Final Report

Using model analyses and surface-atmosphere exchange measurements from the Howland AmeriFlux Site in Maine, USA, to improve understanding of forest ecosystem C cycling (Interagency Agreement No. DE-AI02-07ER64355)

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Background

The overall objective of this research has been to develop the capacity to predict how future climatic variation may affect carbon cycle processes and net CO_2 exchange with the atmosphere at the Howland Forest, a temperate-boreal ecotonal forest that uniquely represents this ecosystem type in the AmeriFlux network. Major goals of the project have been to (1) provide a detailed characterization of C-cycle processes at Howland; (2) develop and test prognostic models to forecast future C-cycle processes; and (3) obtain defensible estimates of the uncertainties in measured and modeled C fluxes and pools.

Whole ecosystem carbon flux measurements began at Howland in late 1995 and continue to this day. Detailed meteorological and ecological studies began in the 1980's. Notable previous results relevant to carbon cycle science from Howland include that this mature (> 140 years old) forest is still vigorously accumulating carbon, that cold autumnal temperatures abruptly and irreversibly reduce photosynthetic capacity until spring, that photosynthetic uptake will occur on warm winter days, that warmer than normal spring temperatures lead to enhanced carbon sequestration while warmer temperatures in the autumn lead to higher carbon losses (e.g. Hollinger et al. 1999, 2004; Piao 2008). Using our unique two-tower design we showed that flux towers make representative and repeatable measurements of forest carbon exchange, quantified the uncertainty in flux measurements, and developed methods for determining uncertainty at single tower sites (Hollinger and Richardson 2005; Richardson et al. 2006, 2007). We also strongly promoted the use of these methodologies, which are an integral part of all data-model fusion efforts (Richardson et al. 2007, 2009; Williams et al. 2009). We investigated the partitioning of C fluxes into gross ecosystem production and respiration, and further partitioned respiration into above- and belowground components and isolated the causes of variation in these fluxes (Davidson et al. 2006; Richardson et al. 2008).

We have produced high quality, comprehensive, and accessible data sets during our entire program. As a result, Howland data have helped inform more than 50 cross-site synthesis studies and Howland was chosen to be the prototype site for the current NACP Site Level Synthesis Project. Howland data are also critical elements in several on-going studies led by other researchers (NASA projects led by S. Ollinger (UNH), S. Saatchi (JPL) and F. Rahman (IU), NSF project led by M. Rudnicki (U. Conn.), and NOAA project led by Richardson (Harvard).

Highlights of our most significant results

We focus here on three areas; long-term trends in C exchange, new understanding of respiratory fluxes, and our development of a comprehensive modeling framework.

Long-term trends in C Exchange. With a fourteen-year record of measurement at Howland, we now find that there is a significant ($P<0.01$) trend of increasing C uptake and storage (sequestration) in this mature forest (Fig. 1, top). Sequestration has been increasing in this mature, unmanaged forest by ~11 (±7) g C m^{-2} y^{-1} (mean and 95% confidence interval). The increasing trend accounts for slightly more than half of the variation observed over time. Partitioning the net flux into photosynthetic uptake (GEP) and ecosystem respiration (R_{eco}), we find, surprisingly, that the trend is not due to increasing photosynthetic uptake but to decreasing respiratory losses ($P<0.01$). This result (decreasing respiration with time) is especially strong during the months of June and August. However, there is no long-term trend in either of the key drivers of respiration (temperature or rainfall) in June, August, or on an annual basis (data not shown). Long-term measures of soil respiration (Fig. 2) also fail to show this trend, suggesting that the aboveground portion of respiration is declining. A potential explanation for these observations is input and subsequent decay of woody debris (branches, needles, standing dead trees) arising from a large-scale ice storm in January 1998. We will continue our efforts to determine whether these observations represent a long-term response from an episodic disturbance or a more fundamental shift reflecting changes in primary drivers such as increasing atmospheric CO_2, temperature, and/or precipitation.

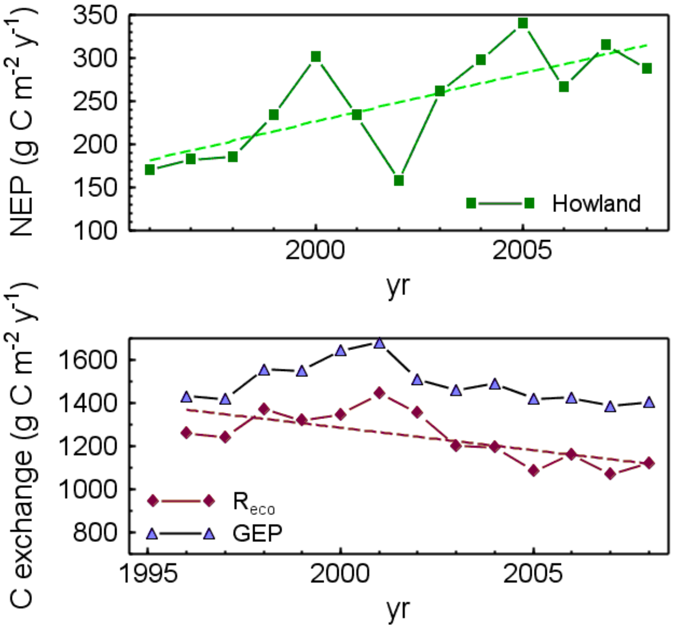

Fig. 1. Significant increases in net carbon sequestration have occurred in the unmanaged "over mature" forest at Howland.

Environmental Controls of Respiration. Soil respiration (R_S) is a combination of autotrophic and heterotrophic respiration, but it is often modeled as a single efflux process, influenced by environmental variables similarly across all time scales. Continued progress in understanding sources of variation in soil CO_2 efflux requires development of R_S models that incorporate environmental influences at multiple time scales. Coherence analysis, which requires high temporal frequency data on R_S and related environmental variables, permits examination of covariation between R_S and the factors that influence it at varying temporal frequencies, thus

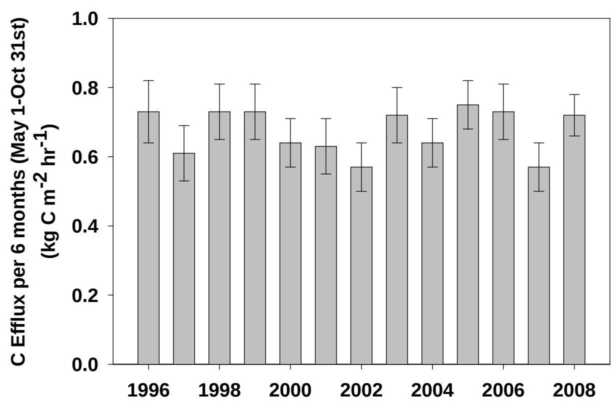

Fig. 2. There has been no significant trend in the soil component of total ecosystem respiration.

isolating the factors important at each time-scale (Savage et al. 2008). Automated growing season R_S measurements, along with air, soil temperature and moisture have been collected at half hour intervals at the Howland Forest since 2005.

We have found (as in other temperate and boreal forests) that seasonal variation in R_S was strongly correlated with soil temperature. The organic and mineral layer water contents were significantly related to R_S at synoptic time scales of 2-3 days to weeks, representing the wetting and drying of the soils as weather patterns move across the region. Post-wetting pulses of R_S were correlated with the amount of precipitation and the magnitude of the change from pre-wet up moisture content to peak moisture content of the organic horizon during the precipitation events. Although soil temperature at 10cm depth and R_S showed strong coherence at a 24-hour interval, calculated diel Q_{10} values for R_S were unreasonably high (6 to 74), suggesting that other factors that covary with soil temperature, such as canopy processes, may also influence the diel amplitude of R_S. Lower diel Q_{10} values were obtained based on soil temperature measured at shallower depths or with air temperature, but the fit was poorer and a lag was needed to improve the fit (peak R_S followed peak air temperature by several hours), suggesting a role for delayed substrate supply from aboveground processes to affect diel patterns of R_S (Savage et al. 2009). The high frequency automated R_S datasets allowed us to disentangle the temporal scales at which environmental factors, phenology, synoptic weather events, and diel variation in temperature and photosynthesis, affect soil respiration processes.

Modeling Framework and Results. A third focus of our recent efforts has been to assemble a comprehensive database of Howland carbon pools and fluxes and to use these data to test various ecosystem carbon models. We have contributed these to the North American Carbon Program (NACP) where because of the quality and completeness of our flux, meteorological, and ecological data, the Howland forest was the first test site of the NACP Data-model comparison project (Schwalm et al. 2010). We have worked with other modelers in the development and testing of the ED2 and Standcarb models, and carried out our own modeling studies (Medvigy et al. 2009; Sierra et al. 2009).

We conducted an inverse modeling analysis (Richardson et al. 2010) using a variety of data streams (tower-based eddy covariance measurements of net ecosystem exchange, *NEE*, of CO_2; chamber-based measurements of soil respiration, and ancillary ecological measurements of leaf area index, litterfall, and woody biomass increment) to estimate parameters and initial carbon [C] stocks of a simple forest C-cycle model, DALEC, using Monte Carlo procedures.

Our analysis focused on: (1) full characterization of data uncertainties, and treatment of these uncertainties in the parameter estimation; (2) evaluation of how combinations of different data streams influence posterior parameter distributions and model uncertainties; (3) comparison of model performance (in terms of both predicted fluxes and pool dynamics) during a four-year calibration period (1997-2000) and a four-year validation period ("forward run", 2001-2004).

We evaluated how well we could model *NEE*, various other carbon fluxes, and the change in woody biomass increment using different sets of measurements to constrain the model during the calibration phase (initial 4-year period, Fig. 3). On the "X" axis the numbers refer to model runs where the model results are constrained by (1) daytime *NEE* alone, (2) day and nighttime *NEE*, (3) #2 plus limits on how fast forest C stocks can change, (4) #3 plus soil respiration, (5) #3 plus LAI, (6) #3 plus litterfall, (7) #3 plus wood increment, and, (8) all previous constraints. We found that biomass data, and, to a lesser degree, soil respiration measurements contribute to marked reductions in uncertainties in parameter estimates and model predictions as these provide orthogonal constraints to the tower *NEE* measurements. However, none of the data are effective at constraining fine root or soil C pool dynamics, suggesting that these should be targets for future measurement efforts. A key finding is that adding additional constraints not only reduces uncertainties (i.e., narrower confidence intervals) on model predictions, but at the same time also results in improved model predictions by greatly reducing bias associated with predictions during the forward run (the last 4 years where the model was no longer constrained by the data). The significant improvement in the forward (unfitted) runs confirms that we have developed a capacity to realistically model variation in ecosystem-atmosphere C exchange.

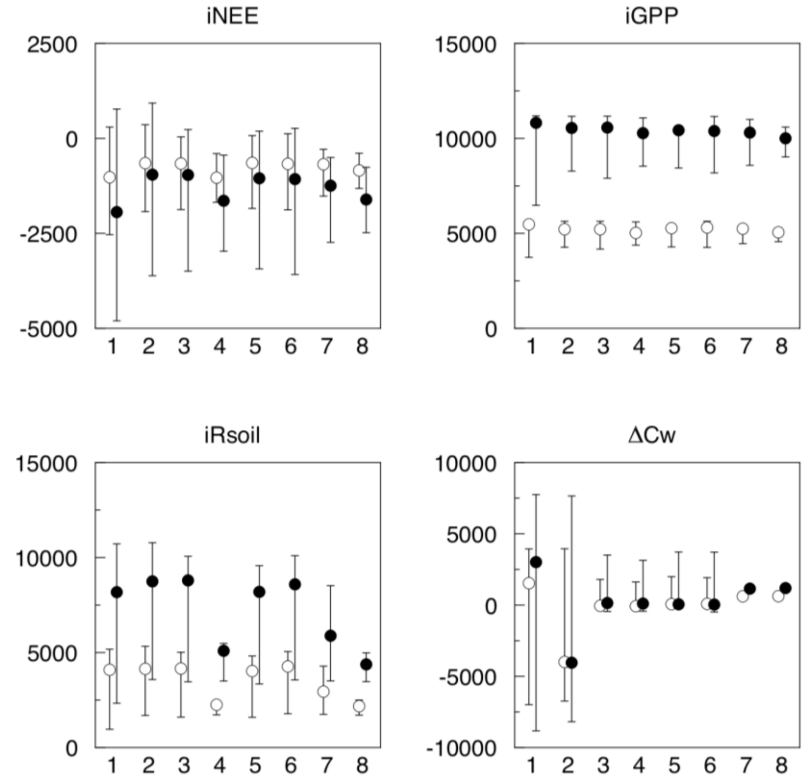

Fig. 3. Predictions of DALEC model, at end of calibration (1997-2000, open circles) and validation (2001-2004, closed circles) periods, constrained with a variety of different data streams (1 through 8, *x*-axis) and run for the Howland Forest. For fluxes, values shown are cumulative integrals for each four-year period, for net ecosystem exchange (i*NEE*), gross primary productivity (i*GPP*), and soil respiration (i*R*soil). Overall changes in pool sizes are shown for woody biomass (Δ*C*w). Error bars indicate 90% confidence intervals. Units (*y*-axis) for all panels are g C m^{-2}.

Other Important Outcomes of this Work.

Automated Phenology Measurements via Webcams. In addition to the on-going collection and analysis of meteorological and flux data, we are continuing studies of ecological aspects of the forest, including leaf area index and canopy phenology. We have pioneered the use of near surface remote sensing using digital webcams to document changes in canopy development and found that the technique works in evergreen forests such as Howland as well as in deciduous forests (pubs 11, 17, 24). We found that daily gross primary productivity (GPP) was highly correlated to changes in the difference between the green and red and blue color channels of the webcam. This work laid the foundation for regional- to continental-scale camera-based monitoring of phenology at network observatory sites, e.g. National Ecological Observatory Network (NEON) or AmeriFlux.

Impact of Nitrogen Deposition. In August 2008 we resampled all of the major biomass pools (foliage, branches, stems, roots, soil) for isotopically labeled nitrogen (^{15}N). This ^{15}N had been applied as part of previous DOE-supported work for 5 years at a rate of 18 kg N ha^{-1} y^{-1} with the goal of determining whether low levels of N fertilization increased forest carbon sequestration. The forest was originally sampled for ^{15}N in 2003 and this work thus represented a following of the original ^{15}N after 5 years. The results of our initial ^{15}N studies have been documented in Dail et al. 2009 (pub 12). In this work we found that of the ^{15}N recoverable in plant biomass, only 3-6% was recovered in green foliage and wood. Tree twigs, branches, and bark constituted the most important plant sinks for both nitrate and ammonium, together accounting for 25 to 50% of ^{15}N recovery for these ions, respectively. Forest floor and soil ^{15}N retention was small compared to previous studies. Retention by canopy elements (surfaces of branches and boles) provides a substantial sink for N that may have been through physico-chemical processes rather than by N assimilation as indicated by poor recoveries in wood tissues. The low recovery in wood tissue indicates that there was little if any initial enhancement in carbon sequestration due to N fertilization.

Participation in the North American Carbon Program (NACP). As part of this project, we have been active participants in NACP synthesis efforts. Because of the quality and completeness of our flux, meteorological, and ecological data, the Howland forest was the first site to be modeled by the NACP Data-model comparison project, with results presented at the 2008 AGU meeting and subsequently (e.g. pub 25). Two of the site investigators (Hollinger and Richardson) were responsible with A. Barr of Environment Canada for determining uncertainty in the flux measurement data for all sites used in this study. This work entailed development of a new method for choosing when to exclude flux site nocturnal data that was subsequently published.

Publications resulting from this Agreement

1) Moffat, A.M., D. Papale., M. Reichstein, D.Y. Hollinger, A.D. Richardson, A.G. Barr, C. Beckstein, B.H. Braswell, G. Churkina, A.R. Desai, E. Falge, J.H. Gove, M. Heimann, D. Hui, A.J. Jarvis, J. Kattge, A. Noormets, V.J. Stauch. 2007. Comprehensive comparison of gap filling techniques for eddy covariance net carbon fluxes. Agricultural and Forest Meteorology 147:209-232.

   This paper reviews and compares gap-filling techniques (including 2 developed with previous DOE support) for eddy flux data and shows that there is little room for additional improvement in gap-filling methods as current approaches are limited by random error inherent in flux data. Recommendations of best gap-filling approaches are made.

2) Richardson, A.D. and D.Y. Hollinger. 2007. A method to estimate the additional uncertainty in gap-filled NEE resulting from long gaps in the CO_2 flux record, Agricultural and Forest Meteorology 147:199-208.

   This paper quantifies the additional uncertainty in annual NEE estimates that arises from long gaps (more than several days) in eddy flux data records.

3) Gaige, E., D.B. Dail, D.Y. Hollinger, E.A. Davidson, I.J. Fernandez, H. Seivering, A. White, and W. Halteman. 2007. Changes in canopy processes following whole-forest canopy nitrogen fertilization of a mature spruce-hemlock forest. Ecosystems 10:1133-1147.

   This paper describes the changes in forest nutrient cycling that occurred following nitrogen fertilization undertaken during previous TCP support.

4) Prabha, T.V., M. Y. Leclerc, A. Karipot, D. Y. Hollinger and E. Mursch-Radlgruber. 2007. Influence of Nocturnal Low-level Jets on Eddy-covariance Fluxes over a Tall Forest Canopy. Boundary-Layer Meteorology 126:219-236.

   This paper investigates the mechanisms of nocturnal atmospheric dynamics on flux transport. Application of these results will help reduce uncertainty in nighttime flux measurements.

5) Piao, S., P. Ciais, P. Friedlingstein, P. Peylin, M. Reichstein, S. Luyssaert, H. Margolis, J. Fang, A. Barr, A. Chen, A. Grelle, D. Hollinger, T. Laurila, A. Lindroth, A.D. Richardson, T. Vesala. 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451(7174):49-53.

   This paper synthesized model results, atmospheric CO2 data, and flux tower results from Howland and several other international sites to show that recent autumn warming enhances respiration (C loss) more than photosynthesis (C uptake). This suggests that enhanced C uptake observed at many sites (including Howland) during warmer springs may be mostly negated by increased autumn C losses.

6) Richardson, A.D., M. Mahecha, E. Falge, J. Kattge, A.M. Moffat, D. Papale, M. Reichstein, V. Stauch, B.H. Braswell, G. Churkina, and D.Y. Hollinger. 2008. Statistical properties of random CO_2 flux measurement uncertainty inferred from model residuals. Agricultural and Forest

Meteorology 148:38-50.

This paper discussed an approach for estimating uncertainty in flux data.

7) van Wijk, M.T., B. van Putten, D.Y. Hollinger and A.D. Richardson. 2008. Comparison of different objective functions for parameterization of simple respiration models. Journal of Geophysical Research 113, G03008.

This paper investigates how a new set of objective (cost) functions could improve the estimates of model parameters and remove bias in inverse analyses studies.

8) Sims, D.A., A.F. Rahman, V.D. Cordova, B.Z. El-Masri, D.D. Baldocchi, P.V. Bolstad, L.B. Flanagan, A.H. Goldstein, D.Y. Hollinger, L. Misson, R.K. Monson, W.C. Oechel, H.P. Schmid, S.C. Wofsy, and L. Xu. 2008. A new model of gross primary productivity for North American ecosystems based solely on MODIS EVI and LST. Remote Sensing of the Environment 112:1633-46.

This paper used remotely sensed reflectance and thermal data to estimate ecosystem gross primary productivity.

9) Xiao, J., Q. Zhuang, et al. 2008. Estimation of net carbon exchange for the conterminous United States by combining MODIS and AmeriFlux data. Agricultural and Forest Meteorology 148:1827-1847.

This paper used a decision-tree methodology to stratify the US using MODIS data and to estimate continental US C sequestration based on AmeriFlux data (including Howland).

10) Ollinger, S.V., A.D. Richardson, M.E. Martin, D.Y. Hollinger, S. Frolking, P.B. Reich, L.C. Plourde, G.G. Katul, J.W. Munger, R. Oren, M-L. Smith, K.T. Paw U, P.V. Bolstad, B.D. Cook, M.C. Day, T.A. Martin, R.K. Monson, and H.P. Schmid. 2008. Canopy nitrogen, carbon assimilation and albedo in temperate and boreal forests: functional relations and potential climate feedbacks. PNAS 105:19335-19340.

This paper found that canopy N could be estimated from remotely sensed albedo data and that these N estimates correlated with maximum canopy photosynthetic (C uptake) capacity. This is an important result that may change how we model land C exchange.

11) Richardson, A.D., D.Y. Hollinger, D.B. Dail, J.T. Lee, J.W. Munger, and J. O'Keefe. 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. Tree Physiology 29:321-331.

Daily gross primary productivity (GPP) was highly correlated to changes in the difference between the green and red and blue color channels of a webcam, which recorded subtle changes in canopy color and density through the seasons.

12) Dail, B., D. Hollinger, E. Davidson, I. Fernandez, H.C. Sievering, N. Scott. 2009. Distribution of ^{15}N tracers applied to the canopy of a mature spruce-hemlock stand, Howland, Maine, USA. Oecologia 160:589-599.

This paper describes the recovery of ^{15}N labeled fertilizer in various ecosystem compartments and concludes that initial carbon sequestration enhancement due to 18 kg N added ha^{-1} y^{-1} for 5 years was low (<5% increase).

13) Savage, K.E., E.A. Davidson, and A.D. Richardson. 2008. A conceptual and practical approach to data quality and analysis procedures for high-frequency soil respiration measurements. Functional Ecology 22:1000-1007.

A methodology for quality controlling automatic respiration chamber data was developed and tested.

14) Savage, K., E.A. Davidson, A.D. Richardson, and D.Y. Hollinger. 2009. Three scales of temporal resolution from automated soil respiration measurements. Agricultural and Forest Meteorology 149:2012-2021.

Variation in soil respiration and environmental data from Howland were analyzed using spectral methods. Variation in respiration occurred on several time scales (diurnal, synoptic weather pattern, seasonal) and was related to variation in soil temperature, moisture, and other factors.

15) Medvigy, D., S.C. Wofsy, J.W. Munger, D.Y. Hollinger, and P.R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: the Ecosystem Demography model version 2. Journal of Geophysical Research 114, G01002, doi:10.1029/2008JG000812.

This paper describes the development, implementation, and validation of the ED2 ecosystem model, which integrates canopy physiology into a demographic model.

16) Sierra, C.A., H.W. Loescher, M.E. Harmon, A.D. Richardson, D.Y. Hollinger, and S.S. Perakis. 2009. Interannual variation of carbon fluxes from a tropical, a temperate, and a boreal evergreen forest: the role of forest dynamics and climate. Ecology 90:2711-2723.

This paper tests the ability of a forest dynamics model to reproduce carbon dynamics in 3 forest ecosystems.

17) Richardson, A.D., B.H. Braswell, D.Y. Hollinger, J.P. Jenkins, and S.V. Ollinger. 2009. Near-surface remote sensing of spatial and temporal variation in canopy phenology. Ecological Applications 19:1417-1428.

Changes in color of an evergreen canopy detected by a webcam were related to changes in forest C exchange.

18) Williams, M., A.D. Richardson, M. Reichstein, P.C. Stoy, P. Peylin, H. Verbeeck, N. Carvalhais, M. Jung, D.Y. Hollinger, J. Kattge, R. Leuning, Y. Luo, E. Tomelleri, C.M. Trudinger, Y.P. Yang. 2009. Improving land surface models with FLUXNET data. Biogeosciences 6:1341-1359.

A conceptual discussion and roadmap of how the next generation of land surface models (the surface portion of global climate models) can be improved with flux tower data.

19) Ollinger, S., S. Frolking, A. Richardson, M. Martin, D. Hollinger, P. Reich, L. Plourde. 2009. Nitrogen-albedo relationship in forests remains robust and thought-provoking. PNAS 106:E17.
A letter addressing questions arising in publication #10.

20) Roman, M.O., C.B. Schaaf, C.E. Woodcock, A.H. Strahler, X.Y. Yang, R.H. Braswell, P.S. Curtis, K.J. Davis, D. Dragoni, M.L. Goulden, L.H. Gu, D.Y. Hollinger, T.E. Kolb, T.P. Meyers, J.W. Munger, J.L. Privette, A.D. Richardson, T.B. Wilson, S.C. Wofsy. 2009. The MODIS (Collection V005) BRDF/albedo product: Assessment of spatial representativeness over forested landscapes. Remote Sensing of Environment 113:2476-2498.

21) Hollinger, D.Y., S.V. Ollinger, A.D. Richardson, T.P. Meyers, D.B. Dail, M.E. Martin, N.A. Scott, T.J. Arkebauer, D.D. Baldocchi, K.L. Clark, P.S. Curtis, K.J. Davis, A.R. Desai, D. Dragoni, M.L. Goulden, L. Gu, G.G. Katul, S.G. Pallardy, K.T. Paw U, H. Schmid, P.C. Stoy, A.E. Suyker, and S.B. Verma. 2010. Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. Global Change Biology 16:696-710.

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24) Richardson, A.D., T.A. Black, P. Ciais, N. Delbart, M.A. Friedl, N. Gobron, D.Y. Hollinger, W.L. Kutsch, B. Longdoz, S. Luyssaert, M. Migliavacca, L. Montagnani, J.W. Munger, E. Moors, S. Piao, C. Rebmann, M. Reichstein, N. Saigusa, E. Tomelleri, R. Vargas and A. Varlagin. 2010. Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philosophical Transactions of the Royal Society B 365:3227-3246.

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