Tree Physiology 29, 321–331
doi:10.1093/treephys/tpn040

Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests

ANDREW D. RICHARDSON,[1,2] DAVID Y. HOLLINGER,[3] D. BRYAN DAIL,[4] JOHN T. LEE,[4] J. WILLIAM MUNGER[5] and JOHN O'KEEFE[6]

[1] *Complex Systems Research Center, University of New Hampshire, Morse Hall, 8 College Road, Durham, NH 03824, USA*

[2] *Corresponding author (andrew.richardson@unh.edu)*

[3] *USDA Forest Service, Northern Research Station, 271 Mast Road, Durham, NH 03824, USA*

[4] *Department of Plant, Soil, and Environmental Sciences, University of Maine, Orono, ME 04469, USA*

[5] *Division of Engineering and Applied Science, Department of Earth and Planetary Science, Harvard University, Cambridge, MA 02138, USA*

[6] *Harvard Forest, Harvard University, Petersham, MA 01366, USA*

Received July 31, 2008; accepted November 13, 2008; published online January 19, 2009

Summary Spring phenology is thought to exert a major influence on the carbon (C) balance of temperate and boreal ecosystems. We investigated this hypothesis using four spring onset phenological indicators in conjunction with surface–atmosphere CO_2 exchange data from the conifer-dominated Howland Forest and deciduous-dominated Harvard Forest AmeriFlux sites. All phenological measures, including CO_2 source–sink transition dates, could be well predicted on the basis of a simple two-parameter spring warming model, indicating good potential for improving the representation of phenological transitions and their dynamic responsiveness to climate variability in land surface models. The date at which canopy-scale photosynthetic capacity reached a threshold value of 12 μmol m^{-2} s^{-1} was better correlated with spring and annual flux integrals than were either deciduous or coniferous bud burst dates. For all phenological indicators, earlier spring onset consistently, but not always significantly, resulted in higher gross primary productivity (GPP) and ecosystem respiration (RE) for both seasonal (spring months, April–June) and annual flux integrals. The increase in RE was less than that in GPP; depending on the phenological indicator used, a one-day advance in spring onset increased springtime net ecosystem productivity (NEP) by 2–4 g C m^{-2} day^{-1}. In general, we could not detect significant differences between the two forest types in response to earlier spring, although the response to earlier spring was generally more pronounced for Harvard Forest than for Howland Forest, suggesting that future climate warming may favor deciduous species over coniferous species, at least in this region. The effect of earlier spring tended to be about twice as large when annual rather than springtime flux integrals were considered. This result is suggestive of both immediate and lagged effects of earlier spring onset on ecosystem C cycling, perhaps as a result of accelerated N cycling rates and cascading effects on N uptake, foliar N concentrations and photosynthetic capacity.

Keywords: AmeriFlux, bud burst, carbon dioxide, eddy covariance, growing season length, phenology, spring onset, start of spring.

Introduction

Reducing uncertainties about the role of terrestrial ecosystems in the global carbon cycle requires a detailed understanding of the spatial and temporal variations in biologically mediated sources and sinks of carbon (C) (Schimel et al. 2001, Wofsy and Harriss 2002). The eddy covariance measurements of surface–atmosphere CO_2 exchange that are being made at research sites around the world (e.g., Baldocchi et al. 2001, Baldocchi 2008) provide the data that are necessary to investigate these patterns. Cross-site studies give strong support for the idea that increases in growing season length are correlated with increases in productivity or carbon sequestration, or both. For example, Baldocchi et al. (2001) showed that, across a range of temperate deciduous sites, a one-day increase in growing season length (as defined by the number of days between source–sink transition in the spring and sink–source transition in the autumn) increased annual net ecosystem productivity (NEP) by 5.7 g C m^{-2}. This value is in close agreement with model predictions (e.g., Lieth 1975, Baldocchi and Wilson 2001).

Whether similar patterns hold for individual sites, in relation to interannual climatic variation, is a question still debated. Early single-site studies (Goulden et al. 1996, Chen et al. 1999, Black et al. 2000, Goldstein et al. 2000) relating

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interannual variation in growing season length to interannual variation in measured NEP, or the component fluxes gross primary productivity (GPP) and ecosystem respiration (RE), were largely anecdotal (e.g., comparing fluxes in a warm, early spring year to those in a cool, late spring year), because with eddy flux time series of only a few years in length, rigorous statistical analysis was impossible. As data records have increased in length, correlation analyses have been increasingly used to develop and test quantitative relationships between anomalies in growing season length and anomalies in integrated C fluxes. However, although the reported trends have generally been in the expected direction, the statistical significance of these trends has often not been especially robust. For example, at a mixed temperate forest, 5 years of data indicated that a one-day increase in the number of days between spring and autumn source–sink transitions was associated with a 3.5 g C m^{-2} (significantly different from 0 at $P = 0.10$) increase in annual NEP (Carrara et al. 2003). At a boreal aspen forest, 9 years of data indicated that a one-day increase in canopy duration was associated with a 6.9 g C m^{-2} ($P = 0.01$) increase in annual NEP (Barr et al. 2004, 2007). Dunn et al. (2007) analyzed an 11-year record from a boreal conifer forest and reported that both earlier spring onset and a longer growing season (both determined by the dates at which GPP reached a specified value) were positively correlated, though not significantly ($P > 0.10$), with increased NEP. Niemand et al. (2005) linked observations from the Tharandt International Phenological Garden to flux measurements in the Tharandt forest and found that earlier emergence of the 'May shoot' of *Larix decidua* Mill. and *Picea abies* (L.) Karst. was correlated with increased productivity, but only when the drought year of 2003 was excluded. In contrast to these studies, Sacks et al. (2007) reported that, in a subalpine conifer forest, annual NEP was decreased by 1.4 g C m^{-2} ($P = 0.37$) for every one-day increase in the number of days between spring and autumn source–sink transitions, because earlier spring onset generally resulted from a shallow snowpack, which translated to reduced soil water content, and ultimately drought, later in the growing season.

These patterns are of special interest to those studying carbon cycling because there is much evidence suggesting that, as a result of recent warming trends, the onset of spring has advanced at a rate between 1 and 2 days per decade over roughly the last half-century (Peñuelas et al. 2002, Badeck et al. 2004, Richardson et al. 2006). Furthermore, indirect evidence (changes in atmospheric CO_2 concentration and remote sensing measures of greenness) is strongly suggestive of increased photosynthetic activity at high latitudes as a result of higher temperatures and consequently an increase in growing season length (Myneni et al. 1997, Randerson et al. 1999).

We evaluated relationships between surface–atmosphere CO_2 fluxes and interannual variation in the arrival of spring at two contrasting forests in the northeastern United States: the coniferous Howland Forest and the deciduous Harvard Forest. Flux data records that date to 1996 and 1991, respectively, are complemented by even longer observer records of bud burst phenology of coniferous and deciduous species. We also considered two alternative phenological indicators derived from the CO_2 flux time series: (1) the spring date at which the ecosystem switches from a CO_2 source to a sink and (2) the spring date at which the maximum rate of canopy photosynthesis reaches a specific threshold value. We predicted that earlier spring has a larger effect on fluxes at Harvard Forest than at Howland Forest, because at peak, daily GPP is about 14 g C m^{-2} day^{-1} at Harvard Forest compared with 10 g C m^{-2} day^{-1} at Howland Forest (Hollinger et al. 2004, Urbanski et al. 2007). This is offset by RE totaling about 6 g C m^{-2} day^{-1} at each site, resulting in NEP of 9 g C m^{-2} day^{-1} at Harvard Forest and 4 g C m^{-2} day^{-1} at Howland Forest. Recognizing that annual patterns may differ from those at shorter time scales (e.g., Goldstein et al. 2000, Suni et al. 2003*a*), and also that there may be indirect or lagged effects of an early (or late) spring, our analysis was conducted for both annual and spring (April, May and June) integrals of NEP, GPP and RE.

Data and method

Study sites

The analysis is based on data from the Howland Forest (45.25° N and 68.73° W, elev. 60 m asl) and Harvard Forest (42.53° N and 72.17° W, elev. 340 m asl) AmeriFlux sites. The Howland tower is located in a boreal-northern hardwood transition forest about 50 km north of Bangor, ME, USA. Forest composition is dominated by the conifers, red spruce (*Picea rubens* Sarg., 44% of basal area) and eastern hemlock (*Tsuga canadensis* (L.) Carrière, 26% of basal area) with lesser quantities of other conifers (21% of basal area) and hardwoods (primarily red maple, *Acer rubrum* L., and paper birch, *Betula papyrifera* Marsh., totaling 8% of basal area) (Hollinger et al. 1999). The Harvard tower is located in a mixed temperate forest, about 110 km west of Boston, MA, USA. Forest composition is dominated by deciduous species, including red oak (*Quercus rubra* L., 36% of basal area) and red maple (22% of basal area), with lesser quantities of other hardwoods (including black oak, *Quercus velutina* Lam., white oak, *Quercus alba* L., and yellow birch, *Betula alleghaniensis* Britton, totaling 14% of basal area). Conifers include eastern hemlock (13% of basal area), red pine (*Pinus resinosa* Aiton, 8% of basal area) and white pine (*Pinus strobus* L., 6% of basal area).

Mean annual temperature is slightly higher at Harvard Forest (6.5 °C) than at Howland Forest (6.1 °C), but mean annual precipitation is comparable (1000 versus 990 mm, respectively). Previous studies have shown both sites to be strong sinks for atmospheric carbon, with the annual C sequestration of 240 g C m^{-2} $year^{-1}$ (mean ± 1 SD) at

Harvard Forest (Urbanski et al. 2007) being roughly 40% greater than the 175 g C m^{-2} $year^{-1}$ at Howland Forest (Hollinger et al. 2004), based on eddy covariance measurements.

CO_2 flux measurements

We used long-term eddy covariance measurements of net ecosystem exchange (NEE) of CO_2 made at each site (Howland, 1996–2004 data; Harvard, 1992–2004 data). Site-specific procedures, including quality control, flux corrections and data editing, are described elsewhere (Howland, Hollinger et al. 1999, 2004; Harvard, Barford et al. 2001, Urbanski et al. 2007). The standard sign convention is that a negative NEE flux is a flux into the system (i.e., net CO_2 uptake). Here, so that the meaning of increases in carbon storage is clear, we instead use the term NEP (NEP = −NEE; see Chapin et al. 2006) and consider the component fluxes RE and GPP both to be positive quantities (i.e., NEP = GPP − RE).

Flux data were assimilated into a simple ecosystem physiology model using a Kalman filter, as described in detail by Gove and Hollinger (2006). Assimilation was used to obtain: (1) continuous partitioning of NEE to its components RE and GPP and (2) time-varying estimates of model parameters for RE, based on the exponential model of Lloyd and Taylor (1994), and GPP, based on the Michaelis–Menten hyperbolic light response function:

$$\mathrm{NEP} = \mathrm{GPP} - \mathrm{RE} = (A_{\mathrm{sat}}) \times \left[\frac{Q}{Q + K_{\mathrm{m}}}\right] - \mathrm{RE}. \quad (1)$$

Here, GPP is driven by incident solar radiation (Q, μmol m^{-2} s^{-1}), with a half-saturation constant of K_m and a theoretical light-saturated rate of photosynthesis (A_{sat}). We use the predicted rate of photosynthesis at Q = 2000 μmol m^{-2} s^{-1} (full-sun conditions) as an estimate of the effective maximum rate of canopy photosynthesis, A_{max}. At both sites, peak A_{max} estimates varied among years but tended to be in the range of ≈ 25 μmol m^{-2} s^{-1}, lower than those previously reported (based on a different model) for Harvard Forest (Urbanski et al. 2007) but higher than those previously reported for Howland Forest (Hollinger et al. 2004); this was compensated for by lower and higher modeled rates of respiration, respectively. However, integrated annual sums for NEE, GPP and RE for both sites were well correlated (all $P < 0.001$) with previously published values (i.e., Hollinger et al. 2004, Urbanski et al. 2007).

We determined the first spring date at which the ecosystem switched from a source to a sink based on a 5-day running mean of the gap-filled daily NEE integral; comparable results (not shown here) were obtained when a sigmoid curve was fit to the NEE time series and used to estimate the source–sink transition date. Following Churkina et al. (2005), we determined the length of the carbon uptake period as the number of days (not necessarily contiguous) in a given year for which the ecosystem was a net sink for atmospheric CO_2, based on the assimilated fluxes integrated to the daily time step.

Field observations of bud burst phenology

Field observations of springtime bud burst phenology have been conducted at both sites since 1990 and are ongoing. At Howland Forest, the mean aggregate (across the dominant species) dates of bud burst by coniferous (hemlock and red spruce) and deciduous (paper birch and red maple) species are estimated from observations made during weekly or twice-weekly site visits. At Harvard Forest, observations of bud burst and leaf development of three or more individuals of 33 woody species have been made at 3–7-day intervals from April through June (see data series HF-003, at http://harvardforest.fas.harvard.edu/, for additional information). Here, we consider deciduous bud burst date to be the mean date for red oak and red maple, and coniferous bud burst date to be the mean date for hemlock and white pine.

Results

Seasonal and annual variation in gross and net fluxes

The standard deviation (SD) of the annual integral of gap-filled and partitioned fluxes, a measure of interannual variation, was twice as large at Harvard Forest (1 SD = 100 g C m^{-2}) as at Howland Forest (55 g C m^{-2}) for NEP, similar at the two sites (85–90 g C m^{-2}) for RE and 50% larger at Harvard Forest (155 g C m^{-2}) than at Howland Forest (105 g C m^{-2}) for GPP. At Howland Forest, interannual variations in RE and GPP were larger during the spring (April, May and June) than during the other seasons, whereas interannual variation in integrated NEP was similar (≈ 20 g C m^{-2}) for spring, summer and autumn periods (Figure 1A). At Harvard Forest, interannual variations in NEP and both component fluxes were largest during the summer (July, August and September) (Figure 1C).

Seasonal flux anomalies, especially summer anomalies, were positively and significantly ($P \leq 0.05$) correlated with corresponding annual anomalies, with two exceptions (Figure 1B and D). First, at neither Howland Forest nor Harvard Forest were winter anomalies for any flux significantly correlated with annual anomalies (all $P \geq 0.05$). Second, the spring NEP anomaly at Howland Forest was not significantly correlated with the annual NEP anomaly, nor was the spring RE anomaly at Harvard Forest significantly correlated with the annual RE anomaly.

Interannual variation in spring onset

At Howland Forest, the photosynthetic capacity of the evergreen canopy began to recover from winter dormancy around Day 80, and the ecosystem switched from a carbon source to a carbon sink 2 weeks later, on Day 93 ± 7 (mean ± 1 SD, calculated across years). This transition

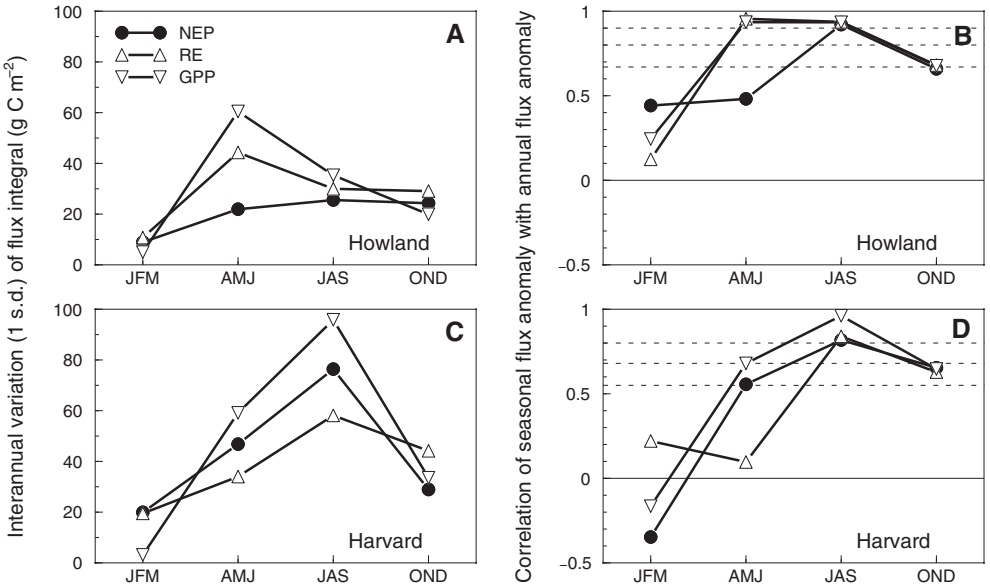

Figure 1. A and C: Seasonal patterns of interannual variation in measured NEP and its component fluxes RE and GPP at the Howland Forest and Harvard Forest AmeriFlux sites. B and D: Correlation of seasonal flux anomalies with annual flux anomalies for NEP, RE and GPP. Dashed horizontal lines indicate varying levels of statistical significance ($P = 0.05$, 0.01 and 0.001), given sample size of $n = 9$ (Howland) and $n = 13$ (Harvard). Labels on x-axis denote months, e.g., AMJ denotes spring months of April, May and June.

preceded bud burst by both deciduous (Day 120 ± 7) and coniferous (Day 139 ± 7) species by almost a month. By comparison, at Harvard Forest, although photosynthetic capacity also began to increase around Day 80 (attributed to photosynthesis by the evergreen conifers accounting for roughly one-quarter of basal area), it remained negligible ($A_{max} < 2$ μmol m^{-2} s^{-1}) until deciduous bud burst occurred on Day 129 ± 6. Conifer bud burst occurred on Day 151 ± 5, roughly coinciding with the source–sink transition at Day 152 ± 8. The date at which canopy A_{max} reached the threshold value of 12 μmol m^{-2} s^{-1} was almost a month earlier at Howland Forest (Day 134 ± 9) than at Harvard Forest (Day 158 ± 8).

There was a general synchrony among the four phenological measures (i.e., deciduous and coniferous bud burst, spring CO_2 source–sink transition date and the date at which canopy photosynthesis first reached a specified threshold) of spring onset at both sites. At both Howland Forest ($r = 0.67$) and Harvard Forest ($r = 0.62$), deciduous and conifer bud burst dates were well correlated (both $P < 0.05$). Similarly, source–sink transition dates were well correlated with the date at which canopy $A_{max} = 12$ μmol m^{-2} s^{-1} at both sites ($r = 0.70$ and $r = 0.77$, respectively; both $P < 0.05$). At Howland Forest, deciduous bud burst dates were significantly correlated ($P < 0.05$) with both source–sink transition dates ($r = 0.67$) and the date at which canopy $A_{max} = 12$ μmol m^{-2} s^{-1} ($r = 0.79$), but these correlations were not statistically significant at Harvard Forest (both $r < 0.40$, $P > 0.20$). This result was not predicted, because we intuitively expected that the phenologies of bud burst and photosynthetic activity would be more tightly coupled in the deciduous forest where the development of new foliage is an essential prerequisite for photosynthesis. The imperfect correlation among measures reflects the fact that each is quantifying a different developmental or physiological state, and each is potentially subject to different environmental drivers and sensitivities.

At both sites, a simple two-parameter spring warming model (following Chuine et al. 1998) fit to the data (with separate parameters fit for each site) described the observed interannual variation in spring onset for each of the phenological measures considered (Figure 2). The two fit parameters were the day (t_0) on which accumulation of forcing units begins and the cumulative amount of forcing required (F^*). In this model, the current state of forcing at time t, $S_f(t)$, is given by the summation of forcing units (based on a sigmoid function of air temperature, with fixed coefficients after Chuine et al. 1998) accumulated from time t_0 as:

$$S_f(t) = \sum_{t=t_0}^{t_1} \frac{28.4}{1 + \exp\left(-0.185 \times T^{air}(t) - 18.4\right)}. \qquad (2)$$

The phenological event being modeled is predicted to occur when $S_f = F^*$.

Root mean square errors (RMSEs) of the fitted models were comparable in magnitude (≈ 4 days) for hardwood and conifer bud burst phenology and also source–sink transition date and the date at which $A_{max} = 12$ μmol m^{-2} s^{-1}. More highly parameterized models involving, for example, parallel or sequential chilling requirements (e.g., Hunter and Lechowicz 1992, Chuine et al. 1998) resulted in lower RMSEs (≈ 3 days) but were generally less well supported by the data, according to Akaike's Information Criterion

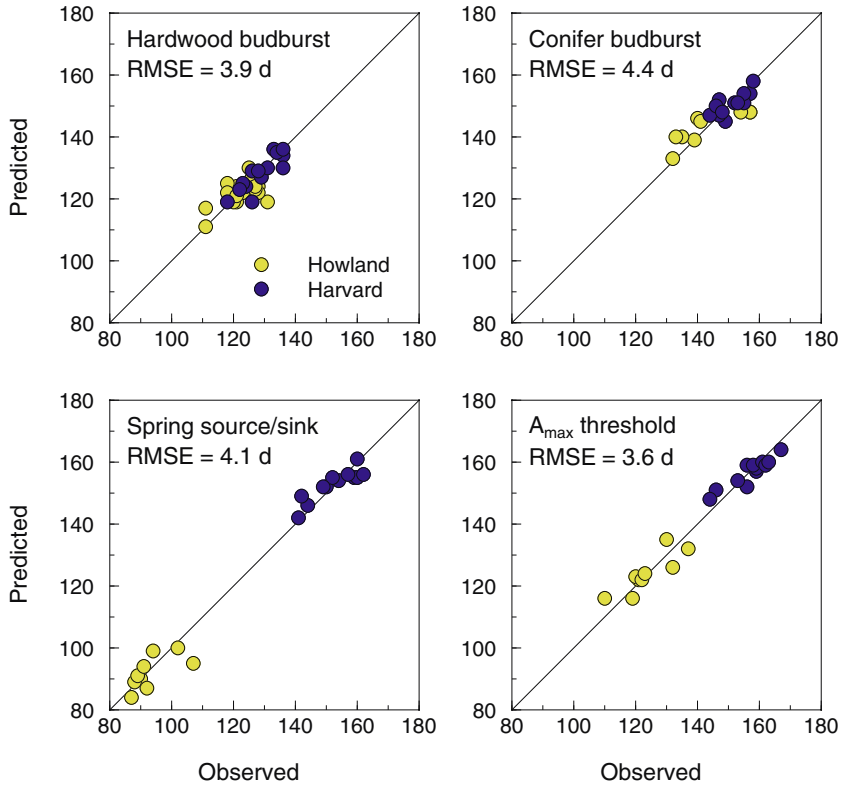

Figure 2. Observed and predicted day of year for four spring phenological measures. Predicted dates are from a two-parameter spring warming model fit to the data, with separate parameters fit for the Howland Forest and the Harvard Forest data.

corrected for small sample sizes (AIC_C; see Burnham and Anderson 2002). Thus, more complex models were likely overfit and did not provide sufficiently improved representation of underlying physiological processes to justify the increased model complexity.

Relationship between spring phenology and flux anomalies

To examine relationships between anomalies in spring onset date and anomalies in integrated fluxes, we analyzed the pooled data for the two sites by simple linear regression. We then tested whether the slope of the regression line differed between Howland Forest and Harvard Forest. For all phenological measures, earlier spring onset resulted in increases in both spring GPP and spring RE; the increase in GPP was always larger than the increase in RE, and so earlier onset also resulted in higher spring NEP at both sites. We obtained comparable results when we used predicted (from the spring warming model described above), rather than observed, dates for each of the phenological measures (results not shown).

The slopes of these relationships and their statistical significance varied among measures of spring onset (Figure 3A). For example, anomalies in the date at which A_{max} = 12 μmol m $^{-2}$ s^{-1} were significantly correlated with increases in springtime GPP (slope = 6.8 ± 0.6 g C day^{-1}, r = −0.93, P < 0.001), RE (slope = 3.2 ± 0.8 g C day^{-1}, r = −0.67, P < 0.001) and NEP (slope = 3.6 ± 0.7 g C day^{-1}, r = −0.76, P < 0.001) (Figure 4A–C). Both hardwood and conifer bud burst date anomalies were significantly correlated with anomalies in the component fluxes, but the correlation with NEP, although in the expected direction, was not significant at the 5% level (e.g., for hardwood bud burst date: slope = 2.2 ± 1.2 g C day^{-1}, r = −0.40, P = 0.06) (Figure 3A).

For all phenological measures studied, the slope of the relationship between phenological anomalies and spring flux anomalies was similar between Howland Forest and Harvard Forest for GPP, less steep at Harvard Forest than at Howland Forest for RE and steeper at Harvard Forest than at Howland Forest for NEE. However, these differences between sites were generally not statistically significant (all P > 0.05), with one exception: the slope of the relationship between anomalies in the A_{max} = 12 μmol m^{-2} s^{-1} threshold date and NEP anomalies was significantly (P = 0.02) lower at Howland Forest (slope = 2.0 ± 0.5 g C day^{-1}) than at Harvard Forest (5.1 ± 1.0 g C day^{-1}) (Figure 4C).

Similar patterns were observed (Figure 3B) when phenological anomalies were related to annual, rather than just spring, flux anomalies, with two important distinctions. First, the statistical significance of the relationships tended to be lower for annual fluxes, because variability in summer and autumn (e.g., Figure 1A and C) contributes to the overall interannual variation, thereby reducing the strength of the correlation between springtime events and annual flux integrals. Second, and perhaps more importantly, the slope of the relationship between phenological anomalies and annual flux anomalies tended to be up to twice as steep as the corresponding relationships between phenological

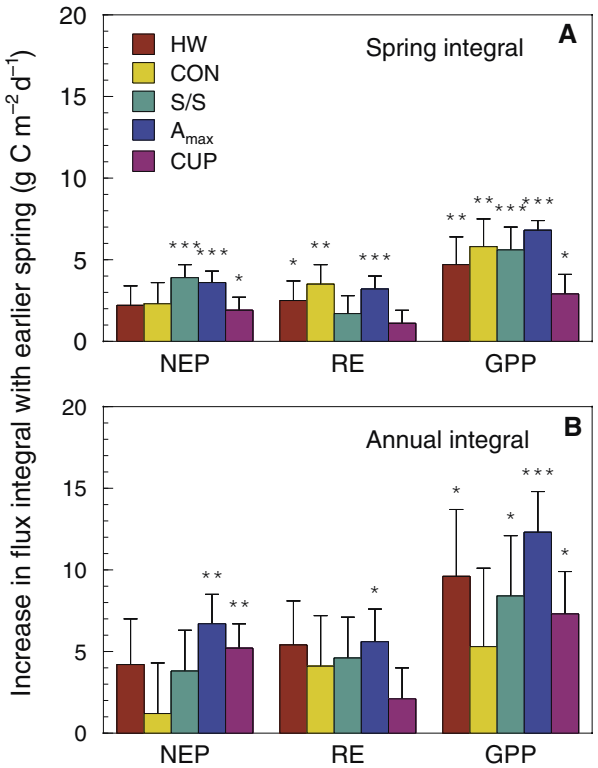

Figure 3. Slopes of the relationships between anomalies in spring onset date and anomalies in integrated CO_2 fluxes, based on eddy flux measurements from the Howland Forest (1996–2004) and the Harvard Forest (1992–2004) AmeriFlux sites. Spring onset was evaluated based on four phenological measures: HW, hardwood bud burst date; CON, conifer bud burst date; S/S, date of ecosystem transition from CO_2 source to sink and A_{max}, date at which canopy-scale photosynthetic capacity reached a threshold value of 12 μmol m^{-2} s^{-1}. Abbreviation: CUP, length of carbon uptake period, defined as the number of days for which the ecosystem was a CO_2 sink. Flux integrals were calculated for both (A) spring months (April, May and June) and (B) the calendar year. Asterisks denote statistical significance of slope estimates (*$P \leq 0.05$; **$P \leq 0.01$ and ***$P \leq 0.001$); error bars denote 1 standard error of slope estimates.

anomalies and spring flux anomalies (Figures 3B and 4D–F). For example, a one-day anomaly in the date at which A_{max} = 12 μmol m^{-2} s^{-1} was associated with a 3.6 ± 0.7 g C day^{-1} increase in spring NEP, but a 6.7 ± 1.8 g C day^{-1} increase in annual NEP, with comparable results being observed for the component fluxes GPP and RE as well (Figure 4) and also for the other phenological measures. This is suggestive of lagged effects of spring phenology — i.e., in addition to increasing spring GPP and NEP, the effects of earlier spring on ecosystem metabolism may also be felt in summer and autumn. However, spring phenological anomalies were only weakly and not significantly correlated with summer flux anomalies (earlier spring leading to increased summer GPP and increased summer RE), presumably because, compared with the lagged effect of antecedent conditions, summer weather (particularly temperature and precipitation) has a larger influence on summer CO_2 uptake and release.

Choice of specific A_{max} threshold

In the above analysis, we used the date at which canopy-level photosynthetic capacity (i.e., A_{max}) reached a threshold value of 12 μmol m^{-2} s^{-1} as another measure of spring phenology. Alternative threshold values could have been selected. We found, however, that anomalies in the dates at which low (e.g., A_{max} = 2 μmol m^{-2} s^{-1}) or high (e.g., A_{max} = 18 μmol m^{-2} s^{-1}) threshold values were reached tended to be less strongly correlated with integrated flux anomalies than dates of intermediate threshold values, particularly those in the range of A_{max} = 8–14 μmol m^{-2} s^{-1} (Figure 5). These patterns were consistent for both spring and annual flux integrals, and differed little among NEP, RE and GPP.

Relationship between length of carbon uptake period and flux anomalies

Anomalies in the length of the carbon uptake period (number of days during which the ecosystem was a sink for atmospheric CO_2) were significantly correlated ($P < 0.05$) with spring and annual anomalies in GPP and NEP, but not in RE (Figure 3B). A one-day increase in the length of the carbon uptake period increased annual GPP by 7.3 ± 2.6 g C and annual NEP by 5.2 ± 1.5 g C. These rates of increase were more than twice the corresponding rates for spring-only flux integrals. Anomalies in the length of the carbon uptake period were more strongly correlated with the source–sink transition date anomalies (r = 0.64, $P < 0.01$) than with either hardwood (r = –0.40, P = 0.06) or conifer (r = 0.29, P = 0.19) bud burst date anomalies.

Discussion

In our analysis, we considered four phenological measures, using data from two contrasting forest types. Two of the phenological measures were based on direct observations of bud burst, whereas measures of the phenology of ecosystem physiological processes (i.e., source–sink transition dates and the date at which canopy A_{max} reached a threshold value of 12 μmol m^{-2} s^{-1}) were inferred from flux measurements (cf. Gu et al. 2003 for other approaches). Building on previous analyses (e.g., Baldocchi et al. 2005), we have shown how traditional measures of phenology, such as bud burst, are related to physiological measures based on functional (C exchange) attributes of the ecosystem, and how these patterns vary between sites. For example, at the coniferous Howland Forest, the ecosystem switches from a carbon source to a carbon sink before bud burst occurs, whereas at the deciduous Harvard Forest, the source–sink transition lags deciduous bud burst by

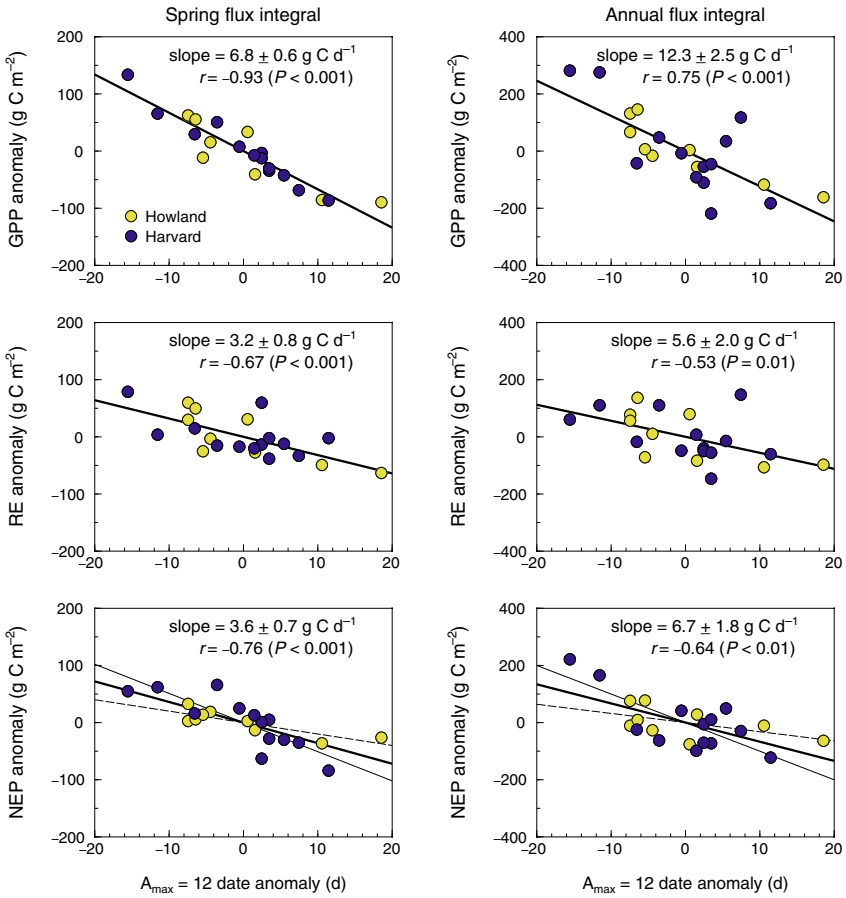

Figure 4. Relationships between anomalies in spring onset date and anomalies in integrated CO_2 fluxes, based on eddy flux measurements from the Howland Forest (1996–2004) and the Harvard Forest (1992–2004) AmeriFlux sites. Spring onset was inferred from the date at which canopy-scale photosynthetic capacity (A_{max}) reached a threshold value of 12 μmol m^{-2} s^{-1}. Flux integrals were calculated for both spring months (April, May and June; left column) and the calendar year (right column). Slope estimates (±1 standard error) and correlation coefficients are reported for pooled data: except for NEP (Howland, dotted line; Harvard, solid line; all data, thick line), slopes of best-fit lines did not differ significantly ($P \geq 0.05$) between sites.

several weeks. This difference is largely because, in evergreen conifer forests, spring recovery of photosynthetic capacity is unrelated to changes in canopy structure but instead requires only sufficiently mild air temperatures (Suni et al. 2003*b*). By comparison, the development of new leaves is a prerequisite for photosynthetic uptake in deciduous forests, and even then photosynthetic capacity continues to increase well after leaf expansion is complete (Barr et al. 2007, Richardson et al. 2007*b*).

Each of the measures of spring onset could be reasonably well predicted with a two-parameter spring warming model. This may provide a simple means by which dynamic phenology (and its relationship to fluxes of carbon, water and energy) could be incorporated into land surface models, although the degree to which these relationships can be extrapolated to other sites needs to be investigated. At present, even the state-of-the art surface schemes typically have a poor representation of vegetation phenology (Kucharik et al. 2006, Morisette et al. 2009).

We examined how phenological anomalies correlated with flux integrals during spring months and for the entire calendar year. This empirical analysis indicated that earlier spring onset tends to increase integrated springtime GPP by 5–7 g C m^{-2} day^{-1}, with concurrent offsetting increases in RE of 1–5 g C m^{-2} day^{-1}, resulting in a modest increase in NEP of 2–4 g C m^{-2} day^{-1} (Figure 3A). At the same time, earlier spring onset tends to increase integrated annual GPP by 5–12 g C m^{-2} day^{-1}, with offsetting increases in RE of 4–6 g C m^{-2} day^{-1} and overall increases in NEP of 1–7 g C m^{-2} day^{-1} (Figure 3B). The finding that GPP and RE both increase with an earlier spring offset has been noted before (e.g., Barr et al. 2002). In contrast, higher autumn temperatures, although delaying the end of the growing season, tend to stimulate RE more than GPP, resulting in reduced rather than increased net C sequestration (Piao et al. 2008).

Because the effect of earlier spring on annual flux integrals tends to be about twice as large as on spring flux integrals, these results are suggestive of lagged effects of the timing of spring onset on ecosystem function. Our findings contrast with what is predicted by ecosystem models. For example, Jolly et al. (2004) used the BIOME-BGC model to investigate the effect of one-and two-week extensions

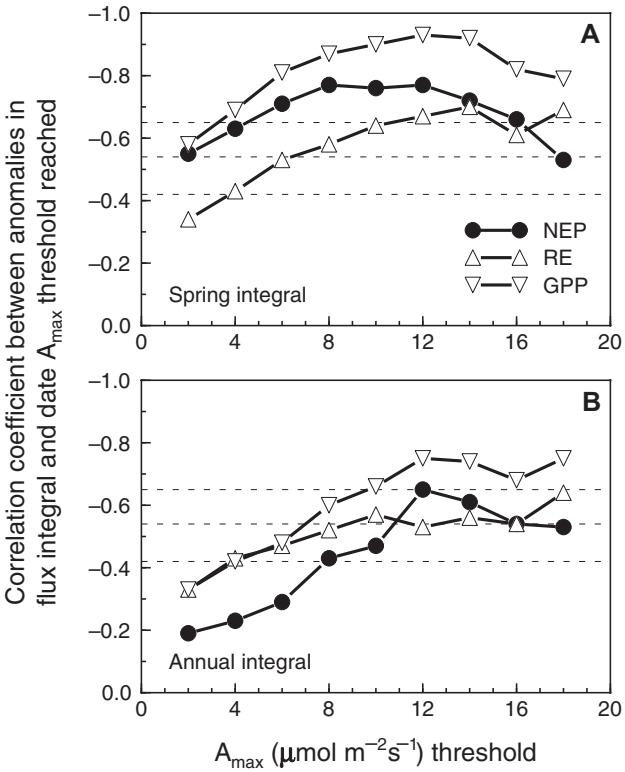

Figure 5. Correlations between anomalies in spring onset date and anomalies in integrated CO_2 fluxes, based on eddy flux measurements from the Howland Forest (1996–2004) and the Harvard Forest (1992–2004) AmeriFlux sites. Spring onset was inferred from the date at which canopy-scale photosynthetic capacity (A_{max}) reached a threshold value; a range of threshold values (from 2 to 18 μmol m^{-2} s^{-1}) was used to identify the strongest correlation. Flux integrals were calculated for both (A) spring months (April, May and June) and (B) the calendar year. Correlation coefficients are negative because earlier spring tends to increase the flux integral. Dotted horizontal lines denote varying levels of statistical significance ($P \leq 0.05$, 0.01 and 0.001).

of the growing season on productivity of a northern hardwood forest. In both scenarios, earlier spring resulted in a modest increase in canopy leaf area index (LAI). Canopy daily NPP increased from Days 100 to 150, but decreased from Days 150 to 280, as the respiratory costs of the increases in LAI more than offset the photosynthetic gains. In contrast, our results suggest that earlier spring results in sustained increases in both GPP and RE over the remainder of the growing season, and that the increase in GPP continues to exceed the increase in RE. Modest increases in LAI would not explain these patterns, because the canopies at both Howland Forest and Harvard Forest, with an LAI of five or more at each site (Hollinger et al. 1999, Urbanski et al. 2007), are already closed and additional leaf area would result in little additional canopy interception of solar radiation. An alternative explanation is that, in years with earlier spring onset, higher temperatures stimulate microbial activity and forest-floor decomposition rates (consistent with our finding that earlier spring onset tends to increase springtime RE) and accelerate rates of N cycling. This could lead to increased N uptake by trees and increased foliar N concentrations, which would enhance both photosynthesis and leaf respiration for the remainder of the growing season. Although we are unaware of studies where interannual variations in N cycling, foliar N and CO_2 exchange have been linked, continent-scale relationships between foliar N concentrations and canopy-level photosynthetic capacity have been documented (Ollinger et al. 2008), and interannual variation in foliar N has been proposed as a factor contributing to variation in GPP (Richardson et al. 2007*a*).

Differences in the seasonality and peak rates of CO_2 exchange in deciduous and evergreen forests are well known (e.g., Falge et al. 2002*a*, *b*, Law et al. 2002). We predicted that the response to earlier spring onset would differ between sites, with the sensitivity to growing season length being more pronounced for the deciduous Harvard Forest than for the coniferous Howland Forest. This expectation was based on previous results indicating that daily sums at the peak of the growing season for GPP and NEP are larger at Harvard Forest than at Howland Forest; we implicitly assumed that these differences would place an upper limit on the value of an extra growing-season day. In addition, leaf phenology is expected to be a more important control on temporal dynamics of GPP and NEP in deciduous-dominated stands, where the development and senescence of the canopy each spring and autumn control, to a large degree, the seasonal patterns of photosynthetic uptake. However, we were unable to detect statistically significant differences in the slopes of relationships between phenological anomalies and flux anomalies for Harvard Forest and Howland Forest, except for the A_{max} = 12 μmol m^{-2} s^{-1} threshold date. For this phenological indicator, earlier spring resulted in an increase in net sequestration (both during the spring months and for the entire year) that was more than twice as large at Harvard Forest as at Howland Forest, consistent with expectations. An interpretation of this result is that a warming climate will favor the growth of deciduous forests over coniferous forests in this region. For the other phenological indicators, the same trend was generally apparent, but not statistically significant. These patterns are in agreement with our observation that year-to-year variability in spring and annual NEP is twice as great at Harvard Forest as at Howland Forest. For the component fluxes, the emerging patterns were more inconsistent. Although interannual variation in spring and annual RE was similar for both sites, earlier spring resulted in a consistently (but not significantly) larger increase in RE at Howland Forest compared with Harvard Forest. And, although interannual variation in annual GPP was 50% larger at Harvard Forest than at Howland Forest, there was no consistent evidence supporting the idea that associated with this increased variability was a stronger response to earlier spring.

The statistical significance of relationships between anomalies in date of spring onset and flux anomalies was

generally larger for spring fluxes than for annual fluxes, although the slope of the relationship was larger for annual fluxes than for spring fluxes. An explanation for this apparent paradox is that the annual fluxes are much more variable because they are affected by weather events (including both direct and indirect effects; see Goldstein et al. 2000, Barford et al. 2001, Hollinger et al. 2004) throughout the year. For Harvard Forest, summertime CO_2 flux anomalies were not only larger, but were also better correlated with annual flux anomalies, than springtime anomalies (Figure 1). Thus, flux anomalies at other times of the year contribute additional variability to the annual sums of NEP and its component fluxes, whereas lagged effects of earlier spring increase the slope of the relationship between anomalies in date of spring onset and these flux sums. Spring phenology is just one of the numerous factors affecting not only annual, but also springtime, flux sums (Baldocchi et al. 2001, Suni et al. 2003*a*), and because both flux measurements and phenology observations are subject to uncertainties (Schaber 2002, Richardson et al. 2008) a less-than-perfect correlation between bud burst anomalies and flux anomalies is to be expected. The relatively short length of most flux time series is a factor that limits our ability to detect statistically significant correlations; even for a 10-year record, a correlation of $r > 0.63$ is required for a significance level of $P \leq 0.05$. Based on the observed correlation between hardwood bud burst date and annual NEP ($r = 0.32$), ≈ 38 years of data would be required to show a significant result at $P \leq 0.05$.

To some extent, our results depended on the measure that was used to define spring onset, because a higher level of statistical significance was typically observed for the relationships with physiological measures compared with bud burst measures. This is perhaps to be expected because (1) the physiological measures were derived from the fluxes themselves and (2) for conifers, bud burst date does not control the onset of photosynthesis. In addition, the somewhat coarse resolution (3–7-day interval between observations) of the bud burst observations may be a contributing factor, because it is a source of random noise that will reduce the correlation between phenological anomalies and flux anomalies. In support of this, when continuous measurements of solar radiation transmitted through the canopy (data available for Harvard Forest, except for 2003, but not for Howland Forest) were used to estimate a spring 50% green-up date (correlation between green-up date and observed hardwood bud burst, $r = 0.74$, $P < 0.01$, $n = 12$), the correlations between phenological anomalies and flux anomalies were as strong, and in some cases much stronger, than when observed bud burst dates were used. This may be a result of the near-continuous temporal resolution of radiometric data, and the elimination of observer bias that is inherent in observer-based records (Richardson et al. 2007*b*).

At the same time, however, we found that patterns were consistent across phenological measures, in that independently of the measure used, earlier spring resulted in larger spring and annual flux integrals (Figure 3). In contrast to our finding, White and Nemani (2003) concluded, based both on model predictions from BIOME-BGC and a shorter time series (through 2001) of Harvard Forest flux tower and phenology data, that canopy duration was not a good predictor of annual carbon balance in deciduous forests. Because it is generally believed that an extra day at the beginning of the growing season is more important than an extra day at the end of the growing season (irradiances and temperatures are higher, and water is generally less limiting in spring than in autumn; Chen et al. 1999), we might expect bud burst dates alone, rather than the total canopy duration, to be a better predictor of integrated C fluxes (e.g., Niemand et al. 2005). Given the findings of Piao et al. (2008), it is clear that the best insights into the role of phenology in regulating C sequestration will arise through considering spring onset and autumn senescence independently, and through partitioning of NEP to its component fluxes, rather than investigating total growing season length and net carbon exchange. Our data clearly show that earlier bud burst resulted in increases in both productivity and RE (Figure 3) but had no significant effect on NEP; however, this does not imply that phenology does not exert a strong control on interannual patterns of C cycling, because with a longer record of observations, correlations between bud burst dates and NEP would likely be statistically significant.

A more comprehensive analysis, based on multi-year data from a large number of sites and including remotely-sensed phenology indices, is planned as a future FLUXNET synthesis (http://www.fluxdata.org/) project. This analysis should provide improved understanding of the role of phenology in regulating ecosystem carbon balance across a range of biomes and forest types.

Acknowledgments

Research at the Howland Forest was supported by the Office of Science (BER), US Department of Energy, through the Terrestrial Carbon Program under Interagency Agreement No. DE-AI02-07ER64355 and through the Northeastern Regional Center of the National Institute for Climatic Change Research. Research at the Harvard Forest was supported by the Office of Science (BER), US Department of Energy, through the Northeast Regional Center of the National Institute for Global Environmental Change under Cooperative Agreement No. DE-FC02-03ER63613 and the Terrestrial Carbon Program, Agreement No. DE-FG02-03ER83751, as well as by the National Science Foundation LTER program, Grant No. DEB-0080592. The Howland and Harvard multi-year CO_2 flux and climate data sets are available at http://public.ornl.gov/ameriflux/Data/index.cfm subject to AmeriFlux 'Fair-use' rules.

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