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Carbon cycling along a gradient of beech bark disease impact in the Catskill Mountains, New York

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Abstract: Exotic pests and pathogens, through direct and indirect effects on forest structure and species composition, have the potential to significantly alter forest ecosystem processes, including C cycling. Throughout the northern hardwood forest, beech bark disease (BBD) is causing widespread disruption in forest structure and composition. In the Catskill Mountains of New York, some forests formerly codominated by American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) are shifting to sugar maple dominance. The effects of BBD and a subsequent shift in species composition on annual aboveground net primary production and soil CO_2 efflux were examined in eight forest plots selected to represent a gradient of BBD impact. There were no significant trends in aboveground net primary production across this gradient. However, growing season soil CO_2 efflux decreased linearly along the BBD gradient, declining by 40%. Although the mechanism controlling this decline is uncertain, the decrease in soil CO_2 efflux with BBD impact and a shift to greater composition of sugar maple in litterfall could significantly alter C cycling in northern hardwood stands in the Catskill Mountains.

Résumé : Par leurs effets directs et indirects sur la structure et la composition en espèces de la forêt, les insectes nuisibles et les organismes pathogènes peuvent altérer de façon significative les processus de l'écosystème forestier, incluant le recyclage du C. Partout dans la forêt feuillue nordique, la maladie corticale du hêtre (MCH) cause une perturbation importante de la composition et de la structure de la forêt. Dans les monts Catskill de New York, certaines forêts jadis dominées par le hêtre commun (*Fagus grandifolia* Ehrh.) et l'érable à sucre (*Acer saccharum* Marsh.) évoluent vers une dominance de l'érable à sucre. Nous avons étudié les effets de la MCH, ainsi que l'évolution subséquente de la composition en espèces, sur la productivité primaire nette annuelle aérienne et l'émission de CO_2 du sol dans huit places-échantillons représentant un gradient d'impact de la MCH. La productivité primaire nette annuelle aérienne ne montrait aucune tendance significative le long de ce gradient. Cependant, l'émission de CO_2 du sol durant la saison de croissance diminuait linéairement de 40 % le long du gradient de la MCH. Bien que nous ne puissions être certain du mécanisme responsable de cette diminution, la diminution de l'émission de CO_2 du sol avec l'augmentation de l'impact de la MCH et l'évolution vers une composition où l'érable à sucre est plus important dans la chute de litière pourraient modifier considérablement le recyclage du C dans les peuplements feuillus nordiques des monts Catskill.

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Introduction

Exotic pests and pathogens have the potential to significantly alter ecosystem processes, either directly by altering nutrient inputs (e.g., via frass inputs; Frost and Hunter 2004) or indirectly by altering species composition (Fahey 1998; Forrester et al. 2003). In the northern hardwood forest of the northeastern United States, differences in nutrient cycling among dominant tree species have been demonstrated (Lovett et al. 2004), strongly suggesting that alterations in tree species composition stemming from exotic pests, particularly those that are host specific, may have ecosystem-scale implications for nutrient cycling and loss. For example, exotic pests could alter net primary production through the stress response of plants or tree mortality. When tree mortality occurs, altered forest structure could have short- or long-term impacts on forest productivity, depending on the rate of reoccupation of the canopy. Soil C storage could also be affected as a result of changes in belowground C inputs and losses, such as alterations in belowground productivity, litter

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quality, and decomposition rate. Because soil CO_2 efflux is one of the largest fluxes in the C cycle (Schlesinger and Andrews 2000), net changes in this flux stemming from exotic pest infestation could have important implications for understanding landscape-scale C cycling.

Beech bark disease (BBD), established in North America in the 1890s in Nova Scotia and first recorded in the United States in the 1930s (Tainter and Baker 1996), is prevalent throughout the northern hardwood forest in southeastern Canada and the northeastern United States (Houston 1984). Where BBD is prevalent, the mortality of large overstory American beech (*Fagus grandifolia* Ehrh.) trees causes major transformations in forest composition and structure. Forests in the Catskill Mountains of New York have been exposed to BBD since the 1940s (Houston 1984). In this region, almost all beech trees >10 cm in diameter have some presence of BBD, and trees in larger diameter classes typically have more advanced symptoms of BBD, such as cankering and girdling (Griffin et al. 2003). Despite the seemingly ubiquitous impacts of BBD in this region, the disease complex remains unevenly distributed, even on relatively small spatial scales (i.e., within a single watershed). These facts provided an opportunity to observe the impacts of BBD over a progression of infestation and stand recovery. Although impacts on forest composition and structure following BBD vary throughout northern hardwood forests in the northeastern United States (Twery and Patterson 1984; Fahey 1998), it appears that mortality caused by BBD in the Catskill Mountains leads to a shift to sugar maple (*Acer saccharum* Marsh.) dominance (Griffin 2005). This shift in species composition could have major impacts on soil CO_2 efflux, because of differences between sugar maple and beech in foliar lignin concentration (Lovett et al. 2004) and litter decomposition rates (Melillo et al. 1982). Furthermore, differences in aboveground net primary productivity (ANPP) could occur because of forest regrowth in response to beech mortality and increased gap formation.

The goal of this study was to examine differences in ANPP and soil CO_2 efflux across a gradient of BBD impact. To accomplish this, a series of plots in a single watershed in the Catskill Mountains representing different points along the gradient were located. The BBD gradient in this region also represents a shift from forest stands codominated by beech and sugar maple to stands formerly dominated by both species, but currently dominated by sugar maple with downed beech logs present (Griffin et al. 2003). It was hypothesized that ANPP would initially increase with BBD impact, as surrounding stems and new stems rapidly fill the gaps created by beech mortality; an attenuation of this effect with advancing stand recovery was expected. Soil surface CO_2 efflux is the sum of belowground heterotrophic and autotrophic respiration and in most systems is thought to be strongly controlled by photosynthate (Hogberg et al. 2001). In this system, it was difficult to predict how soil CO_2 efflux might change with BBD impact, because at various stages in the forest response to BBD, belowground heterotrophic or autotrophic respiration could reasonably be expected to be altered. For example, a shift in species composition from beech to sugar maple could increase soil heterotrophic respiration, because beech litter has slower decomposition rates than sugar maple (Melillo et al. 1982). Alternatively, higher N mineralization rates and more N availability at the sugar maple end of the BBD gradient were expected, which could lead to a reduction in root C allocation and belowground autotrophic respiration.

Methods

Site description

This study was conducted in the Diamond Notch watershed in the northeastern region of the Catskill Mountains (42°9′N, 74°16′W). Climate is characterized by cool summers and cold winters, with a mean annual temperature of 4.3 °C and a mean annual precipitation of 153 cm. Soils are well-drained acidic Inceptisols formed from bedrock consisting of sandstones, shales, and conglomerates of Devonian age (Murdoch and Stoddard 1992). Vegetation is characteristic of the northern hardwood forest and is dominated in the tree stratum by beech and sugar maple. Other tree species include yellow birch (*Betula alleghaniensis* Britt.), striped maple (*Acer pensylvanicum* L.), and white ash (*Fraxinus americana* L.). Sampling plots were located at elevations between ∼545 and 790 m a.s.l.

BBD gradient

During summer 2001, 22 plots representing a gradient of BBD infestation were selected, ranging from healthy mixed beech–maple stands to plots in which beech were only present as downed logs or stumps of former canopy trees. The intensity of the measurements of soil CO_2 efflux coupled with the remoteness of the study sites dictated that a subset of eight plots spanning the gradient were selected for an intensive study of ANPP and soil CO_2 efflux. These plots were 20 m × 20 m, with a 10 m × 10 m subplot embedded on the downslope end for measurement of belowground processes and aboveground production rates.

To develop a BBD gradient, live and dead trees were measured in the 20 m × 20 m plots, leading to a BBD rating for each plot as follows. In each 20 m × 20 m plot, the diameter at breast height (DBH) of every tree (live or dead) >10 cm was measured and identified to species. Trees 2–10 cm DBH were identified to species and tallied. A BBD severity class of 1–12 was assigned to each beech tree, regardless of whether it was a live tree, standing dead, or a downed log (Table 1). The classification for each beech tree was weighted by the basal area of the tree to determine a weighted mean BBD rating for each plot, which ranged across the gradient from 3 to 10. Plots with BBD ratings of 3–5 are representative of a forest codominated by beech and sugar maple. Plots in the middle of the gradient, with BBD ratings of 5–7, represent stands with standing dead beech and gaps in the canopy. Plots with downed beech logs on the forest floor and overstories dominated by sugar maple had BBD ratings of 7–10 (Table 1). While it is impossible to be sure of the cause of mortality of individual trees, >99% of the beech trees in the Catskill Mountains are currently infected with BBD (Griffin et al. 2003), and most of the dying and dead beech in the forests in the study area showed the severe cankering symptoms of BBD.

Annual ANPP

Annual ANPP was estimated as the sum of annual litterfall and annual wood increment. During July 2002, the diameter of every tree >10 cm DBH in the 10 m × 10 m

Table 1. Description of beech tree classes used in determining the severity of beech bark disease (BBD) and establishing a BBD gradient in the Catskill Mountains, New York.

Class	Class description
1	Live tree, healthy, no sign of BBD
2	Live tree, scale insect present, bark beginning to crack, canopy >75% intact
3	Live tree, bark heavily cracked, cankering, canopy 25%–75% intact
4	Live tree, bark severely cracked, large girdling cankers, canopy <25% intact
5	Standing dead tree with fine branches remaining
6	Standing dead tree with only coarse branches remaining
7	Standing dead snag or severe limb loss
8	Downed log, round bole, bark >25% intact, wood solid and hard
9	Downed log, round bole, bark <25% intact, wood solid and hard
10	Downed log, round bole, no bark, wood solid but soft
11	Downed log, elliptical bole, no bark, wood fragmenting
12	Downed log, elliptical bole, wood completely fragmented

Note: Classes 1–4 describe live beech trees, classes 5–7 describe standing dead beech trees, and classes 8–12 describe downed logs.

subplots was measured and cored at breast height using an increment borer. Tree cores were mounted, sanded, and the radial incremental growth measured using a 7–35× continuous zoom microscope. Allometric equations were used to estimate the aboveground woody biomass of each tree in 2002 and 2001, using the DBH minus bark width for each tree in 2002 and the diameter in 2001 estimated from radial increment measurements. The difference in these two values yielded the aboveground woody biomass production for the year. Species-specific allometric equations were used to estimate total aboveground bole and branch biomass for beech, sugar maple, yellow birch, striped maple (Whittaker et al. 1974; Siccama et al. 1994), and white ash (Ter-Mikaelian and Korzukhin 1997), all developed from forests in New Hampshire. The most recent growth rings were immeasurable on about 35% of the cores, because of damage during coring. To estimate the DBH and growth increment for these cores, data from the remaining intact cores were used and a single linear equation for all tree species was developed, using the 2001 DBH as a function of current DBH minus bark ($R^2 = 0.999$, $P < 0.0001$). The difference in biomass of each tree (wood production) was summed for each plot and expressed in $g \cdot m^{-2} \cdot year^{-1}$. To convert biomass to C, it was assumed that wood production was 50% C (Vogt 1991).

The proportion of ANPP contributed by stems <10 cm DBH was excluded in this study and was expected to contribute only about 10% to estimates of ANPP. To estimate the potential importance of these stems to ANPP, the tally of trees 2–10 cm DBH was used and a DBH was assigned to each tallied tree. Each assigned DBH was selected at random from a population of actual trees measured on similar plots for a different study. This approach, rather than applying a fixed DBH or a normal distribution of DBHs, was used because the distribution of DBH in this size class in a mature forest is skewed to the smaller diameter trees. From the DBH of the tallied trees in each plot, the proportion of the basal area contributed by trees <10 cm DBH to that of the total basal area of each plot was estimated as the basal area of trees >10 cm DBH plus the estimated basal area of the trees 2–10 cm DBH. Using this approach, 2%–10% of the estimated basal area was made up of the smaller trees. This proportion was then applied to the estimate of woody

ANPP that could be assumed to have been generated by this pool of stems. The additional (estimated) woody ANPP contributed by these stems did not significantly alter any of the statistical analyses. Therefore, only the woody ANPP estimated from stems >10 cm DBH has been used in this study.

Litterfall, including foliar litterfall, reproductive tissues, and twigs, was collected biweekly from late August to November 2001 using four pairs (total of eight per plot) of 0.226 m² traps per plot. Litter was sorted into beech, sugar maple, other leaf litter, and non-leaf litter and was dried at 60 °C and weighed. A subsample of each component of foliar litterfall was ground using a Wiley mill (20 mesh screen, mesh size 0.85 mm) and then analyzed for total C on a Leco CN-2000 analyzer (St. Joseph, Michigan). To calculate litterfall C, litterfall mass of each basket was multiplied by the percentage of C for each component, and the mean of the eight samples for each plot was taken.

To estimate soil CO_2 efflux, eight permanent PVC collars (5 cm diameter, 6 cm height) were distributed evenly throughout each plot and were inserted into the forest floor horizon to a depth of 2 cm to minimize disturbance during soil CO_2 measurements. Soil CO_2 efflux measurements were made every 3 weeks from May to November 2003, using a LI-COR 6009 soil CO_2 efflux chamber attached to a LI-COR 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, Nebraska) operated in closed-system mode. The calculation of soil CO_2 efflux was dependent on chamber volume, which was based on the depth of the PVC collar that extended above the surface of the forest floor and was incorporated into the estimation of soil CO_2 efflux. Forest floor depth varied between 4.2 and 11 cm and was not significantly related to soil CO_2 efflux ($R^2 = 0.07$, $P < 0.52$). To reduce error associated with declining CO_2 flux rate in response to accumulation of CO_2 in the headspace of the chamber (Davidson et al. 2002b), the CO_2 concentration in the headspace was scrubbed down to ∼20 ppm below ambient and measurements were made from –10 to +10 ppm relative to the ambient atmospheric CO_2 concentration, measured near the forest floor, and readjusted before making measurements at each plot to accommodate diurnal changes in ambient CO_2 concentrations. Minor diurnal variation in

soil CO_2 flux (Newman et al. 2006) and interpolated flux values between measurement dates were assumed to estimate soil CO_2 efflux rates for the period (217 days) from May through November; this timeframe of interpolated soil CO_2 efflux is hereinafter referred to as "growing season soil CO_2 efflux."

Soil moisture, temperature, and N mineralization

During soil CO_2 efflux measurements made between July and October 2003, soil temperature was measured with a temperature probe at a depth of 10 cm proximal to each collar. Soil moisture was measured in July 2003 to determine whether there were differences among plots in soil moisture content. Four soil samples were collected from each plot using a 10 cm diameter soil corer to a depth of approximately 12 cm and included the organic layer. Soils were separated into organic and mineral horizons, sieved, subsampled, weighed, and dried at 60 °C for 48 h to determine gravimetric water content. Potential net N mineralization rates from these plots were measured in organic and upper mineral soil samples in July 2001 with a laboratory assay using the methods of Lovett et al. (2004). Soils were also analyzed for total C on a Leco CN-200 analyzer.
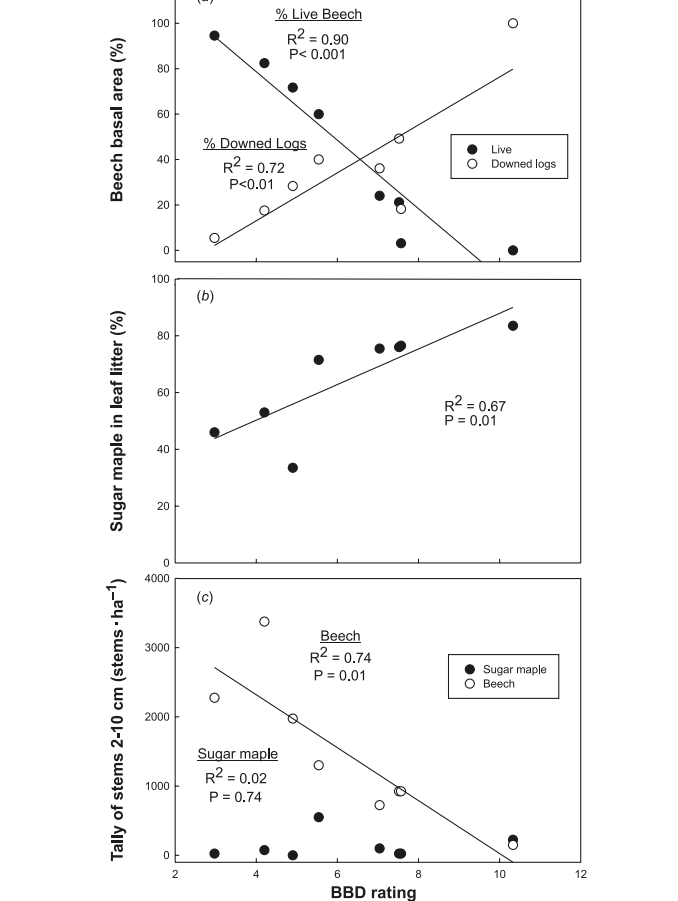
Statistical analysis

Univariate linear and nonlinear regression analyses were used to detect relationships among response variables (e.g., growing season soil CO_2 efflux) and dependent variables (e.g., BBD rating). Cook's D influence statistic was used to determine the influence of individual data points in regression analysis of BBD rating and growing season CO_2 efflux (Cook 1977). A generally accepted cutoff point for identifying influential observations is 1; however, for simple regression that criterion would be lowered to 0.7 (Myers and Well 2003). For this study, Cook's distance for each observation was <0.29, revealing a lack of significant influence of any one data point.

Results

Total live basal area of trees >10 cm DBH ranged between 50 and 113 $m^2 \cdot ha^{-1}$ and did not have a significant linear relationship with BBD rating ($R^2 = 0.02$, $P = 0.74$) or ANPP ($R^2 = 0.05$, $P = 0.59$). Despite the wide range in total live basal area among the plots, the relative basal area of live beech stems within the 20 m × 20 m plots decreased linearly across the BBD gradient ($R^2 = 0.9$, $P < 0.001$; Fig. 1a), while the percentage of beech basal area composed of downed beech logs had a significant positive linear relationship across the BBD gradient ($R^2 = 0.72$, $P < 0.01$; Fig. 1a). Relative basal area of sugar maple increased slightly along the BBD gradient, but the trend was nonsignificant ($R^2 = 0.35$, $P = 0.11$). Despite there being no significant relationship between sugar maple basal area or stem density and BBD rating, the percentage of sugar maple in litterfall did increase significantly with BBD rating ($R^2 = 0.67$, $P = 0.01$; Fig. 1b). Density of stems <10 cm DBH decreased linearly with BBD rating ($R^2 = 0.69$, $P = 0.01$). This trend was strongly driven by density of beech stems <10 cm DBH ($R^2 = 0.74$, $P = 0.01$; Fig. 1c), which mirrored the trend of declining basal area of beech stems >10 cm DBH

Fig. 1. Eight forest stands along a beech bark disease (BBD) gradient in the Catskills Mountains, New York, arrayed by BBD rating. (a) Percentage of total beech basal area (including live trees, standing dead, and the basal area of downed logs when they were standing) that is made up of live or dead and downed log beech basal area; (b) percentage of sugar maple in litterfall; and (c) tally (stems·ha^{-1}) of sugar maple and beech trees 2–10 cm diameter at breast height (DBH). Reported R^2 and P values are from linear regression analysis.

with BBD rating; there was no relationship between sugar maple stems <10 cm DBH and BBD rating ($R^2 = 0.02$, $P = 0.74$; Fig. 1c).

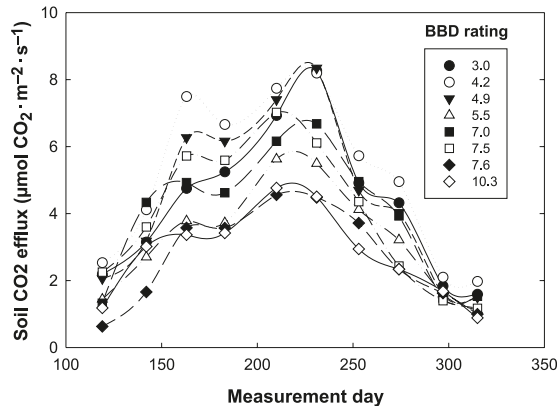Mean growing season soil CO_2 efflux was 873 g $C \cdot m^{-2} \cdot 217$ days^{-1} (±69 g $C \cdot m^{-2} \cdot 217$ days^{-1}; Table 2). Seasonal variation in the instantaneous soil CO_2 efflux rate followed the same general pattern for all eight plots, with higher flux rates measured during the warmer sampling period (Fig. 2). Importantly, differences in growing season soil CO_2 efflux among the eight sites largely reflect the interplot variation expressed across all sampling dates, with differences amplified during the periods of highest flux. Soil CO_2 efflux increased with temperature from July to November 2003 (the period for which soil temperature data was collected). However, there was no significant relationship between soil temperature and BBD rating ($R^2 = 0.16$; $P = 0.70$) or between mean temperature (July–October) and soil CO_2 efflux on a plot basis ($R^2 = 0.11$; $P = 0.41$). Soil moisture (meas-

Table 2. Annual aboveground production rates (litter, wood, and total aboveground net primary production (ANPP)), growing season soil CO_2 efflux rates, and environmental variables across a BBD gradient in the Catskills Mountains, New York.

BBD rating	Litter (g C·m^{-2}·year^{-1})	Wood production (g C·m^{-2}·year^{-1})	ANPP (g C·m^{-2}·year^{-1})	Soil CO_2 efflux (g C·m^{-2}·217 days^{-1})	Soil temp. (°C)	Soil moisture (%)
3.0	138	129	267	975	11.7	34
4.2	175	165	340	1172	11.7	33
4.9	135	272	407	1033	11.5	29
5.5	215	344	559	741	12.2	36
7.0	207	334	541	896	12.3	46
7.5	155	237	392	916	10.7	42
7.6	192	508	700	625	11.6	41
10.3	165	137	302	629	12.3	33
Mean	**172 (±11)**	**244 (±36)**	**436 (±53)**	**873 (±69)**	**11.8 (±0.2)**	**37 (±0.02)**

Note: Values in boldfaced type are means ±SE for the eight plots in the BBD gradient. Litter data represent the mean litter mass for 2 years.

Fig. 2. Seasonal variation in soil CO_2 efflux rate (μmol CO_2·m^{-2}·s^{-1}) for each of eight plots identified by BBD rating along a BBD gradient in the Catskill Mountains, New York.

Fig. 3. Annual aboveground net primary production (ANPP; *a*) and growing season soil CO_2 efflux (*b*) across a BBD gradient in the Catskills Mountains, New York. Reported R^2 and P values are from linear regression analysis.

ured in July 2003) also did not vary significantly across the BBD gradient (Table 2; R^2 = 0.12; P = 0.40). The Palmer drought severity index (www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgr.html) was consistently >1.3, and ranged from 1.36 to 5.42 for the duration of the study, suggesting non-limiting conditions for soil moisture status throughout the study.

ANPP varied widely among the BBD plots, from 267 to 700 g C·m^{-2}·year^{-1} (Table 2), but did not vary in any predictable way along the BBD gradient (R^2 = 0.05, P = 0.60; Fig. 3*a*). There were no significant trends for ANPP with percentage of beech basal area (R^2 = 0.20, P = 0.27) or percentage of sugar maple in litterfall (R^2 = 0.15, P = 0.34). ANPP also did not vary significantly with growing season soil CO_2 efflux (R^2 = 0.24, P = 0.22). Mean foliar litterfall C was 172 g C·m^{-2}·year^{-1} (±11 g C·m^{-2}·year^{-1}). There was no variation in litterfall C across the BBD gradient (R^2 = 0.07, P = 0.54; Table 2).

Growing season soil CO_2 efflux decreased significantly with BBD rating (R^2 = 0.53, P = 0.04; Fig. 3*b*), varying by 40% among plots (Table 2). Soil CO_2 efflux had a significant positive linear relationship with live beech basal area (R^2 = 0.83, P = 0.002; Fig. 4*a*) and a significant negative linear relationship with percentage of sugar maple in litterfall (R^2 = 0.55, P = 0.04; Fig. 4*b*). There was no significant relationship between total litterfall and soil CO_2 efflux (R^2 =

0.01; P = 0.84). There was no significant relationship between BBD rating and N mineralization for organic (R^2 = 0.04; P = 0.62) or mineral soil (R^2 = 0.10; P = 0.45) horizons. N mineralization also was not significantly related to the variation in soil CO_2 efflux along the BBD gradient (R^2 = 0.12; P = 0.40 for organic and R^2 = 0.20; P = 0.27 for mineral horizons). Soil C content (to a 12 cm depth) had a negative linear relationship with BBD rating; however, this relationship was not statistically significant (R^2 = 0.36; P = 0.11). Additionally, soil C in the organic plus mineral soil had a positive, but non-significant, relationship with soil CO_2 efflux (R^2 = 0.26; P = 0.19).

Fig. 4. Relationship of growing season (May–November) soil CO_2 efflux to percentage of total beech basal area (*a*) and percentage of total sugar maple in litterfall (*b*) for eight forest stands along a BBD gradient in the Catskill Mountains, New York.
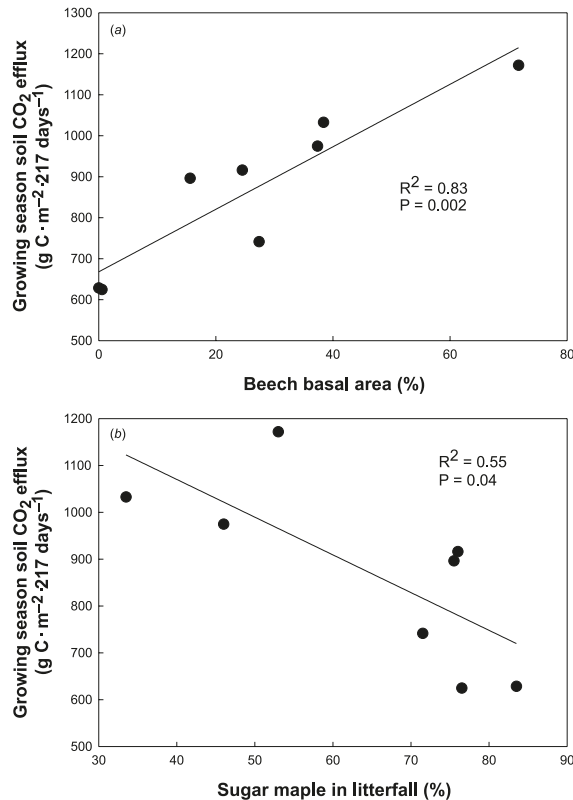
Discussion

The linear decrease in basal area of live beech trees with BBD rating coupled with the increasing basal area of downed beech trees along the same gradient (Fig. 1*a*) provides strong evidence that plots with higher BBD ratings previously had more beech and fewer maple trees. Thus, the BBD gradient established using the rating system applied during plot selection in this study can be treated as a type of chronosequence in a space-for-time substitution (Pickett 1989). The strong linear relationship between BBD rating and percentage of sugar maple in litterfall (Fig. 1*b*) provides evidence that maple trees filled in the canopy gaps from below and from adjacent trees. The gradual filling in of the canopy in response to the slow process of BBD-caused beech mortality likely explains the lack of soil temperature and moisture variability along the BBD gradient.

Mean ANPP (438 ± 53 g C·m^{-2}·year^{-1}) and the two measured components of ANPP (litterfall and wood increment) were within the range reported in other studies in the northern hardwood forest (Nadelhoffer et al. 1985; Fassnacht and Gower 1997). It was hypothesized that ANPP would initially increase with BBD impact as surrounding stems and new stems rapidly fill the gaps created by beech mortality; an attenuation of this effect with advancing stand recovery was expected. However, no significant linear or curvilinear trend in ANPP along the BBD gradient was observed (Fig. 3*a*), suggesting that any effects of altered stand structure on ANPP, if they occurred, had attenuated in the intervening

years since the peak of BBD-caused mortality. With only eight plots of relatively small size, estimates of ANPP in this study have limitations that may preclude effectively testing for a trend in ANPP with BBD rating. Larger plots and a greater number of plots in the middle of the gradient where changes in ANPP may be more likely to occur would provide a stronger test of a potential curvilinear response of ANPP to BBD infestation and recovery.

Mean estimates of growing season soil CO_2 efflux (873 ± 69 g C·m^{-2}·217 days^{-1}) and litterfall (172 ± 10.7 g C·m^{-2}·year^{-1}) in this study were similar to other northern hardwood forests (Davidson et al. 2002*a*; Fahey et al. 2005). We observed a significant decrease in soil CO_2 efflux with BBD rating (Fig. 3*b*). Soil CO_2 efflux along the BBD gradient was positively correlated with percentage of live beech basal area (Fig. 4*a*) and negatively correlated with percentage of sugar maple in litterfall (Fig. 4*b*). These results suggest that lower soil CO_2 efflux across the BBD gradient may be controlled by the change in species composition, through litter quality for example, or by some other factor that covaries with species composition. It was hypothesized that a decrease in soil CO_2 efflux along the BBD gradient would be related to higher N availability at sites dominated by sugar maple, but no significant relationship was observed between N mineralization and BBD rating or soil CO_2 efflux. Although the relationship with soil C along the BBD gradient was nonsignificant, a negative linear trend of soil C with BBD rating and a positive linear trend of soil C with soil CO_2 efflux suggest that increasing sugar maple dominance across the BBD gradient may lead to lower soil C stores and increased soil CO_2 efflux.

Differences among species in root biomass may potentially account for differences in soil CO_2 efflux. However, Templer et al. (2005) reported 40% higher fine root biomass in sugar maple than in beech stands in the Catskill Mountains. While this difference was not statistically significant, it is contrary to what would be expected to explain the lower soil CO_2 efflux in stands dominated by sugar maple in the present study, assuming that higher fine root biomass leads to higher fine root respiration rates.

Beech and sugar maple differ in their mycorrhizal associations; beech form ectomycorrhizal (EM) associations, while sugar maple form arbuscular mycorrhizal (AM) associations. Roots with ectomycorrhizae generally have larger root and mycorrhizal biomass than roots inoculated with arbuscular mycorrhizae (Treseder and Allen 2000), and EM fungal biomass may be more resistant to decomposition compared with AM fungi (Langley and Hungate 2003). While greater fungal biomass might be expected to increase soil CO_2 efflux in EM-dominated forests, the decay resistance may decrease soil CO_2 efflux. Langley and Hungate (2003) reported that forests with EM associations tend to have lower soil CO_2 efflux than those with AM associations, which is opposite of the pattern in soil CO_2 efflux observed in this study

Tree species may also vary in the percentage of roots that are infected with mycorrhizae, which may also affect soil CO_2 efflux rate. For example, Pregitzer et al. (2002) observed the fine root architecture of nine North American tree species and found that of species that formed AM relationships, only 7%–41% of fine roots were infected at one

time; whereas, among species that formed EM associations, >90% of fine roots were infected. The differences between beech and sugar maple in the nature of their mycorrhizal associations could potentially be a cause of the patterns observed in soil CO_2 efflux, although the mechanisms involved are not clear.

Exotic pests and pathogens can have important consequences for ecosystem processes (Lovett et al. 2006). In the case of BBD, the presence of this disease complex can cause important shifts in the structure and composition of northern hardwood forests (Griffin 2005). In the Catskill Mountains, decline of canopy beech stems is often accompanied by an increase in sugar maple (Griffin 2005). No significant relationship between BBD rating and ANPP was found, but a 40% decrease in soil CO_2 efflux across the gradient was observed. The specific mechanisms controlling lower soil CO_2 efflux with increasing sugar maple dominance across a gradient of BBD impact cannot be elucidated from this study. However, this study suggests an important role of an invasive insect in altering C cycling in a northern hardwood forest through a shift in species composition. Understanding the full suite of invasive pest impacts on forest communities and ecosystem processes will require investigation into complex interactions among the pests, their hosts, the consequences for the community, and the influence of plant species on the cycling of C and nutrients.

Acknowledgments

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