

Aboveground sink strength in forests controls the allocation of carbon below ground and its [CO₂]-induced enhancement

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The partitioning among carbon (C) pools of the extra C captured under elevated atmospheric CO₂ concentration ([CO₂]) determines the enhancement in C sequestration, yet no clear partitioning rules exist. Here, we used first principles and published data from four free-air CO₂ enrichment (FACE) experiments on forest tree species to conceptualize the total allocation of C to below ground (TBCA) under current [CO₂] and to predict the likely effect of elevated [CO₂]. 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 [CO₂]-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 [CO₂] 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 CO₂ 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 CO₂ concentration ([CO₂]), 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 CO₂ enrichment experiments (4). Here, we combine new and published data from free-air CO₂ 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 [CO₂], both NPP and forest floor CO₂ efflux (*F_s*), the latter being a major input in the estimation of TBCA, are enhanced under elevated [CO₂] 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 [CO₂] × 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 [CO₂] 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; [CO₂], CO₂ concentration; FACE, free-air CO₂ enrichment; *F_s*, forest floor CO₂ 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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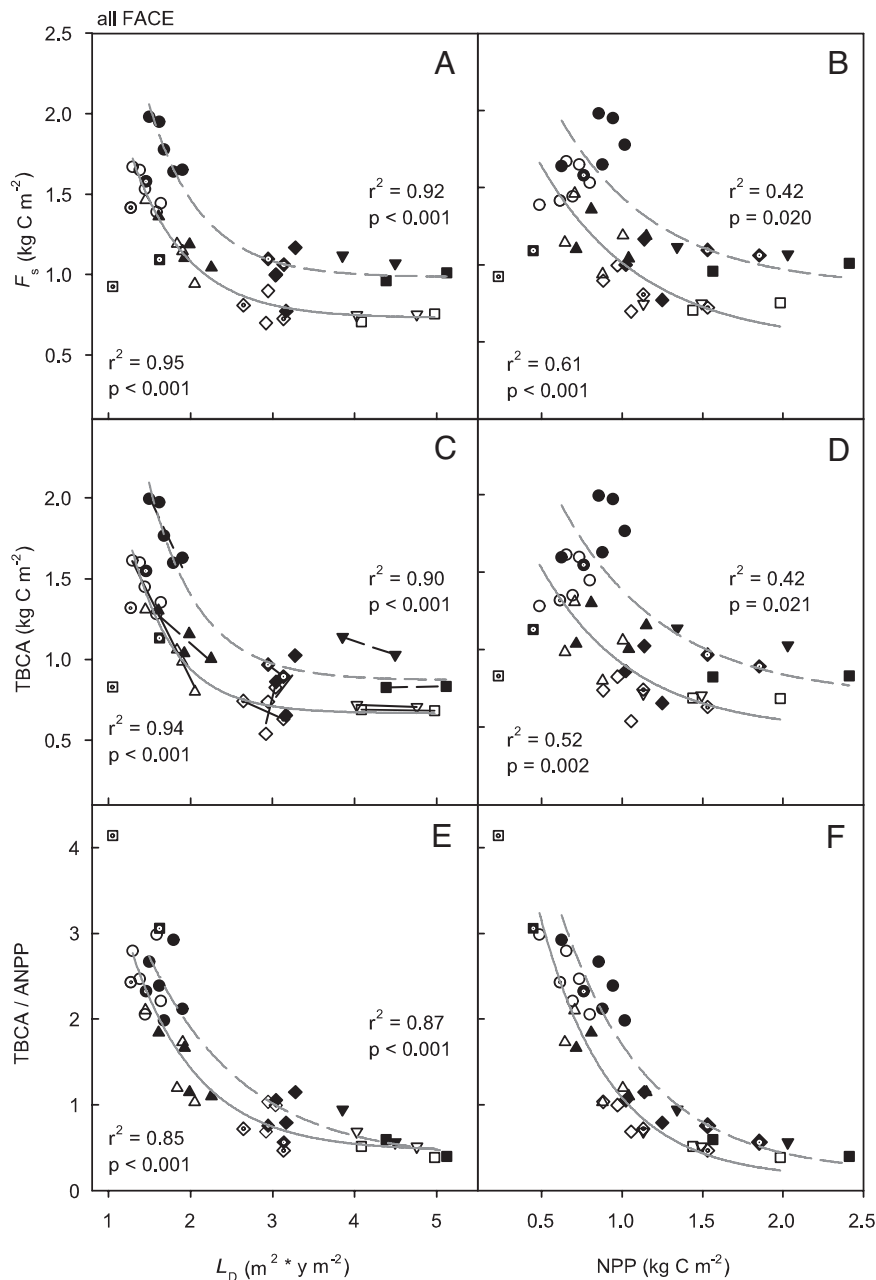


Fig. 2. Forest floor CO₂ efflux (F_s), TBCA, and the ratio of TBCA to ANPP as a function of L_D (A, C, and E) and NPP (B, D, and F). *P. taeda* (open circles and triangles are for fertilized plots), *L. styraciflua* (open diamonds), *P. alba* (open inverted triangles), *P. nigra* (open squares), *P. X euramericana* (dotted diamonds), and *P. tremuloides* / *B. papyrifera* (dotted squares). Filled symbols and dashed lines represent elevated [CO₂]. 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. 1A). The observed relationship was maintained after broadening the analysis to include data from other Duke FACE plots and other FACE sites (Fig. 2C). 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 [CO₂] 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

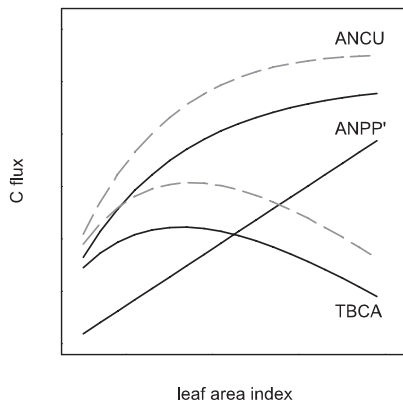


Fig. 3. Conceptual representation of the changes in canopy net photosynthesis minus maintenance respiration of aboveground woody biomass (ANCU), ANPP', and TBCA as a function of leaf area index. Solid lines represent ambient and dashed lines elevated (+200 ppm) [CO₂].

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 [CO₂]-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 [CO₂]-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. 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 [CO₂] and elevated [CO₂]. Under current [CO₂], 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 [CO₂], 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 [CO₂] 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 [CO₂].

Modifying this conceptual model to reflect the known responses of forests to elevated [CO₂] could help predict the effect of [CO₂] on TBCA. Modeling results on canopy-level CO₂ uptake indicate a wide range of enhancement of GPP under elevated [CO₂] (27, 28). On average, the [CO₂]-induced enhancement ratio of canopy CO₂ uptake at a given level of *L* is somewhat less than the FACE-induced enhancement ratio of atmospheric [CO₂] (≈1.5) and decreases with increasing *L* (28). In contrast to NPP (11), ANPP showed no elevated [CO₂]-induced enhancement (10) at a given *L*. With these [CO₂]-induced changes implemented, the conceptual model predicts a convergence of TBCA under elevated and current [CO₂] 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 [CO₂].

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 [CO₂] 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 [CO₂]. 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 CO₂ efflux; *F_a* is litterfall C; Δ*C_{root}*, Δ*C_{litter}*, and Δ*C_{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 ΔC_{litter} .

Duke FACE CO₂ × N Experiment. The Duke FACE experiment is located at the Duke Forest C-H₂O 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 CO₂ 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 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 [CO₂] 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 CO₂ 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_{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). $\Delta(C_{\text{litter}} + C_{\text{soil}})$ 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 [CO₂] did not change over the 4-year investigation and was similar at the initiation of the treatment to that under elevated [CO₂]. 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 CO₂-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 ($\text{m}^2 \times \text{y} \cdot \text{m}^{-2}$). 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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- 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.

