecosystem carbon uptake or STARTNCU) measured at the EMS flux tower in 1992 through 2006. (**b**) Dates of 50% leaf abscission for red oak and red maple, and dates of the last 10-day average NEE below zero (ENDCU) measured at the EMS flux tower for the same years. Dates for STARTCU and ENDCU were calculated from data at: ftp://ftp.as.harvard.edu/pub/nigec/HU_Wofsy/hf_data/final.

3.2 Seasonal Patterns of Net Carbon Exchange in Three Forest Types within Harvard Forest

The three Harvard Forest eddy flux measurement towers show a large difference in the seasonality of carbon uptake between the deciduous sites (LPH and EMS) and the coniferous eastern hemlock forest. While net carbon uptake by the deciduous forests occurs almost exclusively between the end of May and mid-October (approximately days 150–285), in the hemlock stand the peak uptake was in April and May, and declined from June through September before a second carbon uptake peak in late October (Fig. 5). Increased net C uptake by hemlock forest in late October must be due to declining ecosystem respiration rather than increasing photosynthesis, as the latter becomes progressively limited by declining daylength and solar angle in autumn.

More subtle differences in the annual pattern of carbon exchange are visible between the two primarily deciduous forests. For instance, the EMS tower (which

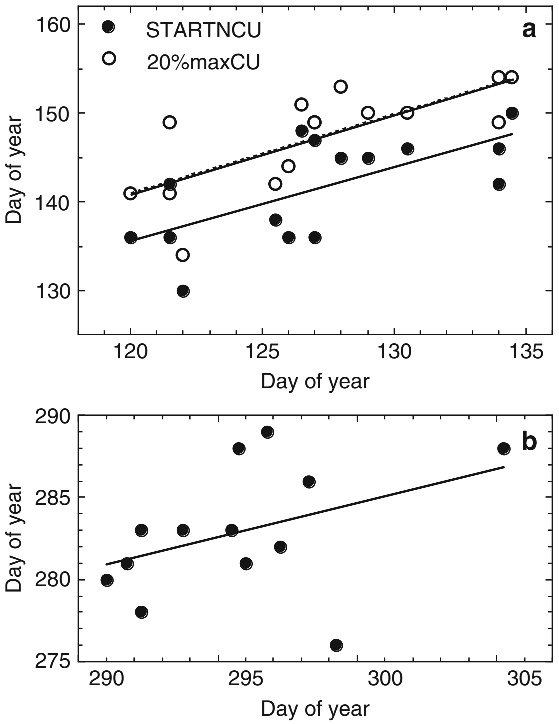

Fig. 4 (**a**) Average bud-break date for red oak and red maple vs. date of first net carbon uptake (*closed circles*) and date at which daily net ecosystem carbon uptake reached 20% of maximum (*open circles*). Regression line for date of first C uptake; y = 0.828x + 36.31, r^2 = 0.45, p = 0.07, regression for date of 20% of maximum daily C uptake; y = 0.889x + 34.3, r^2 = 0.53, p = 0.02. (**b**) Average date of 50% leaf abscission for red oak and red maple in 1993–2005 vs. last date of net carbon uptake. Regression line is y = 0.414x + 160.3, r^2 = 0.17, p = 0.17.

contains slightly under 25% coniferous trees by basal area within 500 m of the tower) shows an accelerating negative trend in NEE, indicating an increasing rate of carbon uptake, beginning around the end of April (day 120) and lasting until mid-June (day 165). In contrast the LPH site shows a sharp upturn in NEE in early May (days 120–130) before the phase of increasingly negative NEE that lasts until the end of June (day 180) (Fig. 5). Some of the difference between the two sites is likely due to the presence of conifers at the EMS site, whose high photosynthetic activity during May masks increasing respiration in the deciduous portion of the forest during the part of May when deciduous leaves are still maturing. With a smaller contribution (7%) of conifers in the footprint of the LPH tower, increasing respiration during early May becomes visible in the NEE trajectory.

The onset of net carbon uptake in the forest at EMS occurred on average about 8 days earlier than the forest at LPH, in the 4 years for which we have data for both sites (Fig. 5, Table 4), which may have been the result of differing rates of snow melt and soil warming. The presence of conifers and more southerly aspect of EMS

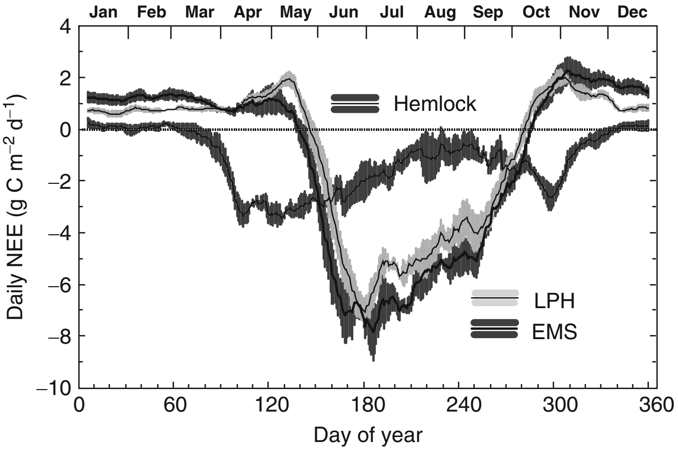

Fig. 5 Mean daily net ecosystem carbon exchange (NEE) for the coniferous eastern hemlock forest in 2001 and 2004–2006 and for the primarily deciduous forests sampled by the LPH and EMS towers in 2003–2006. Negative values indicate net carbon uptake. The lines are plotted from the average running men daily NEE for each day of the year, for 4 years of data at the LPH and EMS towers, and 3–4 years at the Hemlock tower, where a long data gap occurred due to lightning damage in 2005). The gray areas around the lines show standard errors of the mean for values in 3–4 years on a given day of year.

Table 4 First and last day and duration of annual net carbon uptake period at each deciduous forest site, calculated from 10-day running averages

Year	Harvard Forest, Main Tower (EMS)			Harvard Forest, Little Prospect Hill (LPH)			Bartlett Exp. Forest, New Hampshire		
	First	Last	Duration	First	Last	Duration	First	Last	Duration
2003	146	286	140	153	284	131	NA	NA	NA
2004	138	288	150	143	286	143	130	279	149
2005	136	284	148	150	280	130	148	279	131
2006	145	286	141	150	278	128	132	270	138
Average 2003–2006	141	286	145	149	282	133	na	na	na
Average 2004–2006	140	286	146	148	281	133	137	276	139

could have resulted in greater radiation load and lower albedo compared to the north facing purely hardwood stand of LPH. This hypothesis was, indeed, supported by differences in soil temperatures between the two sites (Fig. 6). The W to NW exposure of the LPH site also increases its exposure to NW winds, which in New England tend to be stronger and occur during periods of lower air temperature than other wind directions. For trees at the LPH site, lower soil temperature may slow root growth and any developmental changes requiring elevated metabolism in roots, while the cooling effects of NW winds may also inhibit spring leaf growth. The end of net carbon uptake in October occurred on average 4 days later at the

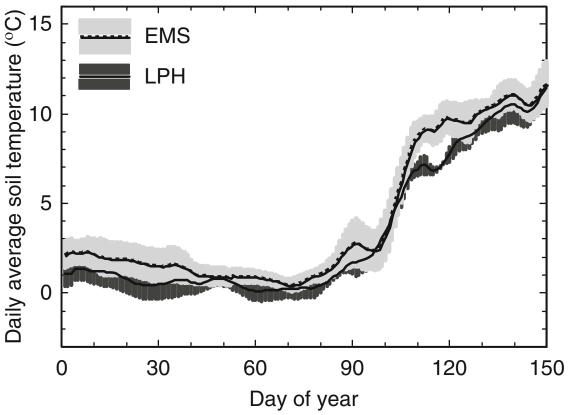

Fig. 6 Seven-day mean soil temperature at 10 cm depth near the HF-EMS and HF-LPH flux towers at Harvard Forest (see Fig. 2) in winter and spring. The *shaded areas* around each line indicate one standard error across 4 years (2003–2006). Soil temperature was measured at 5 m depth at six locations about 250 m SE of the EMS tower, and at 10 cm depth at four locations 200 m SW and 200 m NW of the LPH tower. Soil temperature at 10 cm depth for the EMS tower locations was estimated using the 5 cm measurement plus an adjustment based on a soil temperature profile covering 5–50 cm depths, measured in a location about 4 km away. The mean value at 10 cm for all measurement locations was used for each daily average. (Soil temperatures near the EMS tower and the soil temperature profile courtesy J. Melillo, Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, USA).

EMS site than at LPH (Fig. 5, Table 4), leading to an average annual duration of net daily carbon uptake which was 12 days shorter at the LPH site (Table 4).

3.3 Phenology of Carbon Exchange in Northern vs. Southern New England

3.3.1 Deciduous Forests

In 2 of the 3 years for which there is simultaneous data, net carbon uptake began earlier at the Bartlett Experimental Forest site in New Hampshire than at Harvard Forest about 200 km further south (Fig. 7). Given the difference in latitude, this is surprising; however, the Bartlett site is more than 100 m lower in elevation than the Harvard Forest sites, and in 2004–2006 the average annual temperature measured at the Bartlett flux tower was only about 0.5°C lower than for the Harvard Forest sites (Table 1). The earlier onset of net carbon uptake at Bartlett compared to Harvard Forest in 2 of 3 years is also consistent with earlier leaf development at Hubbard Brook Experimental Forest which is 30 km W of Bartlett, compared to Harvard Forest (Richardson et al. 2006). In the 3 years of simultaneous data however, the difference

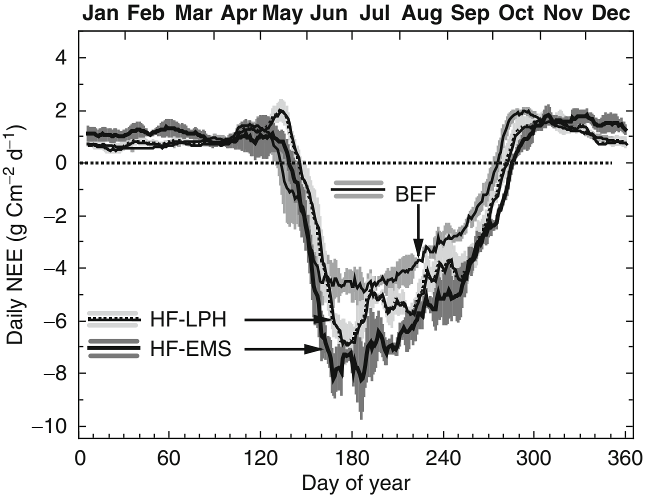

Fig. 7 Average 10-day running means (*lines*) and standard errors (*shading*) of net ecosystem carbon exchange (NEE) for 2004 through 2006 for the predominantly deciduous Harvard Forest sites (HF-LPH and HF-EMS) and the tower at Bartlett Experimental Forest (BEF) in northern New Hampshire. Negative values indicate forest carbon uptake. The *dark* and *light gray bands* for the Bartlett and HF, LPH towers respectively, and the *green band* for the HF main tower (EMS), show standard errors calculated from values on the same day of the year in each of the 3 years.

between the beginning of net C uptake at Bartlett and at the Harvard Forest deciduous sites was very variable. STARTNCU at Bartlett ranged from 13 days earlier to 12 days later than at HF-EMS, and from 18 to 2 days earlier compared to HF-LPH. (The large ranges are due to the year 2005, when net carbon uptake at Bartlett did not begin until May 28, or 16–18 days later than for the other 2 years.) In autumn, the transition from net carbon storage to carbon loss was consistently earlier at Bartlett than at the deciduous Harvard Forest sites (Fig. 7), possibly because the species at Bartlett respond more quickly to decreasing daylength, or because the first hard autumn frosts (below −2°C) came 20–30 days earlier at Bartlett than at Harvard Forest in 2004 through 2006 (day 280–295 at Bartlett, and day 308–315 at Harvard Forest). The average length of the period with net carbon storage at Bartlett was intermediate between the two Harvard Forest sites (Table 4).

3.3.2 Early Photosynthesis in Deciduous Forests Prior to Net Ecosystem Carbon Storage, and Environmental Predictors of Early Photosynthesis and Beginning of Net Carbon Storage

In addition to the date of first net carbon uptake, for each of the deciduous forest sites we calculated the date for the first evidence of strong photosynthesis in spring, as indicated by a daily maximum half-hourly net carbon uptake rate that exceeded the

Table 5 First day of each year in which the maximum 30-min net carbon uptake during day (DAY) exceeded average nighttime carbon efflux, the start of net carbon uptake (24hNET) and the lag between these two dates. Each is derived from a 10-day running average of the respective carbon flux parameter

Year	Harvard Forest, Main Tower			Harvard Forest, Little Prospect Hill			Bartlett Exp. Forest New Hampshire		
	DAY	24hNET	LAG	DAY	24hNET	LAG	DAY	24hNET	LAG
2003	131	146	15	149	153	4	n/a	n/a	n/a
2004	131	138	7	141	143	2	127	130	3
2005	134	136	2	147	150	3	138	148	10
2006	135	145	10	146	150	4	118	132	14
Mean	133	141	8.5	146	149	3.3	128	137	9.0

average nighttime respiration by the forest for that date. From these data, a slightly different picture of the phenology of carbon exchange emerges. Though there was large interannual variation, the date for first strong net carbon uptake preceded the first date of net carbon uptake by about 9 days, on average, at the HF-EMS and BEF sites, but by less than 4 days at the HF-LPH site (Table 5). The shorter lag at the LPH site may be a consequence of later development of photosynthetic capacity at the site, so that it in general leaf development occurred during warmer weather and therefore proceeded faster. The extreme dominance of red oak at the LPH site may also have contributed to the more rapid development of photosynthetic capacity at that site, because at LPH most leaf development occurred synchronously in one species, rather than more slowly in several species with different periods of leaf maturation at the EMS site. The EMS site also has a higher number of understory saplings and shrubs, particularly around the wetland NW of the EMS tower (Fig. 2). Richardson and O'Keefe in current volume report that budburst was slightly earlier in understory species than in canopy trees, although the two groups showed no consistent difference in the date of 75% leaf expansion.

In a search for climatic drivers of the start of net carbon uptake, for each site we calculated daily average soil temperature, cumulative photosynthetically active radiation received after April 1, and "growing degree-days" calculated by summation of daily average temperatures exceeding 4°C. These statistics varied slightly across the years 2003–2006, but also showed marked differences between sites (Table 6). Both for strong daytime net uptake and 24-h net carbon uptake, the HF-LPH site required a larger number of growing degree-days and a higher cumulative PAR than the other sites. The HF-LPH site was less clearly distinguished by the soil temperatures when net carbon uptake became active in spring (Table 6). Thus, HF-LPH site on a northerly slope showed delayed start of net carbon uptake in response to climatic drivers, as well as in respect to calendar date. The Bartlett site tended to require fewer growing degree-days, lower soil temperature and less cumulative PAR prior to the beginning of either strong photosynthesis or daily net

Table 6 Mean and standard error (SE) of cumulative growing degree-days (GDD), daily average soil temperature (T_{soil}; °C), and accumulated PAR (MJ) since April 1 on the date when daily maximum 30-min net carbon uptake exceeded the average nighttime carbon efflux (DAY) or the start of daily net carbon uptake (24h-NET) at the three deciduous forests. Soil temperature was measured at 5 cm depth at HF-EMS and Bartlett, and at 10 cm depth at HF-LPH

Site	Measure of ecosystem carbon uptake	GDD (Mean ± SE)		T_{soil} (Mean ± SE)		PAR (Mean ± SE)	
HF-EMS	DAY	133	1.0	10.5	0.1	1,361	105
HF-LPH	DAY	147	2.4	11.2	0.7	1,778	88
Bartlett	DAY	128	5.8	8.0	1.1	1,209	207
HF-EMS	24h-NET	141	2.5	11.8	1.1	1,657	55
HF-LPH	24h-NET	149	2.1	11.8	0.7	1,860	63
Bartlett	24h-NET	137	5.7	10.1	0.6	1,486	173

carbon uptake compared to other sites. However, a tendency for the forest at Bartlett to require fewer growing degree days, less soil warming, and less incident PAR prior to the initiation of photosynthesis is consistent with the observation by Richardson et al. (2006) that fewer growing degree days accumulated prior leaf development at BEF compared to Harvard Forest. The year-round high hydraulic conductance of diffuse-porous wood in the dominant tree species at Bartlett allows water transport to developing foliage at any time of year, whereas ring-porous red oak, the dominant tree species at Harvard Forest must produce earlywood vessels each year to supply sufficient water to new leaves (see Discussion).

3.3.3 Net Carbon Exchange in Coniferous Forests

Only about 2.5 years of simultaneous data (November 2000 through October 2001, July through December 2004, and 2006) are currently available for the Harvard Forest hemlock forest and the spruce-hemlock dominated forest near Howland, Maine. Daily net carbon uptake at Howland consistently started around day 90. At Harvard Forest net uptake commenced just a few days earlier in 2001, but a full month earlier in 2006 (Fig. 8). Differences in autumn carbon uptake between these sites were observed in all years, with HF-Hemlock showing net carbon uptake for up to two months longer than the Howland site (Fig. 8). The much longer season for carbon uptake at Harvard Forest, especially in 2006, may result from climatic differences. On most days, daily minimum temperatures in October were 2–5°C colder at the Howland site than at Harvard Forest. At Howland in October 2004 and 2006 air temperature fell below 0°C on 8 and 6 days respectively, whereas at

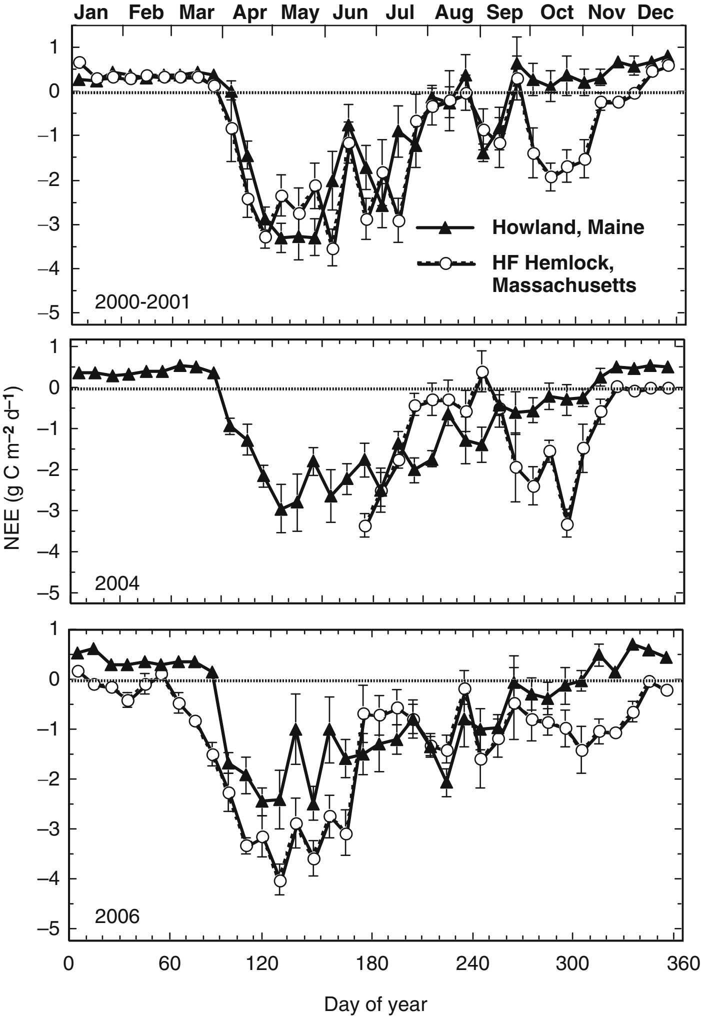

Fig. 8 Daily net carbon exchange averaged over 10-day intervals at the Harvard Forest hemlock site and at Howland, Maine, primarily in 2001, 2004 and 2006. Error bars are standard errors of the ten daily values in each mean; for some winter periods, the error bars are too small to be seen behind the symbols. The last two months in the top panel are in the year 2000, and there were no measurements until late June for the Harvard Forest hemlock site in 2004.

Harvard Forest this happened only once in 2004 and twice in 2006, and then only in late October (Fig. 11). A slightly more open canopy with tree-fall gaps in the relatively old HF hemlock stand may also allow more light to penetrate the canopy at the low sun angles that occur in late autumn, compared to denser canopy in the younger forest at Howland.

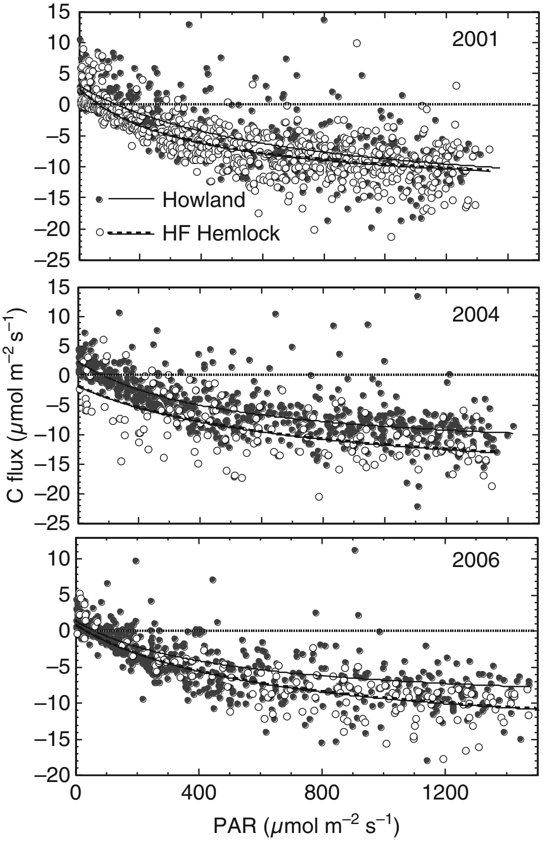

Fig. 9 Response of daytime carbon flux to photosynthetically active radiation (PAR) at the Harvard Forest hemlock site and the Howland, Maine forest in October 2001, 2004 and 2006. Fitted curves are from equations of the form C flux = c + (a × PAR)/(b + PAR), where c is an estimate of daytime ecosystem respiration and a and b describe the shape of the curve.

4 Discussion

4.1 Relationship of Leaf Phenology to Net Ecosystem Carbon Exchange and Local Differences Among Harvard Forest Sites

The start of net carbon uptake at HF-EMS was correlated with budbreak and leaf development (Figs. 3a and 4a), but there was also considerable variation among years. For example, the 4-year period, from 1993 through 1996, exhibited delayed start of net carbon uptake in relation to leaf development than did the rest of the time series. While during the other years, the STARTNCU was within 5 days of the mean of budbreak and 75% leaf expansion, in 1993–1996 STARTNCU lagged by nearly 8–11 days. There are at least two possible reasons that the time interval between leaf development and the beginning of net carbon uptake could vary interannually. Firstly, there is variation in ecosystem respiration, the majority of which comes from soil and can be decoupled from canopy development. Secondly, the contribution of conifers in the EMS tower footprint to measured fluxes during the period of deciduous leaf development could vary from year to year, because the conifers occur almost exclusively to the NW of the flux tower, and conifers therefore have a greater influence on the measured fluxes in years with a greater frequency of NW winds more consistent relationship between leaf phenology and the beginning of daily net carbon uptake at the LPH site, which has very few conifers, would support this hypothesis. The 4 years of carbon flux data from LPH in 2003–2006 show no significant correlation of STARTNCU at LPH with observed dates of either budburst or leaf expansion elsewhere at Harvard Forest; however, leaf phenology was not observed specifically at the LPH site. Lower spring soil temperatures at LPH compared to the EMS site (Fig. 6) could delay leaf development, and exposure of foliage to NW winds, which are associated with air temperatures lower by 2–3°C compared to SW and SE wind in April and May (Harvard Forest meteorological station data) could also delay leaf development at the LPH site.

The relatively weak relationship between dates of leaf abscission and the end of daily net carbon uptake (Figs. 3b and 4b) is not surprising when one considers that leaf fall does not immediately follow leaf senescence, especially in red oak, the predominant deciduous species at the Harvard Forest flux tower sites. It points to the need for a different parameter to accurately predict the cessation of net carbon uptake, possibly leaf greenness from above the canopy or decrease in absorbed PAR (measured as the ratio of below-canopy to above-canopy PAR).

The difference in the annual period of daily net carbon uptake between the primarily deciduous sites at Harvard Forest (EMS and LPH) shows that even fairly small differences in forest composition and location may affect the annual period of net carbon uptake. The two flux towers are only 1.1 km apart and differ in elevation by only about 50 m (Table 1), but showed a consistent difference in the dates at which daily net uptake began and ended. A portion of this difference can be attributed to microclimatic differences including lower Tsoil at the LPH than EMS site in spring (Fig. 6). The presence of conifers in the NW sector of the EMS tower footprint (Wofsy et al. 1993; Goulden et al. 1996), where they form about 40% of the basal area (see ftp://ftp.as.harvard.edu/pub/nigec/HU_Wofsy/hf_data/, "Ecological data") clearly contributes to observations of early-season photosynthesis at the site because data from the nearby Hemlock flux tower show substantial carbon uptake in April (Fig. 5), several weeks before budbreak of the dominant deciduous trees (Fig. 3). The residual differences can be attributed primarily to differences in aspect, canopy structure and microclimate, whereas age effects are likely to be minor (Noormets et al. 2007 and in current volume).

The contrast in the phenology of carbon uptake between the predominantly deciduous Harvard Forest sites and the hemlock forest (Fig. 5) shows how differently the conifer forest functions from the deciduous forests. In the hemlock forest, daily net carbon uptake began in late March, daily maximum rates were reached by mid-April, and a decline in daily net carbon uptake began by late June, about the same time when the deciduous forests were achieving maximum daily uptake. Decreasing daily net uptake for the hemlock stand in July and August had a similar pattern to the decrease for the deciduous forests during the same period (actually, the rate of change for the hemlock forest is slightly smaller), but uptake in the hemlock forest then recovered to a second peak in late October, just before time of maximum net carbon loss from the deciduous forests. Average estimated net annual carbon uptake did not differ significantly between the deciduous and hemlock stands (ranging between 3 and 4 Mg C per ha; Hadley et al. 2008; Urbanski et al. 2007; additional data at web addresses given in Methods), but all of the annual uptake occurred during a single large summertime peak for the deciduous forests, and in two smaller spring and fall peaks for the hemlock forest (Fig. 5).

This pattern in net ecosystem carbon exchange can be attributed to high ecosystem respiration in the hemlock forest relative to its maximum photosynthetic capacity. The maximum instantaneous rate of net carbon uptake by the hemlock forest has been measured at about 15 μmol m^{-2} s^{-1} compared to about 25 μmol m^{-2} s^{-1} for deciduous forest, while average ecosystem respiration in mid-to-late summer is typically around 6–8 μmol m^{-2} s^{-1} in both forest types (Hadley et al. 2002, 2008; Wofsy et al. 1993). Ecosystem respiration occurs continuously during day and night throughout the year, increasing with increasing soil and air temperatures. However, there is high carbon uptake only during sunny daytime periods. As a result, with the limited photosynthetic capacity of hemlock foliage even when conditions are optimum for photosynthesis, warm soil and air temperatures can drive total daily respiration in the hemlock forest to levels approaching or exceeding total carbon uptake. The result is in near-zero daily carbon exchange, as seen for the hemlock forest during some late July, August and early September periods, especially in 2001 and 2004 (Fig. 8).

4.2 *Differences in Phenology of Ecosystem Carbon Exchange Between Southern and Northern New England*

4.2.1 Deciduous Forests

The surprising earlier onset of daily net carbon uptake, as well as the first strong photosynthesis signal, in 2 of 3 years for the Bartlett Experimental forest in northern New Hampshire compared to Harvard Forest sites (Fig. 5, Tables 3–5) could result in part from a difference in the wood anatomy and function of the dominant tree species at the two sites. Red oak, a ring-porous species, forms 46 and 58% of basal area for the Harvard Forest EMS and LPH tower footprints respectively, with diffuse-porous deciduous trees and conifers of secondary importance. In the more diverse forest at Bartlett, red maple and American beech (both diffuse-porous) form the largest fractions of basal area, 28 and 20% respectively, with eastern hemlock third at 17%. The only ring-porous tree in the forest at Bartlett is white ash with just 5% of total basal area. Ring-porous trees depend heavily on the earlywood xylem produced each year for water transport to foliage, and probably in consequence of this, ring-porous trees produce leaves later in spring (Zimmermann and Brown 1971). Although the forest at Bartlett became a net sink for carbon earlier in the year than either of the Harvard Forest deciduous forest sites in 2004 and 2006, it's maximum daily rate of carbon uptake in summer was lower than the Harvard Forest sites, which is consistent with less efficient water transport in diffuse-porous trees (Zimmermann and Brown 1971). Slower water transport may limit stomatal conductance in diffuse porous trees, leading to lower maximum leaf-level photosynthesis by most diffuse-porous species compared to ring-porous oaks (Bassow and Bazzaz 1997) and therefore higher maximum ecosystem-level carbon uptake in forests composed primarily of ring-porous species.

4.2.2 Conifer Forests

The one month delay in the start of net carbon uptake at Howland compared to HF-Hemlock in 2006 is probably mostly a consequence of much earlier spring warming of soil at Harvard Forest in 2006 (Fig. 10) given that Hollinger et al. (1999) showed that the start of the net C uptake season at Howland was coincident with thawing of forest soils. A thaw beginning on March 10, during which the daily minimum air temperature reached 1–7°C for four consecutive nights at Harvard Forest, but reached just 1–2°C for two of these nights at Howland could also have contributed to an earlier start to carbon uptake by hemlocks at Harvard Forest. Leaf conductance to water and carbon exchange in conifers, including eastern hemlock and red spruce, have been shown to exhibit a threshold response to minimum daily air temperature, where air temperatures (and, by inference, foliage temperatures) below freezing can sharply limit stomatal opening and photosynthesis the following day (Fahey et al. 1979; Schwarz et al. 1997; Smith et al. 1984; Hadley 2000). This effect has also been previously seen in ecosystem carbon exchange for the two conifer forests considered here (Hollinger et al. 1999; Hadley and Schedlbauer 2002).

A peak in net carbon uptake in October to early November occurred in the Massachusetts hemlock forest in 2001, 2004 and 2006 but this feature was almost completely absent from the Maine spruce-hemlock forest, aside from a very small increase in C storage in October 2006 (Fig. 8). The autumn carbon uptake at Harvard.

Forest may indicate that the capacity for conifers to store carbon in autumn is expressed in southern but not northern New England, given autumn temperatures typical of the current climate. Previous work at Howland (Hollinger et al. 1999) showed that spruce-hemlock forest C uptake capacity was depressed after air temperatures dropped below a threshold of −2 to −3°C. Similar frost-induced termination of net carbon uptake was observed in a boreal black spruce forest (Goulden et al. 1997). Soil temperature seems unlikely to be limiting to carbon uptake at Howland in October, because the Howland soil temperature at 5 cm depth, although colder than at Harvard Forest, remained above 7°C throughout October in all years (Fig. 10).

However, the fairly small differences in October minimum daily temperatures between Harvard Forest and Howland (Fig. 10) suggest that some other factors may

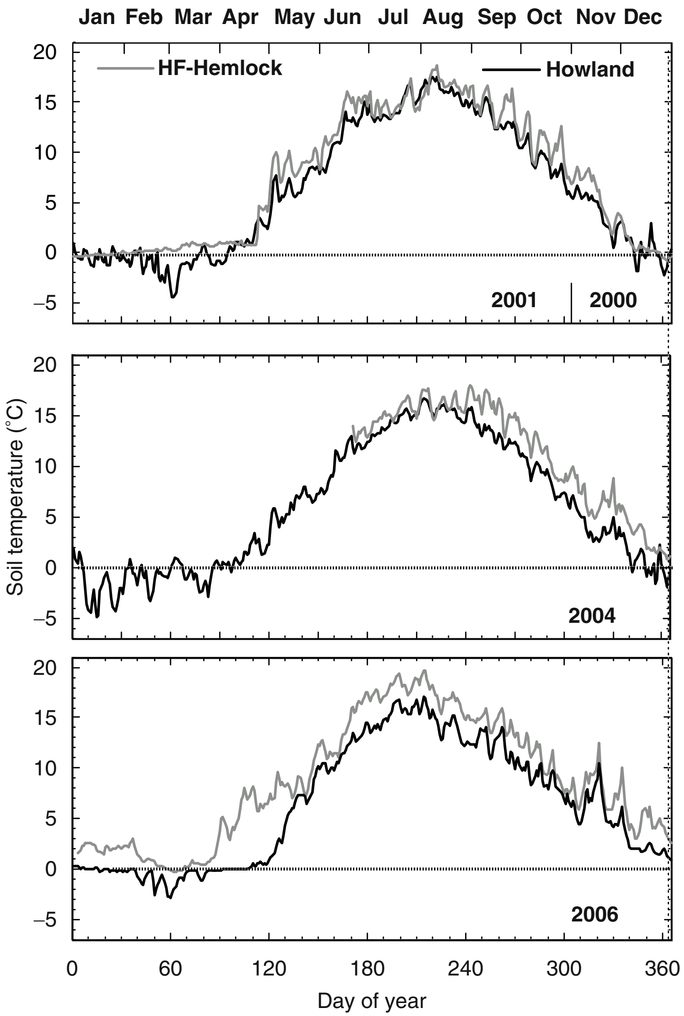

Fig. 10 Measured or estimated soil temperature at 10 cm depth for the HF hemlock and Howland sites in 2000–2001, 2004 and 2006. Values for Howland in 2000, 2001 and 2004 were estimated from measurements at 5 cm, plus a correction based on seasonal temperature gradients between 5 and 20 cm observed in 2006.

also be limiting carbon uptake at Howland in autumn. During most periods, including autumn 2001 and 2004, total daily incident PAR was similar at the two sites, but in the fall of 2006, daily total PAR averaged about 2–5 mol m^{-2} or 10–20% lower at Howland than at Harvard Forest. There was also less net carbon uptake during October at a given PAR level in the Howland spruce-hemlock forest than in the Harvard Forest hemlock stand. This occurred particularly at high PAR values in 2004 and 2006, but also at relatively low PAR values in 2001 and 2004 (Fig. 9).

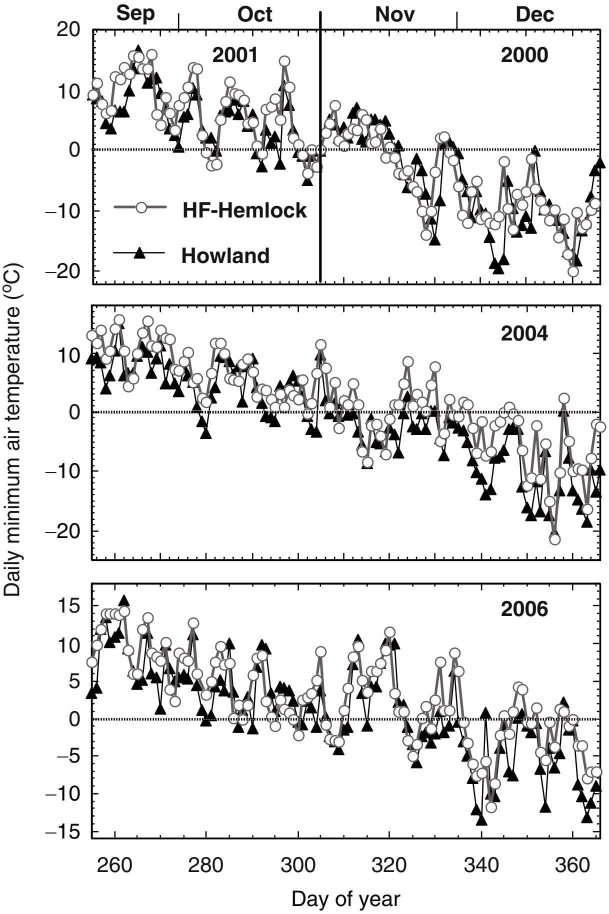

Fig. 11 Mid-September through December daily minimum air temperature for the Harvard Forest hemlock site and the Howland, Maine site. Data for November and December 2000 rather than 2001 are shown in the top panel because the carbon flux data in Fig. 6 are for the earlier year.

In contrast, at high PAR values during summer (July and August) of 2001 and 2006, carbon uptake at Howland was nearly the same as in the Harvard Forest hemlock forest (±1.5 μmol m^{-2} s^{-1}), and C uptake was higher at Howland by about 3 μmol m^{-2} s^{-1} in 2004. The low October carbon uptake capacity at Howland contributed to very low or negative values of daily carbon uptake for the Howland forest beginning in late September of each year, while net carbon uptake by the Harvard Forest hemlock forest continued into or through November.

Greater carbon uptake by the Harvard Forest hemlock forest, relative to the Maine spruce-hemlock stand at Howland, especially in 2004 and 2006, which had higher spring and fall temperatures than 2000 and 2001, suggest that the carbon balance of the more southerly forest could be more stimulated by climate warming at least in the short term. However, the Harvard Forest hemlock forest and the Howland spruce-hemlock forest also differ in age and structure in ways that may affect canopy photosynthesis, especially in autumn. The Harvard Forest hemlock stand is older and has a higher fraction of large, old trees, some of which have died in the last 10 years, creating a very uneven canopy surface with some large gaps. This may allow more light to penetrate the canopy of the Harvard Forest stand, especially at the low solar angles occurring in autumn, compared to the younger, more even-aged forest at Howland. A comparison between more structurally similar forests may be necessary to establish a climate-related difference in spring and fall carbon uptake.

5 Conclusions

The carbon exchange data we summarize here indicate that in inland areas of New England, forest composition and local topography can have stronger effects than latitude on the springtime start of net carbon uptake by deciduous trees. Although there was not a statistically significant difference between the deciduous BEF site in New Hampshire and the Harvard Forest sites in Massachusetts (not surprising given only 3 years of data from BEF), it is striking that the average date for first net carbon uptake at BEF was earlier than for either of the Harvard Forest deciduous sites (Fig. 7, Table 4). The lower average values of accumulated growing degree-days, soil temperature, and accumulated PAR at BEF during spring transitions to carbon uptake (Table 6), indicate a tree species difference, and not primarily a climatic difference, could responsible for the difference in time of first net carbon uptake between BEF and the other sites. This pattern suggests an important influence of tree species, and perhaps particularly xylem anatomy, on the development of leaves and carbon uptake capacity in forests.

The HF-LPH site was the latest to show net carbon uptake, and showed a more consistent difference from HF-EMS than BEF did from either HF site. Some of the difference between HF-EMS and HF-LPH sites is also attributable to forest composition, particularly the presence of some conifers in the HF-EMS flux tower footprint, but microclimate differences (particularly in soil temperature, see Fig. 6) are likely responsible for some of the lag in onset of net carbon uptake in spring at the HF-LPH site compared to HF-EMS. Soil temperature is an important variable to consider in developing models to predict carbon uptake in spring. In autumn, latitude may significantly influence the cessation of net carbon uptake (Fig. 7, Table 4), given that BEF consistently had the earliest date when there was no net uptake, but a possible effect of tree species cannot be dismissed.

In the contrast between coniferous forests (HF-Hemlock vs. Howland), latitude and associated climate parameters seem to play a significant role. The beginning of net carbon uptake at Howland, which is about 300 km further north, was later in both years for which we have spring data to compare (2001 and 2006) though the difference was only about a week in 2001. More significant in terms of annual carbon storage were autumn periods of net carbon uptake in autumn, which occurred in all 3 years only at the more southerly HF-Hemlock site (Fig. 8). With a general climate warming, autumn carbon uptake by conifer forests may be expected to expand further north.

The correlations between the dates of leaf initiation and expansion over 15 years, and the beginning of net carbon at Harvard Forest are not as strong as might be hoped, if such observations are to be used to predict the beginning of carbon storage in other deciduous forest ecosystems. Variation in ecosystem respiration, not associated with leaf development, is one potential cause of this, but the other problem is that the HF-EMS tower does include over 40% conifers by basal area, as well as a wetland within the NW sector of the tower footprint, and these could influence early spring carbon exchange enough to push the changeover from net carbon loss to carbon uptake earlier, in a manner not predicted by the phenological observations which emphasize deciduous trees, and may not have a consistent relationship to photosynthesis in conifers

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