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# Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO<sub>2</sub>]-induced enhancement

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The partitioning among carbon (C) pools of the extra C captured under elevated atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]) determines the enhancement in C sequestration, yet no clear partitioning rules exist. Here, we used first principles and published data from four free-air CO<sub>2</sub> enrichment (FACE) experiments on forest tree species to conceptualize the total allocation of C to below ground (TBCA) under current [CO<sub>2</sub>] and to predict the likely effect of elevated [CO<sub>2</sub>]. We show that at a FACE site where leaf area index (*L*) of *Pinus taeda* L. was altered through nitrogen fertilization, ice-storm damage, and droughts, changes in *L*, reflecting the aboveground sink for net primary productivity, were accompanied by opposite changes in TBCA. A similar pattern emerged when data were combined from the four FACE experiments, using leaf area duration (*L<sub>D</sub>*) to account for differences in growing-season length. Moreover, elevated [CO<sub>2</sub>]-induced enhancement of TBCA in the combined data decreased from ≈50% (700 g C m<sup>-2</sup> y<sup>-1</sup>) at the lowest *L<sub>D</sub>* to ≈30% (200 g C m<sup>-2</sup> y<sup>-1</sup>) at the highest *L<sub>D</sub>*. The consistency of the trend in TBCA with *L* and its response to [CO<sub>2</sub>] across the sites provides a norm for predictions of ecosystem C cycling, and is particularly useful for models that use *L* to estimate components of the terrestrial C balance.

aboveground net primary production | free-air CO<sub>2</sub> enrichment | leaf area index | nitrogen fertilization | soil respiration

In terrestrial ecosystems, the largest and most recalcitrant carbon (C) pools are found in soils (1). Thus, assessing long-term C sequestration potential of these ecosystems requires understanding of the processes that control the dynamics of soil C. The buildup of soil C is controlled in part by the input of aboveground litter and the allocation of C below ground. Belowground C allocation by plants supports root production, respiration, rhizodeposition, and mycorrhizal fungi (2). Only a small fraction of C allocated below ground is retained by soils in recalcitrant pools (3). However, because primary productivity in forests is large, even a small change in the total belowground C allocation (TBCA), e.g., under elevated atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]), can alter terrestrial C storage.

In forest ecosystems, TBCA, i.e., the flux of C belowground, has been shown to be comparable with or greater than, the aboveground net primary productivity (ANPP) (4). Yet the controls of TBCA are poorly understood, leading to unreliable estimates of the soil C dynamics under current climatic and atmospheric conditions. The reliability of estimates decreases further when predictions are made for global change scenarios because few data are available from long-term ecosystem-level CO<sub>2</sub> enrichment experiments (4). Here, we combine new and published data from free-air CO<sub>2</sub> enrichment (FACE) experiments and show that, when canopy leaf area index (*L*) is known, reasonable predictions of TBCA can be made under both current and future climate scenarios.

C allocation is commonly quantified as the partitioning of carbohydrates available in the ecosystem [i.e., gross primary productivity (GPP)] among variously defined pools (4). Mirroring canopy light interception, GPP saturates with increasing *L* (5, 6). At a given *L*, GPP can vary with varying supply of certain site resources, such as water, that can affect the photosynthetic efficiency of foliage. Furthermore, the amount of carbohydrates produced by a given *L* would vary with the length of the growing season. One way of partitioning available carbohydrates is to the C fluxes representing ANPP and associated construction respiration (ANPP'), aboveground maintenance respiration (AR<sub>m</sub>), and all of the belowground processes combined (i.e., TBCA). Thus accounted, GPP = ANPP' + AR<sub>m</sub> + TBCA. In contrast to the saturating response of GPP, NPP and ANPP have been shown to increase linearly over a wide range of *L* (7–10). Thus, over the range of relatively stable (“saturated”) GPP, the variation in TBCA would be determined by the aboveground sink strength for C (i.e., ANPP') as it varies with *L*. Variation in site resources that affect GPP at a given *L*, e.g., water availability, would also affect ANPP, injecting some additional variation to TBCA. Nevertheless, the variation in *L* should dominate ANPP and, thus, TBCA, because drastic or prolonged changes in site resources result in adjustments in *L*.

Although little is known about C allocation to below ground under elevated [CO<sub>2</sub>], both NPP and forest floor CO<sub>2</sub> efflux (*F<sub>s</sub>*), the latter being a major input in the estimation of TBCA, are enhanced under elevated [CO<sub>2</sub>] in forest ecosystems across a broad range in productivity (11, 12). We use detailed measurements performed over 4 years at the portion of the Duke FACE study containing a treatment combination of elevated [CO<sub>2</sub>] × nitrogen (N) addition to assess whether TBCA is inversely related to *L* over a period in which *L* varied considerably because of growing season precipitation and forest recovery from an ice storm (10, 13). We also assessed this relationship and the response of TBCA to elevated [CO<sub>2</sub>] in a broader context based on published data from four FACE experiments in temperate forest stands of up to 20 years of age composed of mostly shade-intolerant species.

## Results

The growing seasons at the four FACE sites differ in length from 5 months (AspenFACE) to 8 months (EUROFACE Tuscania,

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Abbreviations: ANPP, aboveground net primary productivity; ANPP', ANPP plus associated construction respiration; [CO<sub>2</sub>], CO<sub>2</sub> concentration; FACE, free-air CO<sub>2</sub> enrichment; *F<sub>s</sub>*, forest floor CO<sub>2</sub> efflux; GPP, gross primary productivity; *L*, leaf area index; *L<sub>D</sub>*, leaf area duration; TBCA, total allocation of C to below ground.

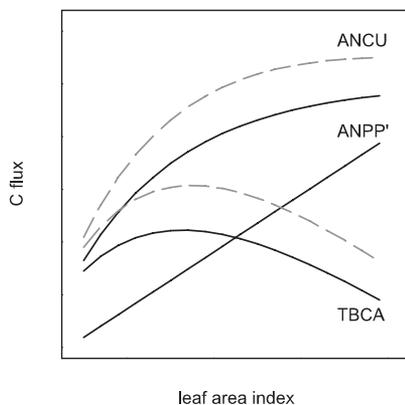
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**Fig. 3.** Conceptual representation of the changes in canopy net photosynthesis minus maintenance respiration of aboveground woody biomass (ANCU), ANPP', and TBCA as a function of leaf area index. Solid lines represent ambient and dashed lines elevated (+200 ppm) [CO<sub>2</sub>].

of individual studies shows that TBCA or belowground NPP (BNPP; roughly 50% of TBCA) (4), may increase, decrease or be insensitive to an increase in ANPP (17–24). These apparently inconsistent responses of TBCA or BNPP to aboveground productivity might be explained by the range of  $L$  in each study and site- and species-specific conditions that control canopy photosynthesis and the aboveground C sink. Narrowing the analysis to a single biome, and even further to young stands of largely shade-intolerant species, as was done here, resulted in TBCA decreasing with NPP (Fig. 2C) and ANPP' (data not shown) in the combined data set from three of the four sites.

Our synthesis adds to previous general findings from the four FACE sites, which encompass a wide range in  $L$  and NPP. The previous syntheses showed elevated [CO<sub>2</sub>]-induced enhancements in NPP (11) and soil respiration (12). Our synthesis demonstrated that the enhancement in TBCA decreased with increasing  $L_D$  and increased with NPP. Over the range of  $L_D$ , the elevated [CO<sub>2</sub>]-induced enhancement of TBCA in the combined data decreased from ≈50% (≈700 g C m<sup>-2</sup> y<sup>-1</sup>) at  $L_D$  of 1.5 to ≈30% (200 g C m<sup>-2</sup> y<sup>-1</sup>) at  $L_D$  of 5. We also showed that the inverse relationship of TBCA with  $L_D$  was maintained when TBCA was normalized by ANPP, generating a ratio of C partitioning between below and above ground (Fig. 2E).

The Duke FACEp was studied in enough detail to assess some aspects of spatial (between treatments) variation in aboveground C sink-source relationship and its effect on belowground allocation. N addition at Duke FACEp increased the aboveground sink under both current [CO<sub>2</sub>] and elevated [CO<sub>2</sub>]. Under current [CO<sub>2</sub>], the average increase in ANPP' with N addition, was balanced by the reduction in TBCA (Fig. 1B). This finding suggests a shift in C partitioning with little effect of fertilization on C source (GPP). However, under elevated [CO<sub>2</sub>], the increase in ANPP' with N addition (≈280 g C m<sup>-2</sup> y<sup>-1</sup>) was ≈100 g C m<sup>-2</sup> y<sup>-1</sup>, less than the decrease in TBCA. This imbalance between the increased aboveground sink and decreased belowground allocation suggests that TBCA under elevated [CO<sub>2</sub>] was misestimated by using the site average of annual C increase in soil pools.

The results from this synthesis are consistent with a conceptual model (Fig. 3) that combines theoretically based expectations of saturating canopy photosynthesis with  $L$  and the empirically observed linearly increasing ANPP' with  $L$  (10). In Fig. 3, we have replaced GPP, or canopy gross photosynthesis, with aboveground net C uptake (ANCU), i.e., net photosynthesis – maintenance respiration of aboveground woody biomass = TBCA + ANPP'. The simple representations of ANCU and ANPP' versus  $L$  should hold if the primary effect of varying site resources, such as water and

nutrients, is to move stands along the relationships with  $L$  (9, 25, 26). On the other hand, both relationships are likely to shift up or down with growing season length, among biomes, species of different shade tolerance, and stands of different stature. Regardless of their exact position, it is the shape of the relationships of ANCU and ANPP' with  $L$  that determines the shape of the gap between the curves (i.e., TBCA). That gap should increase with  $L$  up to the point where most of the available light is intercepted and decrease with increasing  $L$  over the range in which light interception increases little with  $L$ , and thus ANCU (and GPP) is relatively stable. Clearly, this pattern cannot be extrapolated to mean that, at some higher  $L$ , TBCA would drop to zero. These relationships establish a framework for qualitatively assessing changes in TBCA under elevated [CO<sub>2</sub>].

Modifying this conceptual model to reflect the known responses of forests to elevated [CO<sub>2</sub>] could help predict the effect of [CO<sub>2</sub>] on TBCA. Modeling results on canopy-level CO<sub>2</sub> uptake indicate a wide range of enhancement of GPP under elevated [CO<sub>2</sub>] (27, 28). On average, the [CO<sub>2</sub>]-induced enhancement ratio of canopy CO<sub>2</sub> uptake at a given level of  $L$  is somewhat less than the FACE-induced enhancement ratio of atmospheric [CO<sub>2</sub>] (≈1.5) and decreases with increasing  $L$  (28). In contrast to NPP (11), ANPP showed no elevated [CO<sub>2</sub>]-induced enhancement (10) at a given  $L$ . With these [CO<sub>2</sub>]-induced changes implemented, the conceptual model predicts a convergence of TBCA under elevated and current [CO<sub>2</sub>] at high levels of  $L$ . The shape of the decrease in TBCA with  $L$  generated by the model is different from that observed with increasing  $L_D$ , perhaps because  $L_D$  is not a very good surrogate for  $L$  in this analysis. Nevertheless, the conceptual model generates patterns of TBCA that are generally consistent with data under both ambient and elevated [CO<sub>2</sub>].

Despite the large range in  $L$  and NPP represented by these four FACE experiments, these are young temperate stands of relatively shade-intolerant species. The data show little overlap among stands, and the low replication within and among experiments forces the use of repeated measurements as replicates in analyses. Clearly, the model requires testing in other biomes and stands of different stages of development. Furthermore, although this approach can be used to estimate total C allocation below ground, it cannot be used to quantify allocation to specific C pools with different residence times. For example, there was an apparent decrease in the storage of C in the forest floor–soil system under elevated [CO<sub>2</sub>] in stands of two of the three species at EuroFACE (29), whereas most of the apparent ≈100 g C m<sup>-2</sup> y<sup>-1</sup> enhancement at Duke FACE is accumulated in the litter layer (30, 31) and as root biomass. Unlike the relationship between C allocation above ground (as reflected in ANPP') and C partitioning to wood production (10), these observations do not yet lend themselves to a quantitative relationship between C allocation below ground and C storage. Nevertheless, at this time, this model provides a tool for generating caps for TBCA and its enhancement under elevated [CO<sub>2</sub>]. We show that both vary with commonly available ecosystem quantities,  $L$  and net primary productivity, which themselves vary spatially with N availability and temporally with weather conditions.

## Materials and Methods

**Estimation of TBCA.** Annual TBCA was estimated by using a C balance approach (15, 16). Accordingly,

$$TBCA = F_s - F_a + \Delta(C_{\text{root}} + C_{\text{litter}} + C_{\text{soil}}) - F_{\text{tr}}, \quad [1]$$

where  $F_s$  is the C loss from the forest floor as CO<sub>2</sub> efflux;  $F_a$  is litterfall C;  $\Delta C_{\text{root}}$ ,  $\Delta C_{\text{litter}}$ , and  $\Delta C_{\text{soil}}$  are the changes in C pools in roots, litter layer, and soil; and  $F_{\text{tr}}$  is the transport of C off site (all components in g C m<sup>-2</sup> y<sup>-1</sup>). Assuming that annual  $F_{\text{tr}}$  is negligible (30),  $F_s$  reflects the sum of root and microbial respiration and the decomposition of litter, dead roots, fungal hyphae, and root exudates (2).  $F_a$  is the input of decomposable

materials from above ground; material which is not decomposed during the measurement period adds up to  $\Delta C_{\text{litter}}$ .

**Duke FACE CO<sub>2</sub> × N Experiment.** The Duke FACE experiment is located at the Duke Forest C-H<sub>2</sub>O Research Site, in Orange County, NC (35°58'N, 79°08'W). At present, *Pinus taeda* L. (planted in 1983) is the canopy-dominant species together with scattered individuals of *Liquidambar styraciflua* L., with 40 other broadleaf species in the understory. The soil is classified as Enon silt loam, a low-fertility Hapludalf typical of the southeastern U.S. Piedmont (32). The mean annual temperature is 15.5°C, and the mean annual precipitation of 1,145 mm is evenly distributed throughout the year (27).

Duke FACEp and an adjacent ambient reference plot were established in 1993. Since 1994, Duke FACEp has received elevated levels of CO<sub>2</sub> ambient + 200 ppm during daylight hours of the growth season according to the FACE protocol (33). In 1998, a fertilization experiment commenced, where Duke FACEp and an ambient control plot were both subdivided, with half of each plot receiving fertilization (11.2 g of N) annually (34).

$F_s$  was measured continuously for 4 years (2000–2003) at Duke FACEp, and its reference plot.  $F_s$  was measured with the Automated Carbon Efflux System (ACES; U.S. patent 6692970) (35, 36). The measurements, after gap-filling ( $\approx 43\%$  of the time over 4 years), were used to estimate annual  $F_s$  (14). For TBCA calculation at Duke FACEp, the data sources for  $F_a$  and  $\Delta C$  in the soil-litter system as well as the aboveground information (projected  $L$ , NPP, and ANPP) are the same as described below for Duke FACE. For the cross-site analysis, weighed averages of  $L$ , NPP, ANPP', and TBCA were calculated over Duke FACEp and Duke FACE plots over the period where the data sets overlapped (2000–2003).

**Cross-FACE Site Analysis.** There are three other FACE experiments in forest settings: ORNL-FACE in Oak Ridge, TN; AspenFACE in Rhinelander, WI; and EUROFACE in Tuscania, Italy. Although AspenFACE experiences considerably cooler climate (mean annual temperature 4.9°C compared with 14.1 and 14.2°C at the other two sites), all three stands represent young temperate deciduous forests and cover a wide range in  $L$  [2.7–7.4 (11)]. Detailed descriptions of the experimental protocol are provided for ORNL-FACE (37), AspenFACE (38, 39), and EUROFACE (40).

Our analysis on the controls of TBCA was mainly based on combining the data in two recent syntheses on the effects of elevated [CO<sub>2</sub>] on NPP (11) and  $F_s$  (12). For Duke FACE, a more complete data set on NPP (10) and a longer data set on annual  $F_s$  were also available (41), thus covering the years 1998–2003. The temporal overlap of data in the two syntheses, necessary for this analysis, was 3 years from ORNL-FACE (1999–2001; *Liquidambar styraciflua* L.), 1 year from AspenFACE (2001; *Populus tremuloides* Marsh./*Betula papyrifera* Marsh. plot only), and 2 years from EUROFACE (2000–2001; *Populus alba* L., *P. nigra* L., and *P. X euramericana*).

In the soil respiration studies (12, 41),  $F_s$  was measured biweekly or monthly during the period in which CO<sub>2</sub> was enriched. Manual measurements of  $F_s$  and soil temperature were made in the middle of the day with infrared gas analyzers operated in the closed-path mode. Annual estimates were obtained either by linear interpola-

tion between the sample dates or by using fitted Q<sub>10</sub>-temperature responses and a continuous soil temperature record.

Leaf litterfall ( $F_a$ ) was measured with litter traps at Duke FACE (42), ORNL-FACE (43), and EUROFACE (44). At AspenFACE, litterfall was assumed to equal leaf production estimated from allometric functions (45). Note that estimates of leaf production are typically somewhat higher than those of litterfall because of herbivory and other C losses during the growing season (46). For the deciduous species, we calculated annual TBCA using  $F_a$  of that year. For the pine, which unlike the deciduous species tends to accumulate a significant amount of litter on the forest floor, we used  $F_a$  averaged over the 2 years before canopy closure (1998–1999) and the following 4 years (2000–2003).

$\Delta C_{\text{root}}$  was quantified by summing the NPP of coarse roots, assumed to be all accumulating, and the mean annual increment in fine root C. Coarse root NPP was estimated by using site-specific allometric functions [DukeFACE (47), ORNL-FACE (48), EUROFACE (29), and AspenFACE (45)]. Fine root increment was measured by using minirhizotrons and in-growth cores at ORNL-FACE (49) and EUROFACE (50), estimated by using a flow compartment model at Duke FACE (51) and from standing fine root biomass at AspenFACE (45) combined with rates of aspen root turnover (52).  $\Delta(C_{\text{litter}} + C_{\text{soil}})$  was estimated from published data [Duke FACE (30, 31), ORNL-FACE (53), EUROFACE (29), and AspenFACE (54)]. For AspenFACE, we assumed that soil C under current [CO<sub>2</sub>] did not change over the 4-year investigation and was similar at the initiation of the treatment to that under elevated [CO<sub>2</sub>]. When biomass rather than C estimates were available, the fractional C content was assumed to be 0.5.

ANPP was calculated from NPP (10, 11) by subtracting the NPP estimates of coarse and fine roots. Also, for certain analyses, construction respiration [equal to  $0.25 \times \text{ANPP}$  (55)] was added to ANPP (equal to ANPP').

$L$  for Duke FACE was estimated based on data on leaf litterfall mass, specific leaf area, and allometry and for pines was also based on needle elongation rates and fascicle and shoot counts (10). Peak  $L$  was taken from published data for ORNL-FACE (43) and EUROFACE (11, 28). For AspenFACE,  $L$  available under ambient conditions (11) was multiplied by the CO<sub>2</sub>-induced enhancement in leaf biomass (45). Because the growing season length and leaf longevity (deciduous vs. evergreen) varied among the sites,  $L$  was expressed as  $L_D$  ( $\text{m}^2 \times \text{y}^{-1}$ ). For consistency,  $L_D$  was also used in analysis of data from Duke FACEp. For deciduous stands,  $L_D$  was calculated as peak  $L$  multiplied by the fraction of the year that is considered growing season. At Duke FACE, where  $L$  varies considerably during the growing season,  $L_D$  was calculated by using average growing season  $L$  (10).

The relationships among TBCA,  $L_D$ , and NPP were investigated, and between-treatment differences in regression curves were tested by using  $F$  test statistics for extra sum of squares (56). The curve fitting was done by using the nonlinear curve-fitting procedure of SigmaPlot 8.02 (SPSS, Chicago, IL).

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- Schlesinger WH (1977) *Annu Rev Ecol Syst* 8:51–81.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) *Biogeochemistry* 48:115–146.
- Giardina CP, Binkley D, Ryan MG, Fownes JH, Senock RS (2004) *Oecologia* 139:545–550.
- Giardina CP, Coleman MD, Binkley D, Hancock JE, King JS, Lilleskov EA, Loya WM, Pregitzer KS, Ryan MG, Trettin CC (2005) in *Tree Species Effects on Soils: Implications for Global Change*, eds Binkley D, Menyailo O (Kluwer Academic, Dordrecht, The Netherlands), pp 119–154.
- Kira T (1975) in *Photosynthesis and Productivity in Different Environments*, ed Cooper JP (Cambridge Univ Press, Cambridge, UK) pp 5–40.
- Oker-Blom P, Pukkala T, Kuuluvainen T (1989) *Ecol Modell* 49:73–87.
- Gholz H (1982) *Ecology* 63:469–481.
- Oren R, Waring RH, Stafford SG, Barrett JW (1987) *Forest Sci* 33:538–547.
- Gower ST, Vogt KA, Grier CC (1992) *Ecol Monogr* 62(1):43–65.
- McCarthy HR, Oren R, Finzi AC, Johnsen KH (2006) *Proc Natl Acad Sci USA* 103:19356–19361.
- Norby RJ, DeLucia EH, Gielen B, Calafepetra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJ, Ceulemans R, et al. (2005) *Proc Natl Acad Sci USA* 102:18052–18056.
- King JS, Hanson PJ, Bernhardt E, De Angelis P, Norby RJ, Pregitzer KS (2004) *Global Change Biol* 10:1027–1042.

13. McCarthy HR, Oren R, Johnsen KH, Pritchard SG, Davis MA, Maier CA, Kim H-S (2006) *J Geophys Res* 111(D15): Art No D15103.
14. Palmroth S, Maier CA, McCarthy HR, Oishi AC, Kim H-S, Johnsen KH, Katul GG, Oren R (2005) *Global Change Biol* 11:421–434.
15. Giardina CP, Ryan MG (2002) *Ecosystems* 5:487–499.
16. Raich JW, Nadelhoffer KJ (1989) *Ecology* 70:1346–1354.
17. Nadelhoffer KJ, Aber JD, Melillo JM (1985) *Ecology* 66:1377–1390.
18. Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtie RE (1996) *Tree Physiol* 16:333–343.
19. Keith H, Raison RJ, Jacobsen (1997) *Plant Soil* 196:91–99.
20. Raich P, Bolstad P (2001) in *Terrestrial Global Productivity* eds Roy J, Saugier B, Mooney HA (Academic, San Diego), pp 254–283.
21. Gower ST, Krankina RJ, Olson M, Apps M, Linder S, Wang C (2001) *Ecol Appl* 11:1395–1411.
22. Giardina CP, Ryan MG, Binkley D, Fownes JH (2003) *Global Change Biol* 9:1438–1450.
23. Maier CA, Albaugh TJ, Allen HL, Dougherty PM (2004) *Global Change Biol* 10:1335–1350.
24. Litton GM, Ryan MG, Knight DH (2004) *Ecol Appl* 14:460–474.
25. Linder S, Rook DA (1984) in *Nutrition in Plantation Forests*, eds Bowden GD, Nambiar EKS (Academic, London), pp 212–236.
26. Albaugh TJ, Allen HL, Dougherty PM, Kress LW, King JS (1998) *Forest Sci* 44(2):317–328.
27. Schäfer KVR, Oren R, Ellsworth DS, Lai C-T, Herrick JD, Finzi AC, Richter DD, Katul GG (2003) *Global Change Biol* 9:1378–1400.
28. Wittig VE, Bernacchi CJ, Zhu X-G, Calfapietra C, Ceulemans R, DeAngelis P, Gielen B, Miglietta F, Morgan P, Long SP (2005) *Global Change Biol* 11:644–656.
29. Gielen B, Calfapietra C, Lukac M, Wittig VE, DeAngelis P, Janssens IA, Moscatelli MC, Grego S, Cortufo MF, Goldbold D, et al. (2005) *Tree Physiol* 25:1399–1408.
30. Schlesinger WH, Lichter J (2001) *Nature* 411:466–469.
31. Lichter J, Barron SH, Bevacqua CE, Finzi AC, Irving KF, Stemmler EA, Schlesinger WH (2005) *Ecology* 86:1835–1847.
32. Pataki DE, Oren R (2003) *Adv Water Resour* 26:1267–1278.
33. Hendrey GR, Ellsworth DS, Lewin KF, Nagy J (1999) *Global Change Biol* 5:293–309.
34. Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier CA, Schäfer KVR, McCarthy HR, Hendrey G, McNulty SG, et al. (2001) *Nature* 411:469–472.
35. Butnor JR, Johnsen KH, Oren R, Katul GG (2003) *Global Change Biol* 9:849–861.
36. Butnor JR, Johnsen KH (2004) *Eur J Soil Sci* 55:639–647.
37. Norby RJ, Todd DE, Fults J, Johnson DW (2001) *New Phytol* 150:477–487.
38. Karnosky DF, Mankovska B, Percy K, Dickson RE, Podila GK, Sober J, Noormets A, Hendrey G, Coleman MD, Kubiske M, et al. (1999) *Water Air Soil Pollution* 116:311–322.
39. Karnosky DF, Pregitzer KS, Zak DR, Kubiske ME, Hendrey GR, Weinstein D, Nosal M, Percy KE (2005) *Plant Cell Environ* 28:965–981.
40. Miglietta F, Peressotti A, Vaccaro FP, Zaldei A, DeAngelis P, Scarascia-Mugnozza G (2001) *New Phytol* 150:465–476.
41. Bernhardt ES, Barber JJ, Phippen JS, Taneva L, Andrews JA, Schlesinger WH (2006) *Biogeochemistry* 77:91–116.
42. Finzi AC, Allen AS, DeLucia EH, Ellsworth DS, Schlesinger WH (2001) *Ecology* 82:470–484.
43. Norby RJ, Scholtis JD, Gunderson CA, Jawdy SS (2003) *Oecologia* 136:574–584.
44. Cortufo MF, DeAngelis P, Polle A (2005) *Global Change Biol* 11:971–982.
45. King JS, Kubiske ME, Pregitzer KS, Hendrey GR, McDonald EP, Giardina CP, Quinn VS, Karnosky DF (2005) *New Phytol* 168:623–636.
46. Liu L, King JS, Giardina CP (2005) *Tree Physiol* 25(12):1511–1522.
47. Naidu SL, DeLucia EH, Thomas RB (1998) *Can J Forest Res* 28:1116–1124.
48. Norby RJ, Hanson PJ, O'Neill EG, Tschaplinski TJ, Weltzin JF, Hansen RA, Cheng W, Wullschlegel SD, Gunderson CA (2002) *Ecol Appl* 12(5):1261–1266.
49. Norby RJ, Ledford J, Reilly CD, Miller NE, O'Neill EG (2004) *Proc Natl Acad Sci USA* 101:9689–9693.
50. Lukac M, Calfapietra C, Godbold DL (2003) *Global Change Biol* 9:838–848.
51. Matamala R, Schlesinger WH (2000) *Global Change Biol* 6:967–980.
52. Pregitzer KS, Zak DR, Maziasz J, DeForest J, Curtis PS, Lussenhop J (2000) *Ecol App* 10:18–33.
53. Jastrow HD, Miller RM, Matamala R, Norby RJ, Boutton TW, Rice CW, Owensby CE (2005) *Global Change Biol* 11:2057–2064.
54. Loya WM, Pregitzer KS, Karberg NJ, King JS, Giardina CP (2003) *Nature* 425:705–707.
55. Ryan MG (1991) *Tree Physiol* 9:255–266.
56. Ramsey F, Schafer D (1997) *The Statistical Sleuth: A Course in Methods of Data Analysis* (Duxbury, San Francisco).