Effects of Elevated Atmospheric Carbon Dioxide on Soil Carbon in Terrestrial Ecosystems of the Southeastern United States

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As one travels through the rural southeastern landscape, even the most casual observer will note three dominant vegetation types. One cannot help but notice the predominance of forests—both natural and planted—as the Southeast is the nation's "wood basket," producing more wood fiber than any other area of the country. The casual traveler will also see a variety of agricultural row crops being grown. These change from cotton, corn, soybeans, and peanuts to tobacco and vegetables as one visits the varying geographic regions of this diverse area. The final land use one will observe is pasture lands; these may be supporting herds of beef cattle or may be managed to produce hay for winter feeding. All of these types of vegetation have the ability to take carbon from the atmosphere and store it either as standing biomass (including plant roots) or in soil. However, the Earth's atmosphere is changing, and increasing carbon dioxide (CO_2) concentration is one of the most studied and best documented of these changes. How will this rising CO_2 affect the vegetation types of the Southeast and how will these plants impact the continuing rise in the concentration of atmospheric CO_2? Finally, can these varying land uses help mitigate the increase in atmospheric CO_2 by storing C in soil, and can we, as researchers, find ways to manage these systems to increase the amount of CO_2 taken from the atmosphere and stored in the soil? These are the questions that will be investigated and explained in the following chapter.

When considering soil C storage, there are several parameters and processes (as well as impacts on these) that must be taken into account. The first parameter to consider is inputs. Carbon can enter soil via plant processes such as root exudation, sloughing of root cells, and other processes associated with root growth. These inputs, however, are readily decomposable and probably do not add to soil C pools residing more than a few days to weeks. The majority of soil C comes directly from vegetation itself, as aboveground residue or litter and as plant roots. Therefore, it is important to consider plant growth and biomass production processes when attempting to understand soil C sequestration. Not only is

the quantity of plant biomass entering into soil processes important, but so is the quality of these residues. Residue quality can greatly impact the decompositional processes that break down the plant material into C pools, with residence times varying from weeks to months to years. Naturally, environmental conditions (such as resource—N, water, and CO_2—availability) will affect the quantity and quality of plant biomass. Further, it is important to note that not all of the C extracted from the atmosphere by plants is used to produce biomass; some is lost back to the atmosphere through plant (autotrophic) respiration. In addition, insects and microbes involved in decompositional processes also emit CO_2 back to the atmosphere by means of heterotrophic respiration. Therefore, the amount of C able to be sequestered in soil is a sum of plant biomass inputs minus that lost during decomposition.

Biomass

The concentration of CO_2 in the Earth's atmosphere is rising, due primarily to fossil fuel combustion and deforestation, and is projected to double preindustrial levels within this century (Keeling and Whorf, 1994). The fact that most plants increase biomass production when exposed to above ambient levels of atmospheric CO_2 is well documented (Kimball, 1983). In fact, experimentally doubling atmospheric CO_2 has been shown to increase plant biomass, on average, by almost 40% (Poorter, 1993). However, all species do not exhibit equivalent responses to CO_2 enrichment. Leaf morphology (Ceulemans and Mousseau, 1994; Saxe et al., 1998), physiology (Drake, 1992; Poorter, 1993), symbiotic relationships (Hartwig et al., 1996), competition (Bazzaz and Carlson, 1984; Pritchard et al., 2001a; Davis et al., 2002), as well as soil resource availability (Prior et al., 1997c) all influence plant response to CO_2. This chapter examines what is known concerning plant biomass production under elevated atmospheric CO_2 for southeastern crop, forest, and pasture ecosystems.

Crops

Since CO_2 is a primary input for crop growth, there is interest in how the rise in atmospheric CO_2 concentration will affect highly managed agricultural systems. Limited research has been conducted on the responses of several southeastern crops to elevated CO_2; some of these lesser-studied crops include corn (*Zea mays* L.) (Rogers et al., 1983b); cotton (*Gossypium hirsutum* L.) (Rogers et al., 1992; Heagle et al., 1999; Prior et al., 2003a); rice (*Oryza sativa* L.) (Baker et al., 1990); and wheat (*Triticum aestivum* L.) (Heagle et al., 2000). In general, these species demonstrated positive growth (biomass) responses to elevated levels of atmospheric CO_2.

Substantially more work has been conducted with other southeastern crops such as soybean (*Glycine max* L. Merr) (e.g., Allen et al., 1987; Baker et al., 1989; Heagle et al., 1998); as with the previous species, biomass increased for plants grown under high CO_2. Further, we have conducted extensive experiments on soybeans growing under elevated CO_2. Early work using open-top field chambers (Rogers et al., 1983a) and plants growing in containers showed that both corn (a C_4 species) and soybean (a C_3 species) increased biomass production when exposed to above-ambient concentrations of CO_2; soybean tended to show a greater response than corn (Rogers et al., 1983b).

We expanded the early work of Rogers et al. (1983b) for a more-detailed examination of the responses of a C_3 (soybean) and C_4 (grain sorghum; *Sorghum*

bicolor L. Moench) crop to CO_2 enrichment (Prior et al., 2003b, 2004a, 2004b). Prior CO_2 research had been conducted using either C_3 or C_4 crops; however, few previous studies had directly compared these two plant groups growing under similar conditions. A study was conducted over 5 yr and used field plants grown in a loamy sand to remove any potential artifacts associated with root confinement of containerized plants (Arp, 1991). This experiment was conducted using no-till management, and all crop and soil parameters were managed based on local extension service recommendations to resemble, as closely as possible, conditions that would exist on the farm. Further, it should be noted that these two crops were grown in the same plots for five consecutive years, without rotation. Figure 15–1 shows the average yearly biomass production for both sorghum and soybean grown under ambient and twice-ambient CO_2. While average sorghum biomass was greater than that of soybean, the response of soybean to elevated CO_2 was consistently greater than that of sorghum. Soybean seed and total plant dry weights (kg m^{-2} yr^{-1}) increased by 38.5 and 36.3%, respectively, while for sorghum these increases were only 9.2 and 20.9%, respectively. Cumulative biomass inputs to soil for the 5-yr duration of this study are shown in Fig. 15–2. As with average biomass production, the total inputs for sorghum (3.8 kg m^{-2}) were greater than those for soybean (2.7 kg m^{-2}). However, the response of these biomass inputs to elevated CO_2 was, again, greater for soybean than sorghum; nonyield residue (e.g., aboveground biomass minus seed), root, and total input dry weights (kg m^{-2}) increased by 43.0, 28.0, and 35.6%, respectively, while sorghum increased 28.5, 22.6, and 26.2% for these components, respectively. In general, C_3 plants tend to increase growth to a greater extent than C_4 plants (C_3 = 33–40% vs. C_4 = 10–15%) due to their greater photosynthetic response to elevated CO_2 (Kimball, 1983; Bowes, 1993; Amthor, 1995; Fuhrer, 2003). Data from this 5-yr study are in general agreement with these previous reports.
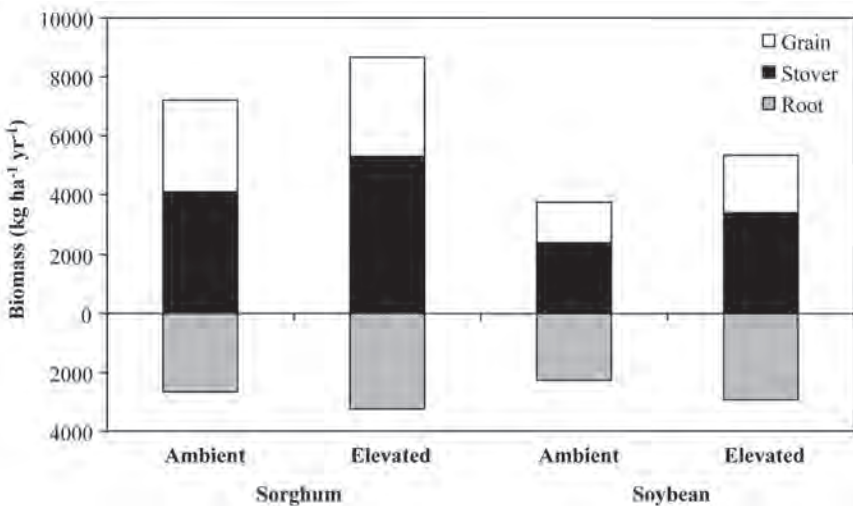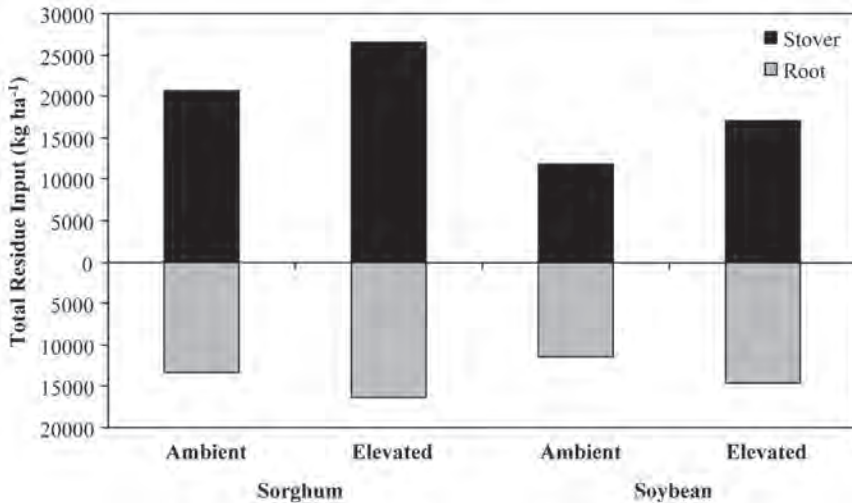

Fig. 15–1. Average yearly biomass production (kg ha^{-1} yr^{-1}) for sorghum and soybean grown under ambient and twice-ambient CO_2. Data above the bisecting line represent aboveground tissues, and data below the line represent belowground tissues. (Data from Prior et al., 2003b.)

Fig. 15–2. Cumulative biomass inputs to soil (kg ha⁻¹) for sorghum and soybean grown under ambient and twice-ambient CO₂ for the 5-yr duration of this study. Data above the bisecting line represent aboveground tissues, and data below the line represent belowground tissues. (Data from Prior et al. 2003b.)

In a separate study, we continued work with row crops to evaluate the interaction of elevated CO_2 with farm management practices (Prior et al., 2005). This study compared the impacts of conventional (spring tillage) versus conservation (no-till) management practice systems on a Decatur silt loam (clayey, kaolinitic, thermic Rhodic Paleudult). In the conventional system, grain sorghum and soybean were rotated each year using conventional spring tillage practices and winter fallow. The conservation system also uses a grain sorghum–soybean rotation, with three winter cover crops: wheat, crimson clover (*Trifolium incarnatum* L.), and sunn hemp (*Crotalaria juncea* L.), which are also rotated. All crops in the conservation system were grown using no-till practices. The wheat served as cover as well as a grain crop. These five species offer contrasting characteristics with respect to photosynthetic pathways (C_3 and C_4), responses to CO_2, rooting patterns, N_2 fixation, decomposition rates, and their impact on soil C and N cycling; most are prominent the world over. As with the research discussed previously, this study employed open-top field chambers for control of the atmospheric CO_2 levels and was conducted in the field to remove potential effects of root confinement.

The effect of management and atmospheric CO_2 concentration on biomass responses over two cropping cycles (4 yr) were evaluated (Prior et al., 2005). In the conservation system, cover crop residue (kg m⁻² yr⁻¹; clover, sunn hemp, and wheat) was increased by elevated CO_2 (22.8, 43.3, and 18.1%, respectively); however, CO_2 effects on weed residue produced during fallow periods in the conventional system were variable. Elevated CO_2 had a greater effect on increasing soybean residue (49.3%) as compared to sorghum (18.9%). Grain yield increases were also greater for soybean (46.1%) than for sorghum (10.0%) or wheat (22.6%) under high CO_2. Differences in 4-yr total sorghum and soybean residue production (kg m⁻²) within the different management systems were small and variable. Cumulative aboveground residue inputs were increased by elevated CO_2 in both conventional
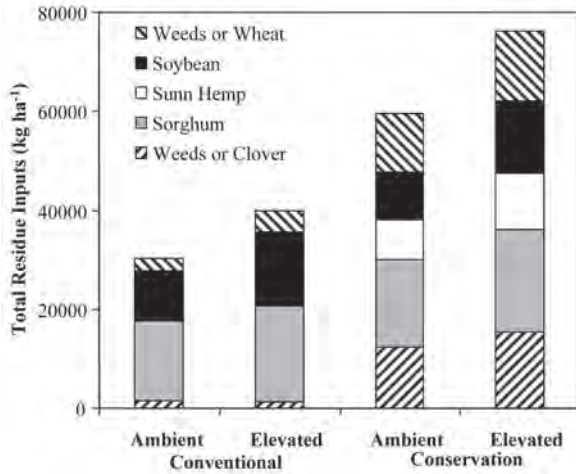
Fig. 15–3. Cumulative aboveground residue production for weeds or clover, sorghum, sunn hemp, weeds or wheat, and soybean grown under ambient or elevated atmospheric CO_2 conditions and under either conventional or conservation management systems after two complete cropping cycles (4 yr). Note that weeds occurred only in the conventional systems, while clover or wheat was grown only in the conservation system. (Data from Prior et al., 2005.)

and no-till systems (Fig. 15–3). Similarly, cumulative inputs were increased by conservation practices in both ambient- and elevated-CO_2 treatments (Fig. 15–3). Results suggest that residue inputs were increased with conservation management or elevated CO_2, with the greatest input occurring for a combination of these treatments. These findings echo results from the previous 5-yr sorghum–soybean study and demonstrate that soil C storage can be impacted both by management and by changes in the Earth's atmosphere.

Forests

As with agronomic crop species, elevated atmospheric CO_2 has the ability to enhance biomass production of forest systems. A review of woody plants showed that growth of most tree species was enhanced by elevated CO_2 (Ceulemans and Mousseau, 1994). Early work demonstrated that growth of sweetgum (*Liquidambar styraciflua* L.) was increased by elevated CO_2 (Rogers et al., 1983b). Further work with sweetgum also showed increased growth under elevated CO_2 (Tolley and Strain, 1984a; Groninger et al., 1995), including increased root growth (Jifon et al., 1995). This research also demonstrated that high CO_2 partially ameliorated the adverse effects of water stress on growth of sweetgum seedlings (Tolley and Strain, 1984b; Groninger et al., 1995). Research with a number of other hardwood tree species occurring in the Southeast has generally shown increased growth under high CO_2; these species include yellow poplar (*Liriodendron tulipifera* L.) (O'Neill et al., 1987a; Norby and O'Neill, 1991; Norby et al., 1992), red maple (*Acer rubrum* L.) (Bazzaz and Miao, 1993; McConnaughay et al., 1996), red oak (*Quercus rubra* L.) (Bazzaz and Miao, 1993), and white oak (*Q. alba* L.) (Norby et al., 1986; O'Neill et al., 1987b; Norby and O'Neill, 1989).

Despite the ecological significance of hardwood species, pines (particularly southern yellow pines) are more economically important in the southeastern United States and are, in fact, the most extensively planted and highly managed tree species in the United States. While of lesser significance than other yellow pines, shortleaf pine (*Pinus echinata* Mill.) seedlings were shown to increase dry weight by 66% under CO_2 enrichment (O'Neill et al., 1987b). Loblolly pine (*P. taeda* L.) is the most economically important and widely planted of the southern yellow pines. Again, early work using open-top field chambers and plants grown in containers demonstrated that growth of loblolly pine seedlings was significantly increased by elevated CO_2 (Rogers et al., 1983b). However, Tolley and Strain (1984a, 1984b) reported no effect of CO_2 enrichment on loblolly pine seedlings in phytotron growth chambers. In contrast, Groninger et al. (1995), also working with loblolly seedlings in growth chambers, reported increased biomass under elevated CO_2. Further, work with loblolly pine seedlings in glasshouses demonstrated increased growth under CO_2 enrichment, including increased root biomass (Larigauderie et al., 1994; King et al., 1996).

Although not as economically important today as loblolly pine, longleaf pine (*P. palustris* Mill.) is a historically and ecologically important southern pine species. Before European settlement, longleaf pine savannahs occupied 37.2 million ha of the southeastern United States (Landers et al., 1995). Since the early 1600s, timber harvesting, fire suppression, and conversion of forests to farmland have reduced the land area of these ecosystems to less than 4% of their original range (Peet and Allard, 1993; Landers et al., 1995). This loss is comparable to that of many endangered communities including the North American tallgrass prairie, the moist tropical coastal forest of Brazil, and the dry forests along the Pacific coast of Central America (Noss, 1989). Longleaf pine ecosystems are also very diverse, with some specific types having the highest reported values for species richness, including many threatened and endangered species, in the temperate Western Hemisphere (e.g., 140 species ha^{-1} for mesic longleaf woodlands [Peet and Allard, 1993]). Longleaf pine forests currently occupy sites at the more xeric end of the moisture continuum in the southeast and are often found on soils with low N availability. Interest in this species has increased dramatically over the last decade, not only due to its ecological significance, but also because of superior lumber quality, fire tolerance, and resistance to some of the more devastating southern forest insects (e.g., bark beetles) and diseases (e.g., fusiform rust).

We have conducted several studies to examine the response of longleaf pine to elevated CO_2. Initially, longleaf pine seedlings were grown in large containers (45 L) to minimize root restriction and exposed to ambient and twice-ambient concentrations of atmospheric CO_2 in open-top field chambers. Within this study, seedlings were also exposed to two levels of N fertilization (0.02 or 0.20 mg N g^{-1} soil yr^{-1}) and two levels of water stress (−0.5 or −1.5 MPa xylem pressure potential). Seedlings were destructively harvested following 4, 8, 12, and 20 mo of CO_2 exposure. Elevated CO_2 resulted in increased photosynthesis (Runion et al., 1999b) and mycorrhizal colonization of longleaf pine roots (Runion et al., 1997), which resulted in greater biomass production (Prior et al., 1997c). Greater biomass production was noted for all longleaf pine plant component parts (Fig. 15–4); however, longleaf pine roots responded to a greater extent to CO_2 enrichment than did aboveground parts (58 and 34%, respectively). Interactions were noted between treatment variables; elevated CO_2 resulted in increased longleaf
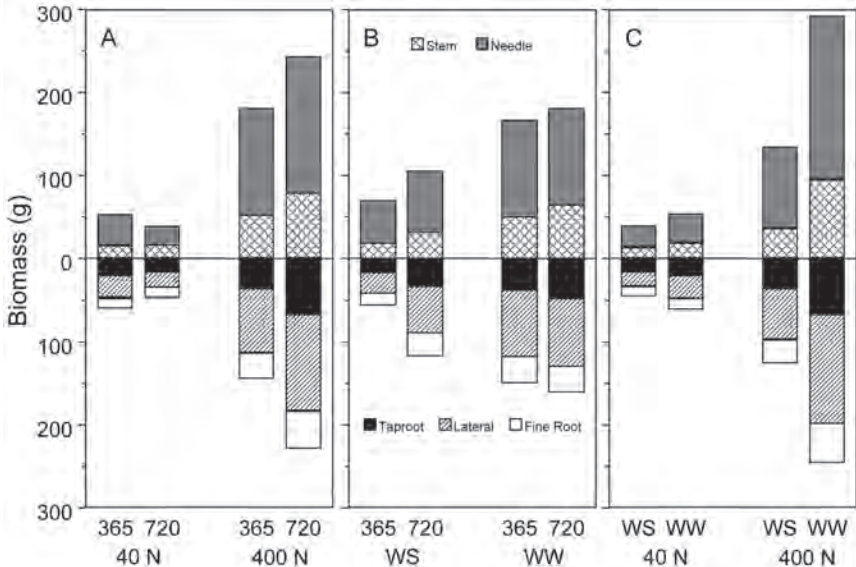
Fig. 15–4. Longleaf pine biomass after 20 mo of treatment as affected by interactions between CO_2 and N (A); CO_2 and irrigation (B); and N and irrigation (C). Data above the bisecting line represent aboveground tissues, and data below the line represent belowground tissues. WS and WW denote water-stressed and adequately watered treatments, respectively; 365 and 720 (μmol mol^{-1}) denote ambient and elevated CO_2 treatments, respectively; 40 N and 400 N denote low-N and high-N treatments, respectively. (Data from Prior et al., 1997c.)

pine biomass only when N was not limiting. High CO_2 tended to ameliorate the adverse effects of water stress, increasing productivity of water-stressed trees (particularly roots); however, this was, again, contingent on sufficient N availability. It was concluded that soil N availability was the overall controlling resource in that a positive response to elevated CO_2 occurred only under high-N conditions, and in that the CO_2 moderation of water response was also contingent on soil N level. It is only under conditions of sufficient N availability that extra CO_2 in the atmosphere can be used for increased seedling growth regardless of soil water availability (Prior et al., 1997c).

Previous research had demonstrated that, while individual plant response to elevated CO_2 may be predicted based on differences in leaf morphology (Ceulemans and Mousseau, 1994; Saxe et al., 1998) and physiology (Drake, 1992; Poorter, 1993), evidence from competition studies consistently suggests that response cannot be reliably predicted when species are grown in communities (Bazzaz and Carlson, 1984; Bazzaz, 1990; Bazzaz and McConnaughay, 1992; Ziska, 2003; Morgan et al., 2004). Given that CO_2–induced shifts in competitive advantages among species may alter species composition and community structure and function (Wray and Strain, 1987; Fajer, 1989; Bazzaz, 1990; Joel et al., 2001; Dijkstra et al., 2002), experiments which examine the effects of CO_2 enrichment on plant communities are critical for furthering understanding of ecosystem response to global climate change.

As for crop plants, we expanded our work with longleaf pine to examine effects of CO_2 enrichment under more natural (i.e., inground) conditions; again, open-top chambers were used for CO_2 enrichment (Pritchard et al., 2001a; Davis et al., 2002; Runion et al., 2006). A model regenerating longleaf pine–wiregrass community was constructed using an assemblage of five early successional forest species representing major functional guilds within a typical longleaf pine–wiregrass community: longleaf pine, a C_3 evergreen conifer; wiregrass (*Aristida stricta* Michx.), a C_4 bunch grass; sand post oak (*Q. margaretta* Ashe ex Small), a C_3 broadleaf tree; rattlebox [*Crotalaria rotundifolia* (Walter) Poiret], a C_3 perennial, herbaceous, N-fixing legume; and butterfly weed (*Asclepias tuberosa* L.), a C_3 non-leguminous, herbaceous perennial. The planting regime used for construction of the model community achieved planting densities reflective of naturally regenerating longleaf pine–wiregrass ecosystems (Hainds, 1995; Jacqmain, 1996). All plants in the open-top chambers were destructively harvested following 3 yr of exposure to either ambient or twice-ambient levels of CO_2.

Elevated CO_2 resulted in significant increases in longleaf pine biomass (88%), did not affect oak biomass production, and decreased biomass for the remaining species (29, 58, and 48% for wiregrass, butterfly weed, and rattlebox, respectively; Fig. 15–5) (Runion et al., 2006). Litter production also increased for pines (77%) and, due to higher plant mortality, for wiregrass (138%); overall, surface litter was increased by 76% under elevated CO_2, primarily due to increases in longleaf pine needle litter.

Community structure was altered by CO_2 enrichment. The percentage of aboveground, belowground, and total biomass composed of longleaf pine was significantly greater (~12%) in CO_2–enriched plots. Biomass components for wiregrass were, concomitantly, lower (8–11%) under elevated-CO_2 conditions. Although butterfly weed and rattlebox comprised small amounts of the overall biomass of the system, these were also significantly lower when grown under elevated than ambient CO_2. As with most other variables, the biomass contribution of sand post oak to the total system did not differ significantly between CO_2 treatments (Runion et al., 2006).

Before initiation of this study, we had hypothesized that differing plants would respond to elevated CO_2 as follows: $C_3 > C_4$; broadleaf plants > conifers; and N-fixers > nonfixers. Data indicated that species within the model community did not always respond in the manner hypothesized. Perhaps this is not surprising given it has often been noted that response of individual species cannot be reliably predicted—even when based on factors known to influence response to CO_2—when species are grown in communities. The most unexpected result in this study was the large biomass increase under CO_2 enrichment of longleaf pine. Longleaf pines were significantly taller in elevated (1.59 m) than ambient plots (1.09 m). This early and rapid height growth under high CO_2 is the most likely reason for the poorer performance of the other species (including the C_3 broadleaves) in this study (i.e., other plants, which did not put on rapid height growth, could not compete for light and succumbed to shading by longleaf pine). It should also be noted that longleaf pine, being an evergreen conifer, is capable of photosynthesis and root growth (thus, exploration for soil resources) during the overwintering period, giving it a possible competitive advantage over neighboring deciduous species.
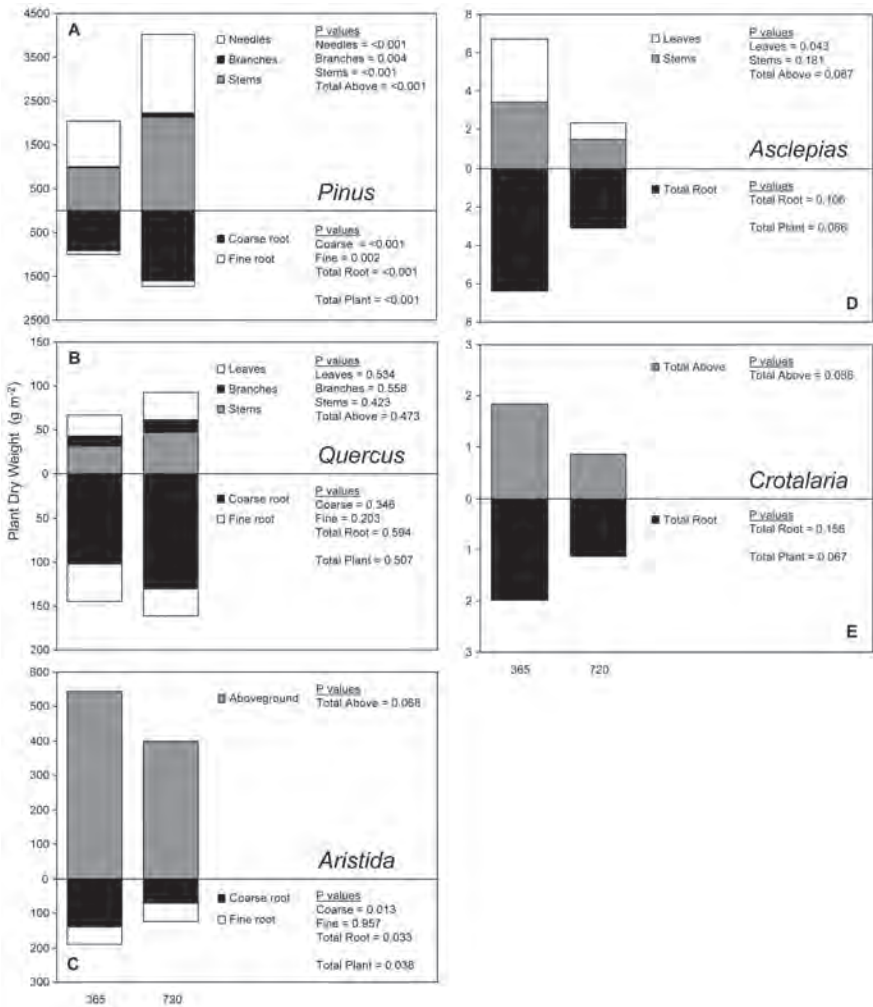
Fig. 15–5. Plant dry weight (g m⁻²) for component plant parts (needles, leaves, branches, stems, total aboveground, coarse roots, fine roots, total roots, total plant as applicable for each species), with associated mean separation statistics, for *Pinus* (A), *Quercus* (B), *Aristida* (C), *Asclepias* (D), and *Crotalaria* (E) when grown together for 3 yr under ambient (365 μmol mol⁻¹) and elevated (720 μmol mol⁻¹) concentrations of atmospheric CO₂. Data above the bisecting line represent aboveground tissues, and data below the line represent belowground tissues. (Data from Runion et al., 2006.)

Although rising CO_2 may alter community structure in ways that could impact ecosystem function, productivity and the ability of longleaf pine forests to sequester C will likely be enhanced by rising levels of atmospheric CO_2. It seems apparent that competition among plants confounds understanding of ecosystem function. This fact highlights the need for additional studies that examine the effects of elevated CO_2 on these processes.

Although data from the previously discussed study are relevant to the effects of rising levels of CO_2 on longleaf communities, it should be noted that these plants started as seedlings and were exposed to CO_2 enrichment for 3 yr. Therefore, these data would be most applicable to early establishment forests (natural or planted) and to reestablishment in gaps in older longleaf forests.

Some work has been conducted with older trees; this research has focused on free-air CO_2 enrichment (FACE) of loblolly pine and sweetgum plantations. It should noted that these plantations were not exposed to CO_2 enrichment from planting; rather, portions of these experimental sites received a step increase in atmospheric CO_2 concentration (200 μmol mol^{-1} CO_2) at 15 or 9 yr of age for the loblolly pine or sweetgum plantations, respectively.

At the Duke FACE site, loblolly pines showed increased growth under high CO_2 for at least the first 6 yr (23–26%); this positive effect of CO_2 on growth rate declined slightly over time (DeLucia et al., 1999; Hamilton et al., 2002). Root production and turnover were examined in situ at this site using minirhizotrons. Modest increases in ecosystem-level root productivity under CO_2 enrichment were observed (Pritchard et al., 2001b). Associated with the increased aboveground growth rate, net primary productivity (NPP) of the forest ecosystem was also enhanced (18–24%) by high CO_2 (Hamilton et al., 2002; Finzi et al., 2006). Also associated with increased growth, litter fall was significantly increased in high-CO_2 plots (DeLucia et al., 1999; Allen et al., 2000), which may or may not suggest an increase in soil C storage in this ecosystem (Schlesinger and Lichter, 2001). Several investigations at this site suggest that CO_2 has had no significant impact on N cycling (Allen et al., 2000; Finzi et al., 2001, 2002; Finzi and Schlesinger, 2003). However, fertilizing half of the FACE prototype ring resulted in an increase in the positive growth response to high CO_2 (Oren et al., 2001). Fertilization is becoming a common practice in intensively managed pine plantations in the Southeast. Another method of redistributing resources in pine plantations is to thin the stand at some point following complete canopy closure. If the loblolly trees within the Duke FACE site had been thinned, as was the remainder of the stand outside of the study, perhaps a positive growth response would have followed. It should also be noted that, while loblolly pine plantations are somewhat common in the piedmont region of the Southeast (as in the Duke FACE site), they are much more prevalent in the coastal plains. Whether or not data from the Duke FACE site are applicable to these coastal plain loblolly pine plantations remains to be investigated.

As with the Duke FACE site, the Oak Ridge sweetgum FACE site also showed that growth was enhanced (24%) by elevated CO_2 in the first 2 yr of exposure (Norby et al., 2001b). Again, as with the Duke loblolly pine FACE site, sweetgum showed a substantial increase in NPP (21%) following 3 yr of CO_2 enrichment (Norby et al., 2002). This NPP response continued through 6 yr, (22%) and a significant portion of the stimulation in NPP could be attributed to a more than doubling of fine root production (Norby et al., 2004). Plantation-grown sweetgum are not common in the Southeast, and whether or not these data are applicable to naturally growing sweetgum (or other hardwood species) is unknown at this time.

Pastures

While the effects of elevated CO_2 on natural grasslands have received some attention, managed pastures—particularly those in the southeastern United

States—remain an understudied agroecosystem (Derner et al., 2005). In a study of a southeastern pasture species, bahiagrass (*Paspalum notatum* Flüggé), conducted in temperature-gradient greenhouses constructed over a field soil, elevated CO_2 increased pasture establishment, ground cover, photosynthesis, and biomass (9%) in the first year of exposure (Fritschi et al., 1999). This species continued to exhibit increased biomass production (15%) over the following 2 yr (Newman et al., 2001); these increases in biomass production are typical for the response of C_4 plants to elevated CO_2 (Kimball, 1983). Throughout this period, bahiagrass also exhibited a positive growth response to increased temperatures (1.5, 3.0, and 4.5°C above ambient) under high-CO_2 conditions (Fritschi et al., 1999; Newman et al., 2001). In a continuation of this bahiagrass study, N was applied at two rates (80 or 320 kg ha^{-1} yr^{-1}). Biomass was not affected by CO_2 treatment at the low N rate; however, biomass increased under high CO_2 (7 and 17%, for the first and second years of study, respectively) when N was not limiting (Newman et al., 2006).

We initiated a study of bahiagrass response to elevated CO_2, using open-top chambers over a field soil, in 2005. This study will run for a minimum of 10 yr and will examine not only biomass production and soil C, but will also assess root growth and monitor soil trace gas efflux (CO_2, CH_4, and N_2O). After a 1-yr establishment period, during which the bahiagrass was harvested once, a N treatment was applied. Half of all ambient and elevated plots received N [(NH$_4$)$_2$SO$_4$] at 90 kg ha^{-1} 7 mo before the first harvest following initiation of the N treatment and following each subsequent harvest; the remaining plots received no N fertilization. These two treatments represent improved or managed pastures versus unimproved pastures; both types of pastures are common in the Southeast.

Biomass was harvested in fall of 2005. Biomass production in the first year, which was representative of the establishment phase of an unimproved pasture, was unaffected by CO_2 treatment (Fig. 15–6). Two harvests have been conducted
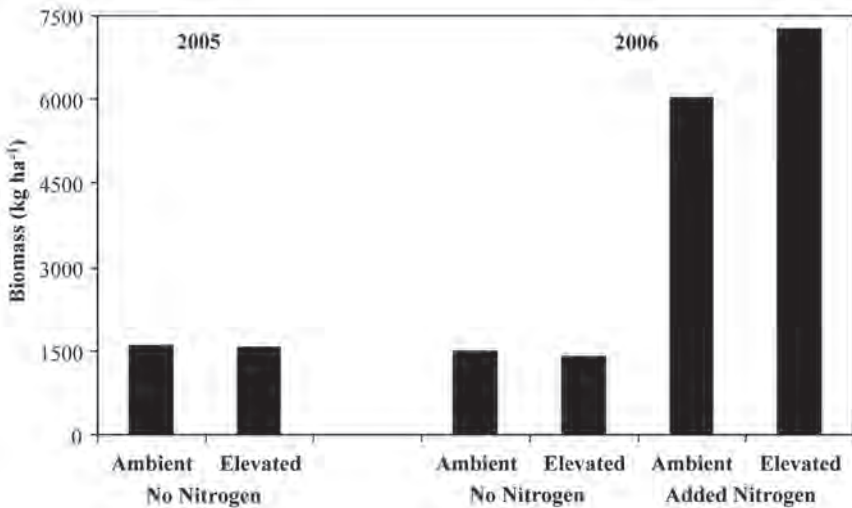
Fig. 15–6. Cumulative yearly bahiagrass biomass production (kg ha^{-1}) for ambient (365 μmol mol^{-1}) or elevated (550 μmol mol^{-1}) CO_2 treatments for one harvest in 2005 (before N treatments) and for two harvests in 2006, following initiations of N treatments. No Nitrogen, no N; Added Nitrogen, 90 kg ha^{-1}.

since N treatment initiation; both occurred in summer 2006. There was, naturally, a strong effect of the N treatment (360% increase with N) on cumulative biomass production. There was also, overall, a significant CO_2 effect (16% increase with high CO_2). There was a significant ($p = 0.027$) interaction between treatments. In the no-N treatment, elevated CO_2 had no impact on bahiagrass production, as was observed in the first year; however, with added N, biomass production increased (21%) with high CO_2 (Fig. 15–6).

As was mentioned previously, a primary component of soil C comes as a result of inputs from vegetation. As was clearly demonstrated in this section, elevated atmospheric CO_2 increases plant biomass production in most cases. In some instances, plants do not respond to increased atmospheric CO_2; this is particularly true when soil resources, such as N, are a limiting factor. Increased plant biomass production should, logically, lead to the potential for increasing soil C in these southeastern systems. However, other factors play a role in determining the fate of this additional plant biomass.

Litter Quality and Decomposition

In addition to increases in the quantity of plant biomass entering into or onto the soil, elevated atmospheric CO_2 can alter the quality of these tissues. One commonly seen alteration in plant tissue chemistry under high CO_2 is a reduction in tissue nutrient (especially N) concentration; this reduction is generally greater for green plant material than for naturally senesced material (Norby et al., 2001a). However, due to greater biomass inputs, the total amounts of nutrient entering the soil can remain unchanged or can increase. For example, in the ongoing pasture study, tissue C concentration was unaffected by CO_2 treatment, while N concentration was reduced (6%) under high CO_2 (Fig. 15–7). However, the total C content of the bahiagrass harvested in summer 2006 was significantly higher (25%) under elevated CO_2; the total N content was unaffected by growth in high CO_2 (Fig. 15–7). Changes in residue C and N generally result in an increase in the tissue C/N ratio under elevated CO_2 (Mellilo, 1983; Cotrufo et al., 1998; Torbert et al., 2000). Changes in tissue C and N in the bahiagrass study increased the C/N ratio in the no-N treatment, regardless of CO_2 level. There was, however, an interaction between the N and CO_2 treatments; plants grown in high CO_2 had a lower C/N ratio than plants grown in ambient CO_2 in the no-N treatments, but the opposite effect was noted in the N-fertilization treatment (Fig. 15–8). This bahiagrass data were from recently harvested (green) plant material. Similar results were found for tissue C and N content using senesced material from the previously mentioned 5-yr sorghum–soybean study. Tissue C content was increased under high CO_2 for leaves, stems, and roots in both species, while tissue N content was more variable. Root N content was increased in both species, stem N content was unaffected in both species, and leaf N was increased in soybean but not sorghum under elevated CO_2 (Prior et al., 2004b).

Plants grown in elevated concentrations of CO_2 may exhibit alterations in other aspects of tissue chemistry, including higher concentrations of carbohydrates (Runion et al., 1999a; Booker et al., 2000), changes in quantity and quality of foliar epicuticular waxes (Thomas and Harvey, 1983; Graham and Nobel, 1996; Prior et al., 1997a), changes in quantity of lignin and higher lignin to N ratios (Runion et al., 1999a; Norby et al., 2001a), and increased levels of defense compounds
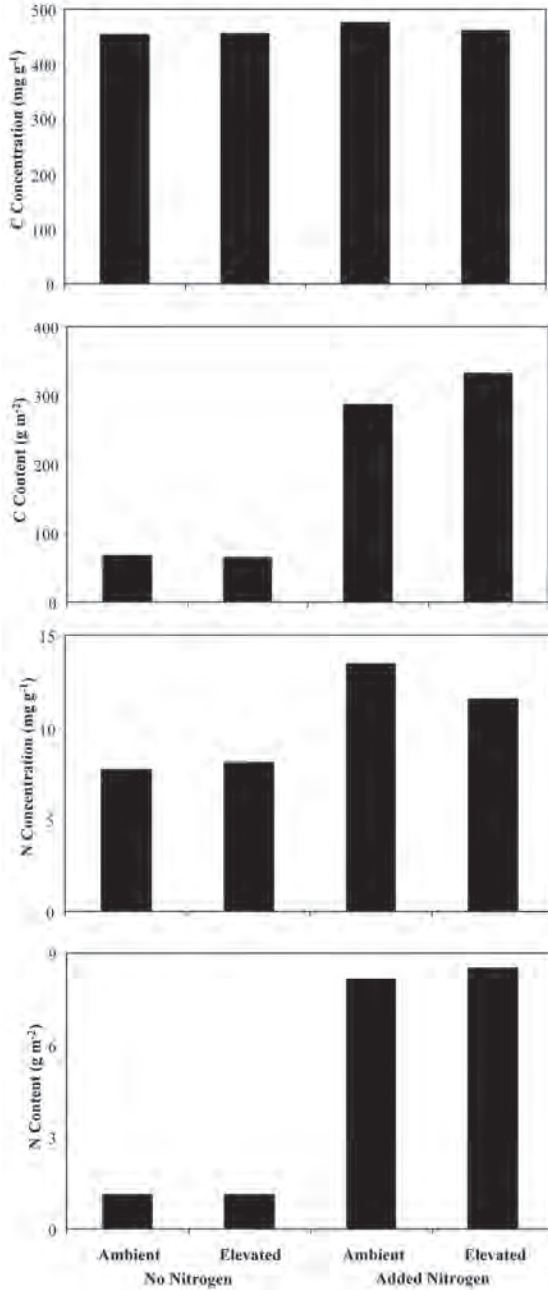
Fig. 15–7. Pasture C and N concentration, and content for bahiagrass grown under all combinations of ambient (365 μmol mol^{-1}) and elevated (550 μmol mol^{-1}) CO$_2$ and either no N or added N (90 kg ha^{-1}). Data are for two harvests in 2006, following initiations of N treatments; C and N concentration were averaged for the two harvests, while C and N content were totaled for these harvests.
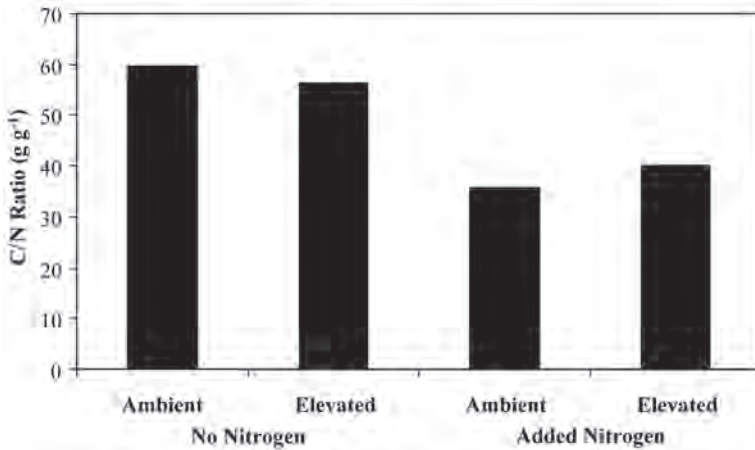
Fig. 15–8. Pasture C/N ratio for bahiagrass grown under all combinations of ambient (365 μmol mol^{-1}) and elevated (550 μmol mol^{-1}) CO_2 and either no N or added N (90 kg ha^{-1}). Data are for two harvests in 2006, following initiation of N treatments; C/N ratio is averaged for the two harvests.

such as tannins and phenolics (Mellilo, 1983; Pritchard et al., 1997; Entry et al., 1998; Runion et al., 1999a; Booker et al., 2000). Again, these data are generally derived from green plant material and may not hold for senesced material found under natural conditions.

Changes in tissue chemistry are particularly important in regard to potential impacts on decompositional processes. In particular, the manner in which changes in tissue chemistry impact plant–detritivore and plant–microbe interactions will have major effects on decomposition of these plant materials, as these are the primary decomposers. Elevated atmospheric CO_2 has been shown to alter both litter (Coûteaux et al., 1991) and rhizosphere (Runion et al., 1994) microbial community composition and/or activity, which could impact decomposition; these changes were indirect and generally related to alterations in tissue chemistry, particularly lower tissue N concentration and higher C/N ratio.

Lamborg et al. (1983) have argued that increased soil microbial activity, resulting from greater biomass C inputs in an elevated-CO_2 world, could lead to increased soil organic matter decomposition (i.e., the "priming effect") and, therefore, atmospheric CO_2 enrichment would not result in accumulation of soil organic C. Alternatively, Goudriaan and De Ruiter (1983) proposed that increased soluble, easily decomposed C inputs (as a consequence of CO_2 enrichment) would accentuate substrate preferences among soil microbes. They further speculated that preference for easily decomposable substrates would retard the decomposition of recalcitrant plant debris and native soil organic matter. The end result would be an accumulation of soil organic matter. Results from Lekkerkerk et al. (1990) support the contention of Goudriaan and De Ruiter (1983) in that they found that turnover of the more resistant soil organic matter was reduced under elevated CO_2 due to increased microbial preference for easily decomposable root-derived material. Coûteaux et al. (1991) demonstrated similar results for an initial decomposition period; however, in the long term, shifts in the decomposer

population (i.e., increased microfauna and white-rot fungi) increased decomposition of CO_2–enriched material. Verburg et al. (1998) also reported that high CO_2 initially increased microbial respiration due to decomposition of fresh root exudates; however, overall respiration was lower for elevated-CO_2 soils due to dominance of decomposition of more recalcitrant root material in the long term.

The C/N ratio is thought to play an important role in determining the rapidity with which plant materials will break down. Further, this increase in C/N ratios of plant tissues produced under elevated CO_2 led to the hypothesis that decomposition rates in an elevated-CO_2 environment will be slower (Bazzaz, 1990) and will limit plant response to CO_2 enrichment and long-term C storage (Strain and Bazzaz, 1983). This work may be more applicable to natural ecosystems due to the ability to supply N in managed systems. It has also been suggested (Ball, 1992; Ball and Drake, 1997) that higher C/N or lignin/N ratios under high CO_2 can slow decomposition of C_3 (but not C_4) plant material; however, this may depend on the duration and method used to study the decomposition processes. Variability in research findings, coupled with the debate noted above, demonstrate the need for further exploration into the effects of elevated CO_2 on decompositional processes.

Investigations into decompositional processes have employed three primary methodologies: laboratory incubations of plant material grown in elevated CO_2 with subsequent C and N mineralization and immobilization measured; litter bag studies using plant material produced under elevated CO_2 to assess mass, C, and N loss over time; and measurements of soil CO_2 efflux conducted under elevated CO_2.

Laboratory incubation studies were conducted on cotton material produced under ambient and elevated CO_2. To examine the effects of elevated CO_2 on residue decomposition independent of the cumulative impact to the soil, plant parts (leaf, stem, and root) were added separately to three different soil series (Blanton loamy sand [loamy, siliceous, thermic Grossarenic Paleudult], Decatur silt loam [clayey, kaolinitic, thermic Rhodic Paleudult], and Houston clay loam [very fine, montmorillonitic Typic Chromudert]) common to the Southeast that had not been previously exposed to elevated-CO_2 conditions (Torbert et al., 1995). Results indicated that, contrary to the effect commonly hypothesized, decomposition rates were similar for both CO_2 treatments (despite elevated residues having higher C/N ratios). Further, it was found that increased levels of easily decomposable components (e.g., proteins, starch, sugars, organic acids, and pectin) in high-CO_2–grown residues compensated for higher C/N ratios, resulting in the similar decomposition rates.

While soil C mineralization showed little effect of atmospheric-CO_2 concentration (Fig. 15–9), the net N immobilization and mineralization rates were impacted (Fig. 15–10). The release of inorganic N into the soil solution was slower for elevated-grown material, resulting in an increase in the net N immobilization under high CO_2. These data indicate that CO_2–induced changes to the plant material may impact the availability of N in the plant–soil system. This would support the contention of Strain and Bazzaz (1983) that plant response to CO_2 fertilization may be limited by N immobilization in an elevated-CO_2 world. Results from this study also indicated that differences in soil series could exert an important control on decomposition rates of plant residue produced under elevated CO_2 (Fig. 15–10). The rate of decomposition seemed to be controlled by the ability of the soil to supply nutrients (especially N).
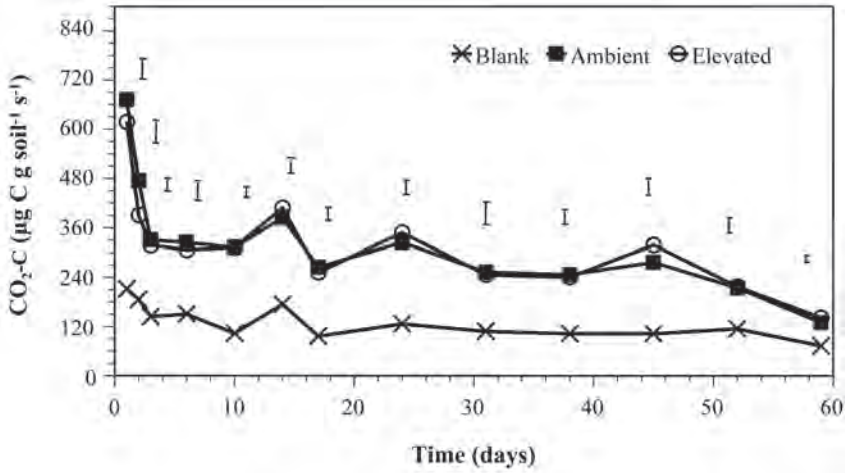
Fig. 15–9. Soil respiration rates (μg C g soil^{-1} s^{-1}) from a laboratory incubation study using soil amended with either elevated- or ambient-CO_2–grown cotton plant residue, averaged across soil series and plant residue type. (Data from Torbert et al., 1995.)

Additional incubation studies were conducted utilizing material produced from the sorghum–soybean cropping system study. Plant parts were examined separately by adding the material to soil that had not been previously exposed to elevated-CO_2 conditions. In this study, while differences were observed between plant parts and species, no significant difference was observed for C mineralization due to elevated CO_2 when green tissue was collected at physiological maturity (Henning et al., 1996). This study, however, did not consider changes due to the potential priming effect as defined by Lamborg et al. (1983). To address this priming effect, the impact of elevated CO_2 on decomposition was examined using elevated-CO_2–produced plant residues in amounts similar to that used for ambient-CO_2 material, as well as at a rate proportional to the increased biomass production observed under high CO_2 (Torbert et al., 1998). Further, this study combined all aboveground nonyield residue inputs and used senesced material. Carbon mineralization with the ambient-CO_2 tissue was higher than that of elevated-CO_2 tissue regardless of the amount of tissue added for both plant species. This indicates that decreases in residue quality due to elevated CO_2 may slow residue decomposition. However, the relative difference between CO_2 treatments was lower when more plant material was added; this may indicate that a priming effect occurred due to the increase in biomass additions, as predicted by Lamborg et al. (1983).

Data from this study also indicated that low soil N availability limited microbial decomposition in both grain sorghum and soybean, with net N immobilization occurring throughout the incubation period (Torbert et al., 1998). Also, as was observed with cotton, the release of inorganic N into the soil solution for soybean was slower in the elevated-CO_2 treatment. The limitations on inorganic N meant that, in general, N availability was imposing an important controlling effect on the residue decomposition processes in soil, but the level of this control was plant species dependent.
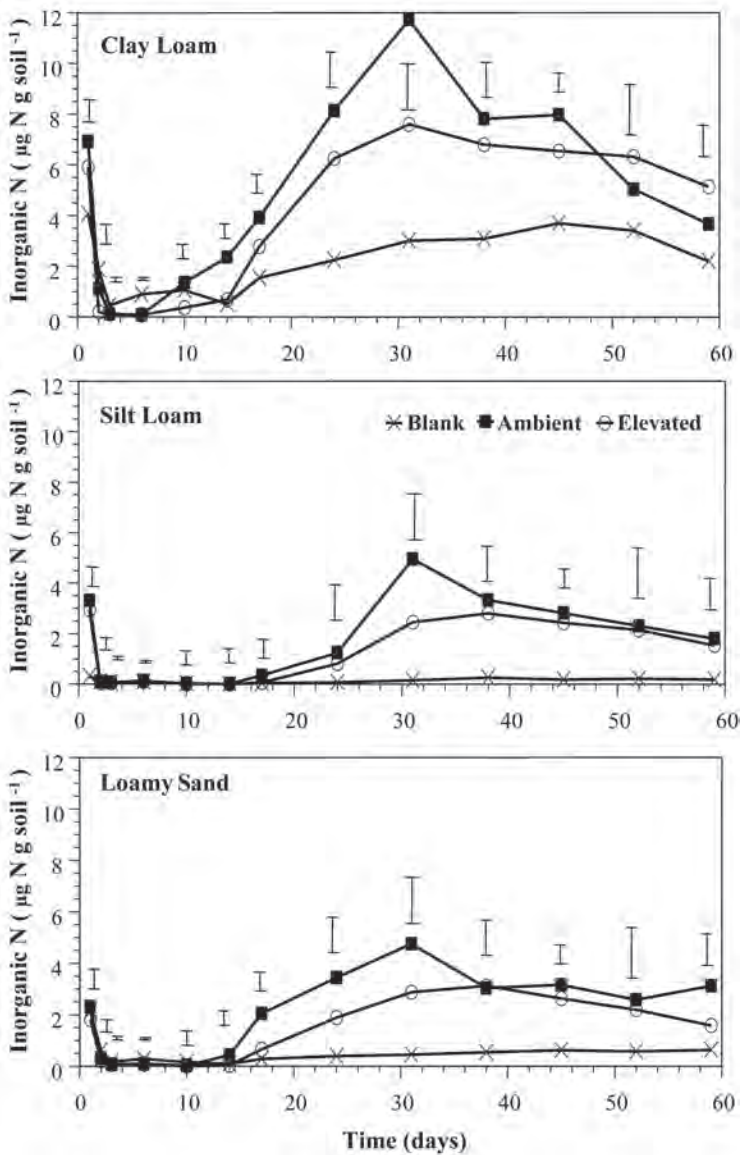
Fig. 15–10. Inorganic N concentration (μg N g soil^{-1}) in leachate from a laboratory incubation study using three soils (clay loam, silt loam, and loamy sand) amended with either elevated- or ambient-CO_2–grown cotton plant residue. (Data from Torbert et al., 1995.)

Intermediate-length studies were undertaken to examine the impact of elevated CO_2 on plant decomposition processes over the winter fallow period using a litter bag technique (Prior et al., 2004b). Measurement of mass losses from leaves and stems of sorghum and soybean indicated a species effect that varied by tissue type for the percent residue biomass recovery (Fig. 15–11). While there was a
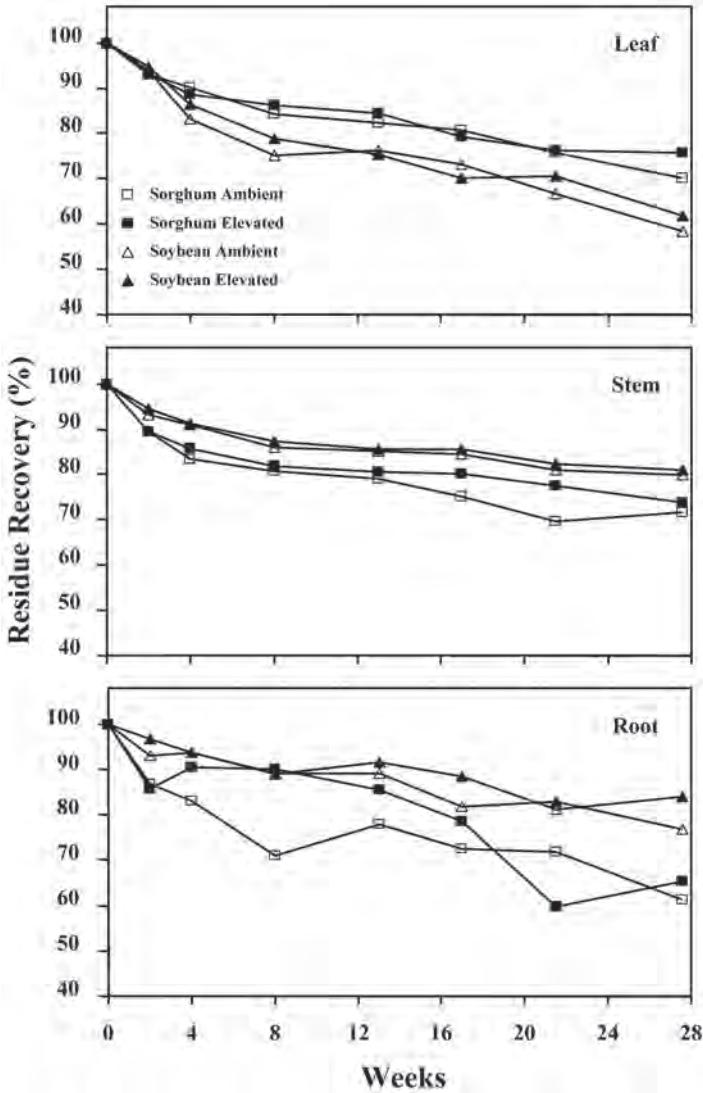
Fig. 15–11. Percent recovery of mass from a litter bag study using ambient- or elevated-CO$_2$–produced soybean and sorghum leaf, stem, and root residue during an overwintering period. (Data from Prior et al., 2004b.)

significant increase in percent ground cover measured under elevated-CO$_2$ conditions, there was no significant effect on percent biomass recovery due to elevated CO$_2$ in the litter bags. For leaf tissue, decomposition of soybean proceeded more rapidly than did decomposition of sorghum, as would be expected since soybean had a lower C/N ratio; however, the opposite pattern was observed with stem tissue. This was consistent with findings from the incubation studies in that differences were noted between plant parts, but no elevated-CO$_2$ effect was
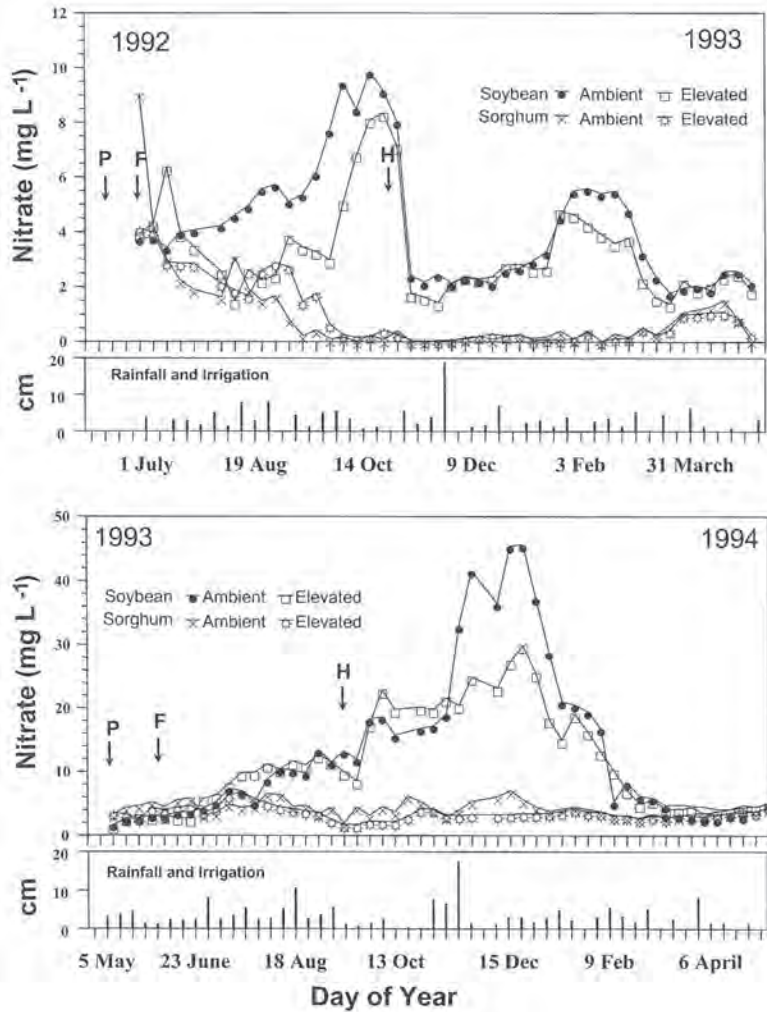
Fig. 15–12. Soil solution NO_3–N collected from a 90-cm depth for grain sorghum and soybean plots grown under ambient or elevated atmospheric CO_2 concentrations from 1 July 1992 to 28 April 1994. Planting date (P), fertilizer application date (F), and final harvest date (H) are noted. Means are for three replications. (Data from Torbert et al., 1996.)

observed. Even though CO_2 concentration did not affect percent biomass recovery, greater production under elevated CO_2 resulted in more biomass remaining after the overwinter fallow period.

An investigation using suction lysimeters placed at 90 cm depth was conducted within the previously mentioned sorghum–soybean cropping study to monitor the level of NO_3 movement below the rooting zone (Torbert et al., 1996). Results indicated that crop species and atmospheric-CO_2 concentration will both affect NO_3–N moving to groundwater (Fig. 15–12). The NO_3–N concentrations below the rooting zone of soybean were generally higher than those for sorghum,

most likely the result of higher N input into the soil system due to symbiotic N_2 fixation in soybean and of lower C/N ratios of soybean plant residue. The observed reduction in NO_3–N concentrations below the root zone under CO_2–enriched conditions during the growing season were likely a result of increased root proliferation under elevated CO_2 (Prior et al., 1994a, 1994b), resulting in increased N interception for plant growth. During the winter fallow period, reduced NO_3–N concentrations under CO_2 enrichment could be due to a reduction in N released due to slower decomposition of plant biomass. It should be noted that these field observations correspond to inorganic N responses seen in the incubation studies, indicating that changes in N release from plant material was responsible for most of the observed effect. These results suggest that reduced N leaching may impact residue decomposition processes and further indicate that a reduction in the degradation of groundwater quality beneath CO_2–enriched agroecosystems (due to lower NO_3–N concentrations below the root zone) could be expected.

We examined the short-term soil CO_2 efflux from field plots before planting within the sorghum–soybean cropping system study (Prior et al., 1997b). Elevated atmospheric CO_2 resulted in increased soil CO_2 efflux in soybean plots but had no effect on sorghum plots. These soil CO_2 efflux measurements were consistent with CO_2 evolution from crop residue decomposition in the incubation studies (Torbert et al., 1998).

Soil CO_2 efflux had been measured within the current cropping system study (conventional vs. conservation tillage) for the past 4 yr using the automated carbon efflux system (ACES) (Butnor et al., 2003). Briefly, ACES is an open-flow chamber–based, multiport respiration measurement system designed with pressure equilibration ports to ensure that differences in chamber pressure do not compromise the quality of the respiration measurement (Fang and Moncrieff, 1996). In general, both conservation management practices and elevated atmospheric CO_2 have increased seasonal soil CO_2 efflux by greater than 50% (unpublished data). The interactive effects of CO_2 and management on soil CO_2 efflux remain to be elucidated. These increases are a result of the greater biomass inputs under high CO_2 and conservation management. Despite higher respiration rates, greater amounts of residue remain in elevated-CO_2 plots and conservation management plots to date.

The ACES were previously employed within the model regenerating longleaf pine–wiregrass community for the 90-d period before harvesting for this study (Fig. 15–13). Soil CO_2 efflux, averaged across the entire 90-d measurement period, was significantly higher (26.5% or a total increase of 60 g C m^{-2}) in elevated-CO_2 plots. Soil CO_2 efflux showed a strong positive relationship to soil temperature in both ambient- and elevated-CO_2 plots. The increase in soil CO_2 efflux seen in this study is comparable with the increase of 178 g C m^{-2} reported by Butnor et al. (2003), who used the ACES over a 220-d period in a 17-yr-old loblolly pinestand; it is also consistent with other reports in the literature (e.g., Zak et al., 2000).

Despite increases in CO_2 efflux from soil, alterations in residue quality, and any changes in decompositional processes, greater biomass inputs due to growth in elevated atmospheric CO_2 remain an overriding factor impacting potential C storage in terrestrial systems. However, the capacity of terrestrial systems to store C in an elevated-CO_2 environment, particularly in soil, requires long-term evaluation of C inputs and losses.
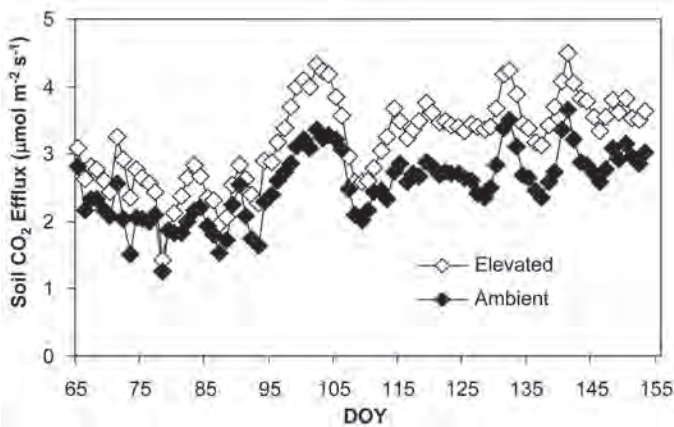
Fig. 15–13. Daily average soil CO$_2$ efflux (μmol CO$_2$ m^{-2} s^{-1}) for ambient (365 μmol mol^{-1}) and elevated (720 μmol mol^{-1}) CO$_2$ plots containing a model regenerating longleaf pine community.

Soil Carbon

Agricultural experiments comparing effects of management practices (e.g., crop rotations, manure inputs, conventional vs. conservation-tillage systems, etc.) on soil physicochemical properties, such as soil C, are generally evaluated after long periods (e.g., decades) of management (Reeves, 1997; Dick and Durkalski, 1998; Dick et al., 1998; Lal et al., 1998; Potter et al., 1999; West and Marland, 2002; West and Post, 2002). However, to date, very few elevated-CO$_2$ experiments have been conducted under consistent conditions for extended periods of time.

In the sorghum–soybean cropping system comparison, carbon isotopic techniques (δ^{13}C) were used to track the input of new C into the soil system following two growing seasons under elevated or ambient atmospheric CO$_2$ treatments (Torbert et al., 1997). At the end of 2 yr, shifts in δ^{13}C content of soil organic matter C were observed to a depth of 30 cm; however, the effects of elevated atmospheric CO$_2$ on changes in soil C dynamics were crop species dependent. New soil C was greater for sorghum under elevated CO$_2$ (162 and 29 g m^{-2} for elevated and ambient CO$_2$, respectively). With grain sorghum, the high C/N ratio led to slower microbial decomposition, resulting in increased new soil C and an overall increase in total soil C. In comparison, with soybean the new C in soil organic matter was less for elevated CO$_2$ (120 and 291 g m^{-2} for elevated and ambient CO$_2$, respectively). The low C/N ratio of soybean residues promoted microbial decomposition of new biomass inputs. This is consistent with the priming effect proposed by Lamborg et al. (1983). However, the increased decomposition of new C inputs under elevated CO$_2$ did not lead to a reduction in total soil C; instead, total soil C was higher under elevated CO$_2$ due to a reduction in decomposition of old C.

The differences observed between species (soybean and sorghum) for plant decomposition mechanisms are likely driven by N availability in the residues of the two species. Green et al. (1995) reported that additions of NO$_3^-$ following corn production promoted corn residue decomposition but suppressed C mineralization from native soil organic matter. Differences in N availability between the two

plant species in this study could result in the same type of preferential decomposition as observed in their field study. Regardless of differences in the effects of N on decomposition, data from this study suggest that elevated CO_2 may result in increased storage of C in soil in both systems over the long term.

At the end (5 yr) of the sorghum–soybean cropping system study, total soil C content was increased under CO_2–enriched conditions (Fig. 15–14) for both sorghum and soybean (16 and 29%, respectively) (Prior et al., 2004a). Further, aggregate stability was greater in both systems under elevated CO_2; there was also a trend for a system by CO_2 interaction, suggesting more of a CO_2–induced increase in aggregate stability for soybean (Fig. 15–14). Aggregate stability can affect soil C storage, as C within soil aggregates is physically protected from decomposition (Schlesinger, 1991).

We evaluated changes in soil C concentration following 4 yr (two cropping cycles) within a long-term crop management study (Prior et al., 2005). Across both cropping cycles, elevated CO_2 increased cumulative residue production by ~30% regardless of management practice. Use of conservation practices led to an increase in cumulative residue production of ~90%. Increases in cumulative inputs resulted in changes in soil C concentration (Fig. 15–15). Both elevated CO_2 and conservation management resulted in increased soil C concentration, particularly in the surface increment (0–5 cm). Further, a $CO_2 \times$ management interaction was noted; elevated CO_2 resulted in a dramatic increase in soil C concentration (44%) compared to ambient CO_2 in the conservation management treatment. The effect of elevated CO_2 was also higher in the conventional treatment, but this was not statistically significant. The effects of CO_2 and management were significant for other depth increments, but these differences were not as dramatic as observed at the top depth. Changes in soil N concentration followed a similar pattern as observed with soil C concentration over the depth increments evaluated. These results suggest that, with conservation management in an elevated-CO_2 environment, greater residue amounts increased soil C storage. A further evaluation of soil C, as well as other soil physicochemical properties, will occur following 10 yr of treatment (five cropping cycles).

An incubation study using soil from the model regenerating longleaf pine–wiregrass community experiment was conducted following 3 yr of exposure to elevated CO_2 (Torbert et al., 2004). This soil was not amended with plant residues and reflected only natural inputs during the 3-yr period. While soil C concentration was slightly increased by elevated atmospheric CO_2, differences were generally not significant; soil N concentration was also unaffected by CO_2 treatment. The large increase in plant litter observed in this study (Runion et al., 2006) might indicate that soil C could have increased further had the experiment run for more than 3 yr. The fact that C mineralization and C turnover (C mineralization and total C) were both reduced for soil from elevated-CO_2 plots suggests an additional potential for soil C sequestration.

A recent study (Allen et al., 2006) using bahiagrass grown in field soil within temperature-gradient greenhouses found only a slight (nonsignificant) increase in soil C due to elevated atmospheric CO_2 following 6 yr of exposure despite significantly higher biomass production. While changes in soil C have not yet been assessed within the recently initiated bahiagrass pasture study, which will compare not only the impact of atmospheric CO_2 level but also the effects of N additions (unimproved vs. managed pasture systems), soil C will be assessed
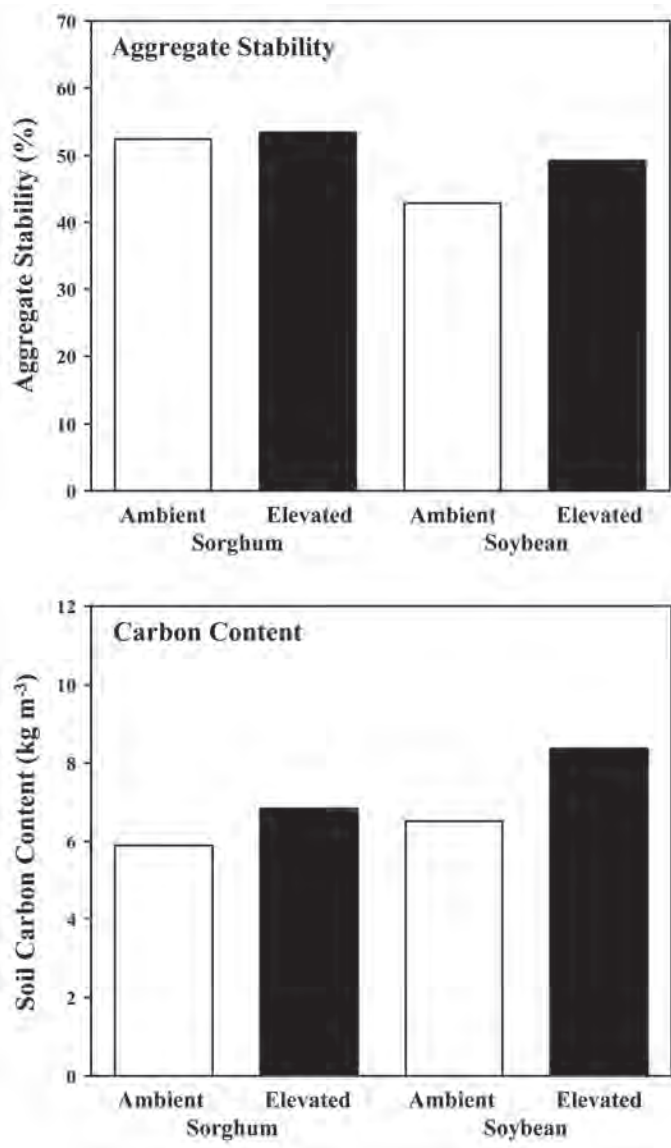
Fig. 15–14. Effect of atmospheric CO$_2$ concentration (ambient or elevated) on soil C content (kg m^{-3}) and soil aggregate stability (%) in sorghum or soybean cropping systems (*n* = 3). (Data from Prior et al., 2004a.)

following 5 and 10 yr of treatment. It should be noted that aboveground biomass is removed periodically within these studies to simulate foraging systems. Therefore, only belowground biomass is available to contribute to soil C sequestration, which will likely be lower than in other terrestrial plant systems.
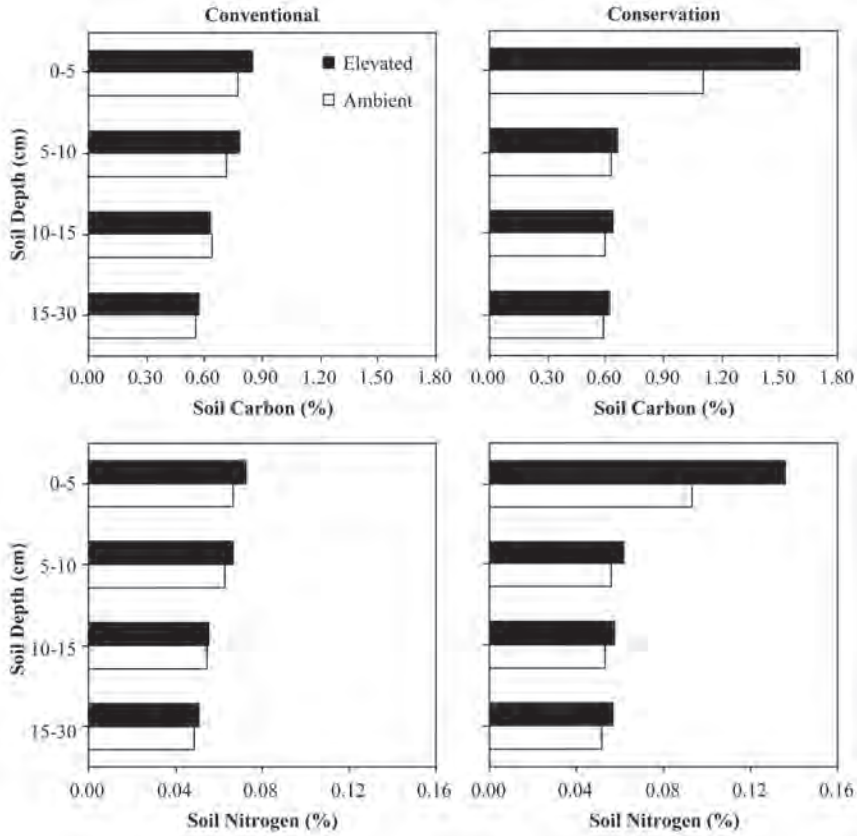
Fig. 15–15. Soil C and N concentrations (%) at various depth increments as affected by atmospheric CO_2 level (ambient and elevated) and management system (conventional and conservation) after two complete cropping cycles (4 yr). (Data from Prior et al., 2005.)

Conclusions

In today's world, it is important to enhance soil C sequestration. Using plants to extract C from the atmosphere and store it in soils represents a great opportunity to help mitigate potential climate change (Follett, 1993). Increasing soil C also has the potential to improve soil quality. Increased soil C has important positive effects on soil physical properties such as hydraulic conductivity, bulk density, porosity, aggregate stability, water retention, and rainfall infiltration. These positive effects on the soil physical conditions could also lead to a positive feedback to plant productivity. However, since soil C sequestration is a slow process, long-term studies are needed to assess the effects of various treatments (e.g., cropping sequence and tillage operations) on the potential of terrestrial ecosystems to accumulate C.

Long-term studies are also needed to assess the effects of elevated atmospheric CO_2, alone or in combination with ecosystem management options, on soil C sequestration. It has been shown that elevated CO_2 will increase biomass

production in most plant systems; this will lead to greater inputs of C to the soil. Elevated CO_2 also has the potential to alter the quality of these inputs, as well as decompositional processes; all of these factors will interact to determine the quantity of plant C entering the soil system. Within this chapter, we have shown that both plant species and N cycling within plant–soil systems are critical factors controlling C storage in terrestrial systems.

Given the CO_2–induced increases in biomass observed within terrestrial ecosystems of the southeastern United States (crops, forests, and pastures), there is little doubt that these systems have a potential for increased soil C storage. A major research objective continues to be to increase understanding of how best to manage these systems to maximize soil C sequestration, while also providing food and fiber to a growing population.

Acknowledgments

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