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Aboveground sink strength in forests controls the allocation of carbon below ground and its $[CO_2]$-induced enhancement

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The partitioning among carbon (C) pools of the extra C captured under elevated atmospheric CO_2 concentration ($[CO_2]$) 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_2 enrichment (FACE) experiments on forest tree species to conceptualize the total allocation of C to below ground (TBCA) under current $[CO_2]$ and to predict the likely effect of elevated $[CO_2]$. 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_D) to account for differences in growing-season length. Moreover, elevated $[CO_2]$-induced enhancement of TBCA in the combined data decreased from ≈50% (700 g C m^{-2} y^{-1}) at the lowest L_D to ≈30% (200 g C m^{-2} y^{-1}) at the highest L_D. The consistency of the trend in TBCA with L and its response to $[CO_2]$ 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_2 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 mychorrhizal 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_2 concentration ($[CO_2]$), 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_2 enrichment experiments (4). Here, we combine new and published data from free-air CO_2 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_m), and all of the belowground processes combined (i.e., TBCA). Thus accounted, $GPP = ANPP' + AR_m + TBCA$. 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 $[CO_2]$, both NPP and forest floor CO_2 efflux (F_s), the latter being a major input in the estimation of TBCA, are enhanced under elevated $[CO_2]$ 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 $[CO_2]$ × 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 $[CO_2]$ 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; $[CO_2]$, CO_2 concentration; FACE, free-air CO_2 enrichment; F_s, forest floor CO_2 efflux; GPP, gross primary productivity; L, leaf area index; L_D, leaf area duration; TBCA, total allocation of C to below ground.

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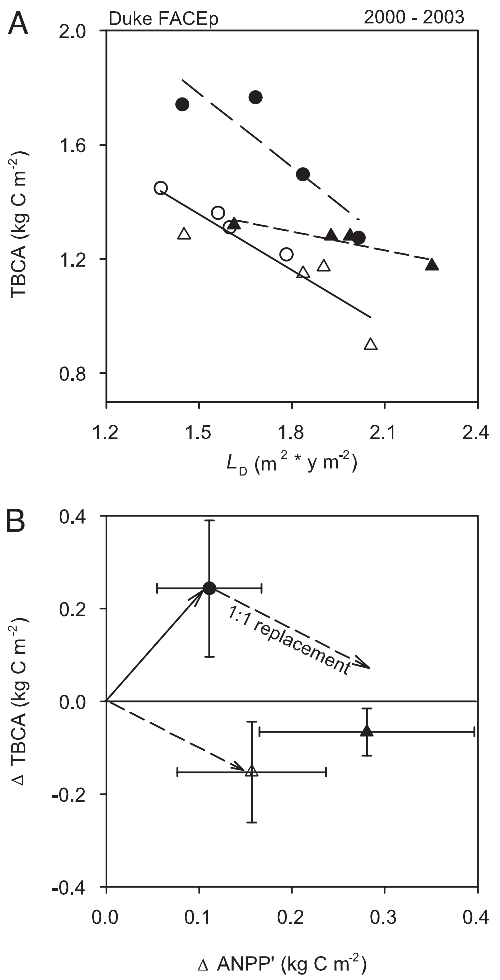

Fig. 1. TBCA as a function of L_D at Duke FACEp elevated [CO$_2$] × nitrogen addition experiment. (*A*) Open circles represent unfertilized plots, diamonds represent fertilized plots, and filled symbols represent plots under elevated atmospheric [CO$_2$] conditions. Changes in TBCA as a function of changes in the ANPP plus construction respiration (ANPP$'$). (*B*) TBCA and ANPP$'$ of the unfertilized current [CO$_2$] treatment are subtracted from the values of the other three treatments (indicated as ΔTBCA and ΔANPP$'$) and averaged over the study period. Error bars are one standard deviation among years.

Italy) (11). To facilitate comparisons among sites, we converted L to leaf area duration (L_D), a variable that integrates the display of leaf area over the growing season, thus accounting for the differences in the length of the active photosynthesis and growth period. For consistency, we used L_D in all of the analyses, including analyses in which data from only Duke FACE prototype (Duke FACEp) were used.

Duke FACE CO$_2$ × N Experiment. L_D at Duke FACE increased from 2000 to 2001 and decreased to the lowest level after a severe drought (growing season of 2002) and an ice storm (December, 2002) (refs. 10 and 13; Fig. 1*A*). ANPP$'$ (equals ANPP plus construction respiration) varied linearly with L_D, and, at a given L_D, was lower in drought years (10). Across treatments, drought-induced reduction in TBCA, estimated as the difference between measured F_s and modeled potential F_s (14), was 10% in 2001 and 20% in 2002. Because the response of L_D to drought lags behind that of microbial activity, in this first analysis, we used the potential F_s in the calculation of TBCA. TBCA decreased linearly with increasing L_D in the two elevated [CO$_2$] treatments (maximum P = 0.10). The two current [CO$_2$] treatments shared a single relationship (P = 0.50). The relationships under current [CO$_2$], unfertilized elevated [CO$_2$], and fertilized elevated [CO$_2$] significantly differed from one another ($P < 0.01$). The relationship under current [CO$_2$] (TBCA = 2.336 − 0.653 × L_D; r^2 = 0.82) and unfertilized elevated [CO$_2$] (TBCA = 3.066 − 0.858 × L_D; r^2 = 0.71) converged at high L_D. When N was added under elevated [CO$_2$] and L_D was low, TBCA was similar to that under current [CO$_2$]. At high L_D, TBCA showed a more similar enhancement to that under unfertilized elevated [CO$_2$].

Next, we assessed how much the changes in ANPP$'$ are reflected in opposite changes in TBCA. In this analysis, TBCA should not be corrected for the effect of drought on F_s. Using the unfertilized current [CO$_2$] as a reference, we assessed the [CO$_2$]-induced changes in the allocation of C to aboveground productivity versus total belowground C flux. In each year, we subtracted TBCA and ANPP$'$ of the unfertilized current [CO$_2$] treatment from those estimated for the other three treatments, and averaged these treatment differences over the 4-year study period. Fertilizing under current [CO$_2$] reduced TBCA by an amount equivalent to the increase in ANPP$'$ (Fig. 1*B*). Increasing atmospheric [CO$_2$] stimulated both TBCA and ANPP, but the flux to below ground increased twice as much as that to aboveground productivity. Adding N under elevated [CO$_2$] reduced TBCA more than it increased ANPP$'$.

Comparisons Among FACE Sites. In the combined data set, growing season length varied by a factor of ≈1.5, and L varied by a factor of ≈3. Thus, the variation in L_D is dominated by that in L, and GPP is expected to saturate with increasing L_D as it would if only L varied. Over that range of relatively stable ("saturated") GPP, the variation in TBCA should be determined by the aboveground sink strength for C (ANPP$'$) as it varies with L_D. Data within the low L_D range (AspenFACE and the 2003 average from Duke FACE), where GPP is likely to be far from saturation, are shown in the figures but were excluded from the analyses.

Combining the data from three of the four FACE sites, F_s was inversely related to L_D, with higher fluxes under elevated [CO$_2$] (Fig. 2*A*). Similar but weaker relationships were observed with NPP (Fig. 2*B*). F_s and TBCA are very similar quantities; not only is F_s the largest component in the calculations of TBCA, but the amount of litterfall C subtracted from F_s in the calculations can be balanced by the amount of C accumulated in the forest floor and soil, which is added to F_s. Thus, the magnitude of TBCA was similar to F_s, but the variations were not identical. For a given species (black lines in Fig. 2*C*), TBCA either decreased or was invariable with increasing L_D and appeared to be higher under elevated [CO$_2$] at a given L_D. Combining the data from three of the four sites showed an overall decrease in TBCA with increasing L_D and NPP (Fig. 2 *C* and *D*). The relationships were stronger with L_D than NPP. At Duke FACE, which was the only site with sufficient data to make such analysis, TBCA was unrelated to NPP (minimum P = 0.16), in contrast to the relationship observed with L_D (Fig. 1*A*). Under elevated [CO$_2$], the overall relationships of TBCA with both L_D and NPP were above those for current [CO$_2$] (maximum P = 0.02).

The ratio of TBCA to ANPP is an indication of the partitioning of GPP between the aboveground and belowground processes. TBCA/ANPP decreased nearly 8-fold for a 3-fold increase in L_D and a 4-fold increase in NPP (Fig. 2 *E* and *F*). The ratio TBCA/ANPP under elevated [CO$_2$] was higher than under current [CO$_2$] (P = 0.02). Note that strong correlation between ANPP and NPP improves the correlation between TBCA/ANPP with NPP because of autocorrelation, and we do not provide the coefficient of determination for this relationship. Data and parameters of the nonlinear regressions shown in Fig. 2 are tabulated [see supporting information (SI) Tables 1 and 2].

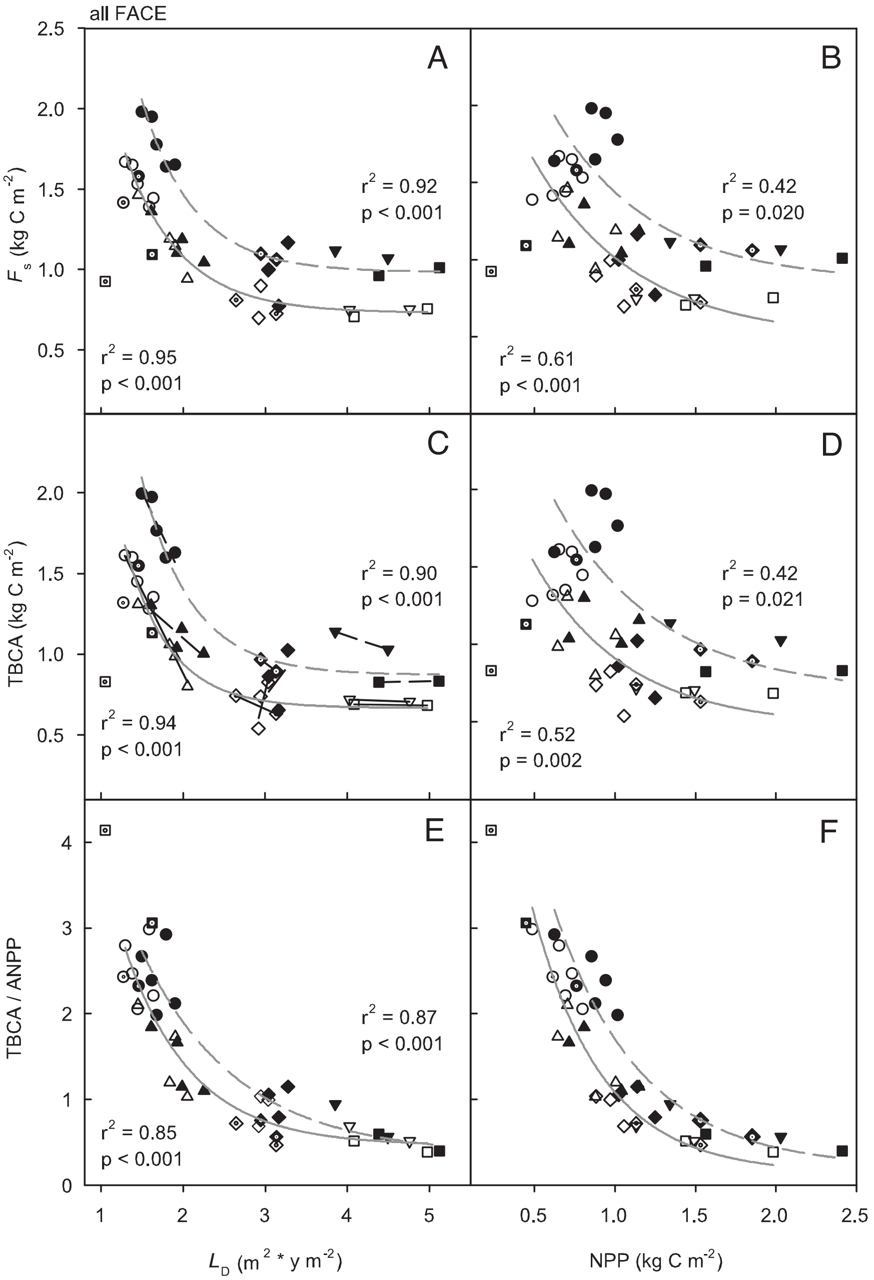

Fig. 2. Forest floor CO_2 efflux (F_s), TBCA, and the ratio of TBCA to ANPP as a function of L_D (*A*, *C*, and *E*) and NPP (*B*, *D*, and *F*). *P. taeda* (open circles and triangles are for fertilized plots), *L. styraciflua* (open diamonds), *P. alba* (open inverted triangles), *P. nigra* (open squares), *P. X euramericana* (dotted diamonds), and *P. tremuloides* / *B. papyrifera* (dotted squares). Filled symbols and dashed lines represent elevated [CO_2]. In *C*, black lines are within sites. Data on *P. tremuloides*/*B. papyrifera* and *P. taeda* for 2003 (dotted circles) were not used in regression analysis.

Discussion

Understanding what controls belowground allocation is hampered by methodological barriers to the accurate estimation of C fluxes and pools in the soil at requisite frequencies (4). We used a recently developed mass–balance approach to estimate TBCA, which has the advantage of accounting for all of the belowground C fluxes and changes in C pools in soil and forest floor (15) and related TBCA to productivity indices that integrate site conditions. At Duke FACE, L_D was higher in plots fertilized with N, was reduced by prolonged droughts and an ice storm, and increased as the stand recovered from these events (10). These changes in L_D were positively correlated with the aboveground sink for C, ANPP′ (ANPP plus construction respiration) (10), and inversely correlated with TBCA (Fig. 1*A*). The observed relationship was maintained after broadening the analysis to include data from other Duke FACE plots and other FACE sites (Fig. 2*C*). At very low L_D, there is a hint (based on a single datum from AspenFACE and another from Duke FACE after a prolonged drought and an ice storm) that TBCA might be increasing with L_D. After canopy closure (corresponding to an average L of ≈ 3 and interception of $>70\%$ of incoming light), TBCA first decreased with increasing L_D and then stabilized. Moreover, at Duke FACEp and generally in the combined data from the other sites, the difference in TBCA between current and elevated [CO_2] decreased with increasing L_D.

Syntheses of data from boreal to tropical forest ecosystems suggest that the total belowground C flux increases with aboveground productivity (4, 16). However, a closer assessment

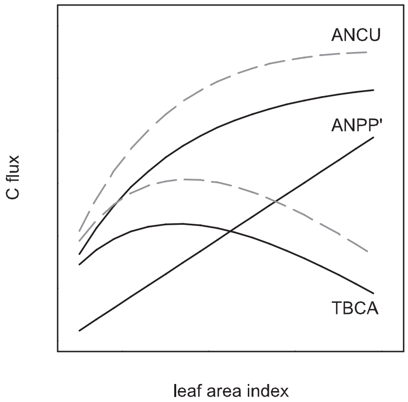

Fig. 3. Conceptual representation of the changes in canopy net photosynthesis minus maintenance respiration of aboveground woody biomass (ANCU), ANPP′, and TBCA as a function of leaf area index. Solid lines represent ambient and dashed lines elevated (+200 ppm) [CO_2].

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. 2*C*) 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_2]-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_2]-induced enhancement of TBCA in the combined data decreased from ≈50% (≈700 g C m^{-2} y^{-1}) at L_D of 1.5 to ≈30% (200 g C m^{-2} y^{-1}) 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. 2*E*).

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_2] and elevated [CO_2]. Under current [CO_2], the average increase in ANPP′ with N addition, was balanced by the reduction in TBCA (Fig. 1*B*). This finding suggests a shift in C partitioning with little effect of fertilization on C source (GPP). However, under elevated [CO_2], the increase in ANPP′ with N addition (≈280 g C m^{-2} y^{-1}) was ≈100 g C m^{-2} y^{-1}, less than the decrease in TBCA. This imbalance between the increased aboveground sink and decreased belowground allocation suggests that TBCA under elevated [CO_2] 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_2].

Modifying this conceptual model to reflect the known responses of forests to elevated [CO_2] could help predict the effect of [CO_2] on TBCA. Modeling results on canopy-level CO_2 uptake indicate a wide range of enhancement of GPP under elevated [CO_2] (27, 28). On average, the [CO_2]-induced enhancement ratio of canopy CO_2 uptake at a given level of L is somewhat less than the FACE-induced enhancement ratio of atmospheric [CO_2] (≈1.5) and decreases with increasing L (28). In contrast to NPP (11), ANPP showed no elevated [CO_2]-induced enhancement (10) at a given L. With these [CO_2]-induced changes implemented, the conceptual model predicts a convergence of TBCA under elevated and current [CO_2] 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_2].

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_2] in stands of two of the three species at EuroFACE (29), whereas most of the apparent ≈100 g C m^{-2} y^{-1} 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_2]. 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,

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

where F_s is the C loss from the forest floor as CO_2 efflux; F_a is litterfall C; ΔC_{root}, $\Delta C_{\mathrm{litter}}$, and ΔC_{soil} are the changes in C pools in roots, litter layer, and soil; and F_{tr} is the transport of C off site (all components in g C m^{-2} y^{-1}). Assuming that annual F_{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 $\Delta C_{\mathrm{litter}}$.

Duke FACE $\mathbf{CO_2}$ × N Experiment. The Duke FACE experiment is located at the Duke Forest C-H_2O 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_2 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 (≈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 ΔC 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_2] 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_2 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 interpolation between the sample dates or by using fitted Q_{10}-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).

ΔC_{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). $\Delta(C_{\mathrm{litter}} + C_{\mathrm{soil}})$ 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_2] did not change over the 4-year investigation and was similar at the initiation of the treatment to that under elevated [CO_2]. 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 × 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_2-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} ($\mathrm{m}^2\times \mathrm{y}\cdot\mathrm{m}^{-2}$). 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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