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Decreasing photosynthesis at different spatial scales during the late growing season on a boreal cutover

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Summary The relationship between photosynthesis and accumulated cold degree days (CDD) over the late growing season was examined at the shoot, ecosystem and landscape scales in a boreal cutover in eastern Canada predominated by black spruce (*Picea mariana* Mill. BSP), lowbush blueberry (*Vaccinium angustifolium* Ait.) and sheep laurel (*Kalmia angustifolia* L.). We calculated CDD as the sum of minimum daily temperatures below a 5 °C threshold.

Light-saturated photosynthesis at the shoot level (A_{max}) of black spruce and *V. angustifolium* decreased steadily with increasing CDD once temperatures below the CDD threshold value became frequent in mid-September, whereas *K. angustifolia* showed a more irregular pattern. Tissue acclimation played an important role in the decrease in A_{max} as the season progressed, but only *V. angustifolium* showed decreasing foliar nitrogen concentrations.

Based on eddy covariance flux tower data, maximum daily gross primary productivity (GPP_{max}-tower) at the ecosystem level was more strongly related to CDD ($r^2 = 0.59$) than was maximum daily net ecosystem exchange ($r^2 = 0.32$). The GPP_{max} was likely influenced by both tissue acclimation and the direct effects of changing temperatures and irradiances on physiological rates. Mean daily GPP, calculated for consecutive 8-day periods for a 25 km^2 area around the tower by the MODIS MOD17A2 Collection 4 satellite algorithm (GPP-MODIS), decreased more rapidly with increasing CDD than did GPP_{max}-tower. Although GPP-MODIS was closely correlated with mean daily GPP from the tower (GPP_{daily}-tower, $r^2 = 0.95$) over the late growing season, the former was about twice as high. Although MODIS estimates of air temperature closely tracked the ground data, the maximum light-use efficiency parameter used by the MODIS algorithm was much higher than that indicated by the tower measurements. There was a 3% decline in GPP_{max}-tower with an increase of 10 CDD, corresponding to the percent decline in branch-level A_{max} of black spruce and *V. angustifolium*.

Keywords: carbon flux, eddy covariance, forest harvest, frost, gross primary productivity, MODIS, net ecosystem exchange.

Introduction

Boreal forests cover about 11% of the terrestrial land surface (Bonan and Shugart 1989) and contain about 13% of terrestrial carbon stocks (Schlesinger 1991). Thus, it is important to estimate the current state of this biome's carbon cycle and to predict its response to future climate scenarios (Schimel et al. 2000). Several ecosystem models have been developed in recent years to understand and predict the underlying processes affecting terrestrial carbon cycling, e.g., Forest-BGC (Running and Coughlan 1988, Running and Gower 1991), Biome-BGC (Running and Hunt 1993, White et al. 2000), BIOMASS (Bergh et al. 1998), PnET (Aber and Federer 1992, Aber et al. 1995), SiB-2 (Sellers et al. 1996) and 3-PG (Landsberg and Waring 1997). These models describe the controls on the exchange of CO_2 between forests and the atmosphere through photosynthesis and respiration.

Low temperatures are a key environmental constraint on ecological processes in boreal ecosystems. Linder and Flower-Ellis (1992) and McMurtrie et al. (1994) proposed that process models for northern ecosystems should accurately account for three physiological phenomena related to low temperatures: (a) the beginning of photosynthetic activity in spring; (b) the direct impact of severe frost events during the growing season; and (c) the reduction in photosynthetic activity in autumn. In autumn, the reduction in photosynthetic activity in boreal forests is associated with decreasing photoperiods and air temperatures, leaf senescence for deciduous species, and increasing frost hardiness. In a nursery experiment, Gaumont-Guay et al. (2003) proposed an algorithm to describe the strong correlation they found between the accumulation of low temperature events, expressed as cold degree days (CDD), and tissue acclimation manifested as decreasing photosynthetic capacity of black spruce during autumn. A logical next step is to determine to what extent the types of photosynthetic measurements that can be made at larger spatial scales are consistent with these earlier results.

It is now possible to obtain estimates of photosynthetic gas exchange at the scale of branches, ecosystems and landscapes. Portable gas exchange systems have been in common use for several decades and provide photosynthetic measurements for individual branches and leaves (Field et al. 1989). More recently, the development of eddy covariance flux towers has permitted the estimation of the turbulent flux of CO_2 between an ecosystem and the atmosphere at 30-min time steps over multiple years. Eddy covariance measurements are typically obtained for spatial scales ranging from several hundred meters up to a kilometer (Schuepp et al. 1990, Baldocchi 1997). These measurements can then be used to estimate ecosystem-level photosynthesis (gross primary production; GPP) (Fan et al. 1995, Waring et al. 1995, Aber et al. 1996, Goulden et al. 1997). At spatial scales extending from landscapes to the globe, satellite remote sensing of vegetation now permits estimates of photosynthesis (GPP) at weekly time steps (Running et al. 2000, Heinsch et al. 2003). The MODIS sensor on the Terra satellite is currently being used for 8-day daily mean estimates of GPP globally, and these estimates can be extracted for spatial scales of 1–5 km. Turner et al. (2003) have used flux tower data from mature deciduous and conifer forest sites to validate these estimates. The different approaches to measuring different aspects of photosynthesis, e.g., photosynthetic capacities under set environmental conditions, photosynthetic rates under the most favorable environmental conditions for a given period, and actual photosynthetic rates over a given period. Combining simultaneous measurements of photosynthesis on branches, ecosystems and landscapes has the potential to provide a useful synergy of information that can be used to enhance our understanding of carbon assimilation by terrestrial surfaces.

The first objective of this study was to determine whether branches showed acclimation of photosynthetic capacity with increasing CDD over the late growing season in an early successional cutover in the boreal forest of eastern Canada. Branch-level measurements were made on black spruce (*Picea mariana* (Mill.) BSP), lowbush blueberry (*Vaccinium angustifolium* Ait.) and sheep laurel (*Kalmia angustifolia* L.). The second objective was to quantify and compare the decrease in photosynthetic rates as measured at the shoot, ecosystem and landscape levels.

Materials and methods

Study area

The study area is located at the Québec boreal cutover flux site of the Fluxnet-Canada Research Network in the Ashuapmushuan Reserve (49.267° N, 74.037° W), about 70 km south of the town of Chibougamau. The site was harvested in August 2000 using the most common harvesting practice in the region, a cut with protection of regeneration and soils. In this technique, logging equipment is restricted to skid trails comprising around one third of the surface area, thus protecting the natural regeneration and minimizing soil impacts on the remaining two thirds. The harvested stand contained a mixture of black spruce and jack pine (*Pinus banksiana* Lamb.), whereas the current natural tree regeneration is comprised almost exclusively of small (< 1 m tall) black spruce of layer origin. On a leaf area basis, the vegetative cover is 11.1% *K. angustifolia*, 7.2% *V. angustifolium*, 6.1% *Ledum groenlandicum* Retz., 5.5% *P. mariana*, with primarily mosses (*Pleurozium schreberi* (BSG) Mitt., *Sphagnum* spp.), lichens (*Cladina* spp.) and bare ground accounting for the remainder of the vegetative cover.

The plants were chosen randomly within the approximate 400-m radius of the tower footprint and were marked in the field by their GPS coordinates. Sixty sheep laurel (*K. angustifolia* L.), 60 lowbush blueberry (*V. angustifolium* Ait.) and 72 black spruce plants were selected. The black spruce plants were between 30 and 100 cm tall. For each plant, the individual shoots of black spruce, *K. angustifolia* and *V. angustifolium* were randomly selected within the upper third of their crown and from all orientations. Shoots of the two ericacious species (*K. angustifolia* and *V. angustifolium*) were from the current year, whereas the black spruce shoots were 1 year old.

Air temperature

Air temperatures were measured on the flux tower 7 m above ground from the time the study was established (June 5, 2002) until the end of the experimental period (October 29, 2002) with a temperature and relative humidity probe (Model HMP45C, Campbell Scientific, Edmonton, AB, Canada). Temperatures were also measured with copper-constantan thermocouples connected to a CR-10 data logger (Campbell Scientific) and installed 1 m above ground.

Conclusions

Combining simultaneous measurements of photosynthesis on branches, ecosystems and landscapes has the potential to provide a useful synergy that can help us better understand carbon assimilation by terrestrial surfaces. For a recent boreal forest cutover in eastern Canada, we showed that A_{max} of black spruce and *V. angustifolium* shoots decreased in parallel with increasing cold degree days, but that the A_{max} of *K. angustifolia* had a more variable pattern. The results suggest that tissue acclimation played an important role in this decrease as the season progressed.

Although the decreases in photosynthesis at the ecosystem and landscape scales over the autumn were closely linked, landscape photosynthesis obtained from the MODIS MOD17A2 photosynthesis algorithm was estimated to be double the daily GPP measured by the tower. Differences in maximum LUE estimated by the tower versus that used in the MODIS algorithm appear to be the principal reason for this discrepancy. Maximum ecosystem-level GPP declined around 3% for an accumulation of 10 CDD and this corresponded to the available data for A_{max} of shoots of black spruce and *V. angustifolium*.