Elevated Carbon Dioxide in the Atmosphere

What Might It Mean for Loblolly Pine Plantation Forestry?

Research with loblolly pine suggests that projected increases in atmospheric CO_2 concentration will accelerate early growth and could result in shorter rotation length, reduced time until first commercial thinning, higher optimal planting density, and possibly higher maximum stocking level in managed stands. We discuss some of the physiological processes and stand dynamics that underlie these changes, as well as silvicultural strategies that may serve to ensure sustainability of intensively managed forest systems in the face of increasing CO_2 and possible climate change.

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To achieve long-term management goals, foresters need to account for subtle variations in the environment. The forests of the last two centuries have grown under steadily increasing concentrations of atmospheric carbon dioxide (CO_2) attributable to the combustion of fossil fuel reserves and other human activities. Although atmospheric CO_2 concentrations have fluctuated in the geologic past, the rate of increase we are experiencing today is unprecedented. Present-day concentrations average 365 parts per million (ppm), an increase of 35 percent over pre–Industrial Revolution levels of 270 ppm. By 2050, concentrations are expected to equal or exceed 550 ppm—an additional increase of at least 50 percent (Wigety al. 1'996). Because of the rapid increase in atmospheric CO_2 and the fundamental importance of CO_2 to all photosynthesizing plants, the implications for forestry are potentially profound.

Although public attention has focused on the potential effects of increased CO_2 on plant life in forests with minimal or no management, litde has been written about possible impacts on managed forest ecosystems. The distinction is important if forest manages, in the course of working to sustain forest productivity, can use silvicultural manipulations to harness the benefits and mitigate the problems associated with atmospheric CO_2 increases. Among managed forest systems, loblolly pine plantations deserve special attention because of our nation's increasingly heavy reliance on intensive management of this species, and in fact, the effects of CO_2 on loblolly pine have been well studied. The ideas discussed here may be applicable to other managed forest ecosystems as well.

Research with Loblolly Pine

Research has shown that loblolly pine grows faster with increasing CO_2 concentrations, largely through the enhancement of photosynthesis (Mickler and Fox 1998; Saxe et al. 1998), except under conditions of extreme nitrogen deficiency (Johnson et al. 1998). Criticisms of some of the research include the short duration of the studies compared with the length of a rotation, use of seedlings as experimental material, and artificial growing conditions (growth chambers, small pot size, artificial soil mixtures). Research models are summarized in *table 1*. Two obvious and practical questions need to be answered:

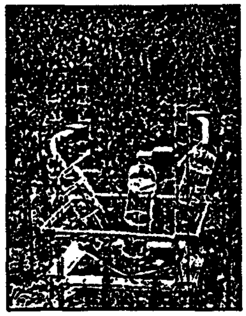
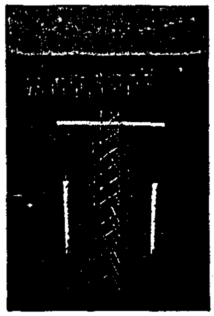
- Can we predict the response of managed loblolly pine forests to elevated CO_2?
- Will stand management strategies need to be adapted to a high-CO_2 world?

After more than 20 years of research in thii area and improvements in experimental methodologies, several common threads have emerged, and unifying theories explaining possible. impacts of elevated CO_2 on forest management may now be discussed.

Physiological Response

Under CO_2 concentrations within predicted future ranges, photosyn-

Table 1. Comparison of experimental research models for elevated CO_2 effects.

	Controlled environment	Open-top chamber	Branch chamber	Free-air CO_2 enrichment
	 John W. Groninger	 Rod Kindlund	 Tim Albaugh	 David S. Ellsworth
Pros	Repeatable control of all environmental conditions, large potential sample sizes and treatments, replication costs are intermediite.	Particularly useful for seedlings and saplings but trees can also be used, soil conditions are natural, costs are intermediate.	Permits work on mature trees, relatively low costs allow large sample sizes.	Most natural conditions, full stands are exposed, entire ecosystem responses can be evaluated.
Cons	Restricted to seedling stage, potential pot-binding effects, difficult to simulate true field conditions.	Fans create unnatural turbulence, ambient conditions difficult to maintain as trees get larger.	Fans create unnatural turbulence, only part of tree is treated, eliminating potentially important feedback effects	Very high costs discourage large sample sizes.
Examples	Lewis et al. 1994, Groninger et al. 1995 and 1996, Will and Teskey 1997.	Burdick 1996, Tissue et al. 1996 and 1997, Fetcher et al. 1988.	Liu and Teskey 1995, Teskey et al. 1995 and 1997, Murthy et at. 1996 and 1997.	Ellsworth et al. 1995, Hendrey et al. 199%

thetic rates initially accelerate through two primary mechanisms: greater availability of CO_2 and greater photosynthetic efficiency. Because forest tree photosynthesis and thus growth are limited by the availability of CO_2, increasing atmospheric CO_2 essentially behaves as a fertilizer, perhaps analogous to the effect of applying nitrogen fertilizer to a nitrogen-deficient site. Photosynthetic efficiency is increased because a higher concentration of CO_2 in the air decreases the antagonistic effects of oxygen on CO_2 uptake by rubisco, the plant enzyme primarily responsible for capturing CO_2 from the atmosphere for producing carbohydrate building blocks for growth. In seedlii and mature trees, increased photosynthetic rates have translated into increased growth shortly after CO_2 concentrations were elevated and kept high for as long as four years (*fig. 1, p. 6; see also* Tissue et al. 1997). How long these initial growth-enhancing effects of elevated CO_2 *are* sustained, *however, has* not been determined.

The increase in photosynthesis and gmwth under elevated CO_2 sometimes decreases in magnitude as other essential resources are depleted—a phenomenon known as photosynthetic acclimation (Gunderson and Wullschleger 1994). Early misinterpretation of this phenomenon led to speculation that with increases in atmospheric CO_2, acclimation would lead to eventual decreases in tree biomass production. Although acclimation brings lower photosynthetic rates than those initially found under elevated CO_2, there is no indication that total tree photosynthetic production *or* net tree growth is lowered to rates observed with present-day CO_2 concentrations (Saxe et al. 1998). Rather, shii of nitrogen away from rubisco that may occur with acclimation would result in more efficient nitrogen use and allow more of the tree's resources to be expended on producing biomass instead of acquiring nitrogen, thereby contributing to more rapid tree growth.

In greenhouse and growth chamber studies, acclimation has been attributed to pot binding or nutrient and water limitations (Thomas and Strain 1991; Tiiue et al. 1993; Will and Teskey 1997). In forests growing under present-day CO_2 concentrations, natural reductions in photosynthetic and grow& rates are observed as stands reach carrying capacity, apparently due at least in part to reductions in soil resource availability (Murty et al. 1996). Therefore, rather than being a direct response to growth in an elevated CO_2 environment, it appears that acclimation is more likely a consequence of accelerated resource depletion by faster-growing, and therefore larger, trees. Because elevated CO_2 increases the growth rate of trees and accelerates stand development, the onset of photosynthetic and growth reductions associated with aging or crowding is also hastened.

This phenomenon should in no way be considered a detriment to land managers concerned with timber production: forest stands will simply reach their product size classes sooner.

Although the effect of elevated CO_2 on photosynthesis of individual leaves exposed to abundant light has been well studied, the effect on light-liited foliage is less known. Of Particular interest is how CO_2 affects crown morphology, light distribution, and photosynthetic rates in the lower canopy. These are important considerations because total carbon gain (i.e., productivity) is a function of total canopy photosynthesis. Canopy photosynthesis depends on canopy structure (e.g., total leaf area index, distribution of leaf area, and leaf morphology), the amount and distribution of nitrogen, and the resulting availability of light within the crown. Loblolly pine canopies are typically sparse and have a relatively low projected leaf area index-3 to 5 for closed canopies (Vose et al. 1994)—allowing light sufficient to maintain positive photosynthetic rates to permeate the canopy. Despite the relatively deep penetration of light, leaf morphology (e.g., specific leaf area), foliar nitrogen concentration, and leaf physiology are known to vary with crown position (Porte and Loustau 1998; Ellsworth unpubl. data; Maier unpubl. data).

All those factors are Potentially affected by elevated CO_2. Recent work with loblolly pine shows that maximum rates of photosynthesis increase throughout the crown because, of elevated CO_2 (Maier unpubl. data). Exposure to elevated CO_2 lowers dark respiration rate and light compensation *point* of foliage regardless of crown position, indicating possible benefits in photosynthesis for shaded foliage. In addition, leaf area and shoot extension increase, and foliar density (leaf area per 'unit stem length) decreases (Kress and Johnsen, unpubl. data). These changes in branch structure, combined with the potential for lower light compensation points and greater foliar retention, may result in

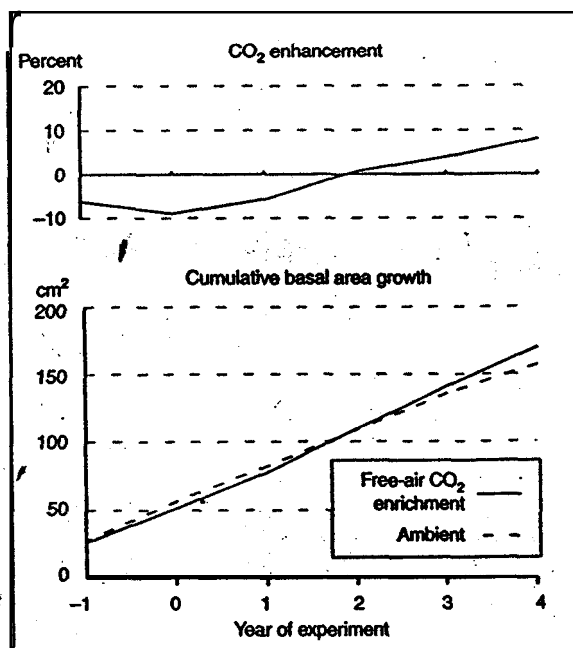


Figure 1. Cumulative basai area growth in individuai dominant iobioiiy pine trees growing in a singie free-air CO_2 enrichment plot under elevated CO, and in nearby ambient-grown trees from two different plots in the same stand at Duke Forest, North Caroiina.The results are from four summer seasons of CO, enrichment to 550 parts per million. Year I corresponds to the first growing season of elevated-CO_2 exposure for trees in the plot, when trees were 12 years old. Enhancement is the ratio of cumulative basai area growth of the elevated-C& trees to growth of ambient trees. Data are from increment cores for 32 select' dominant&es that were 14 cm DBH at the start of the study. Methodology and initial data are in Ellsworth et al. (I 995); remaining data are unpublished.

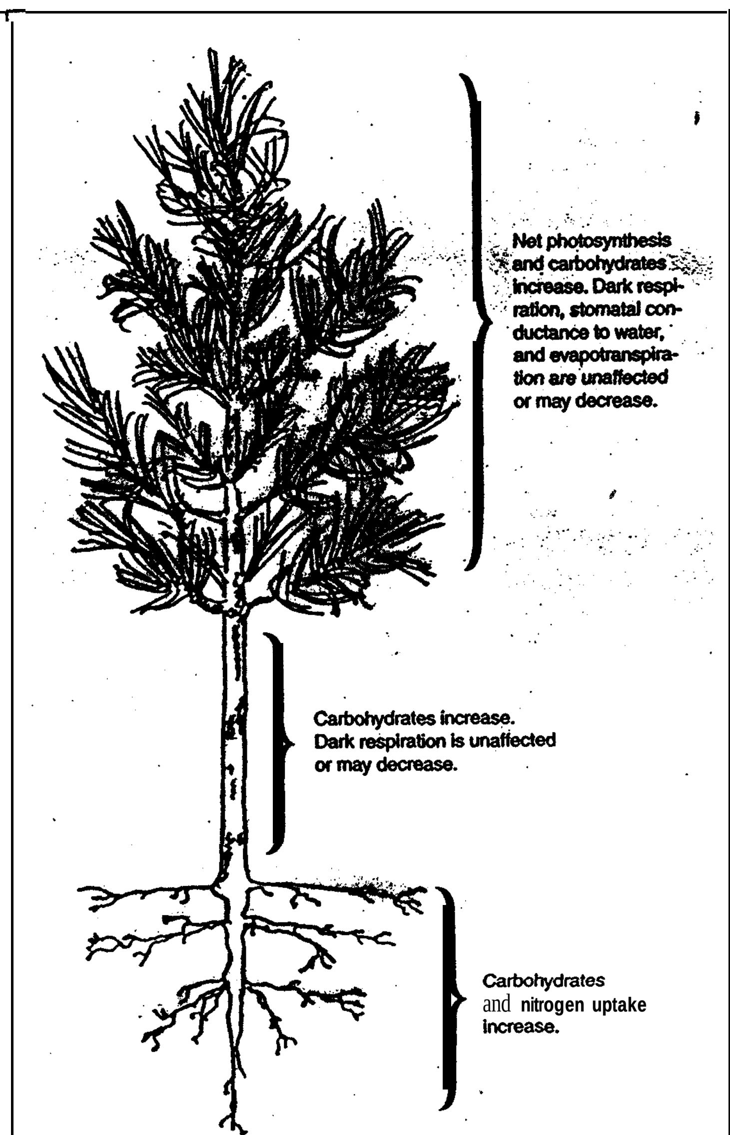


Figure 2. Summary of principal processes in trees, loblolly pine in particular, exposed year-long to elevated CO_2. The effects are based on published studies for seedlings and mature trees (see references in Mickier and Fox 1998 and Saxe et al. 1998).

deeper crowns and more complete interception of solar radiation.

Often, an increase in resource availability that enhances tree growth, such as water and nutrients, also decreases the growth of roots relative to aboveground biomass. However, most seedling studies indicate that elevated CO_2 either does not change or increases dry matter partitioning to roots. Thus, elevated CO_2 may or may not result in trees that can better withstand extreme drought and acquire nutrients for a given amount of aboveground biomass. A 30-year summer drought had similar effects on water relations of elevated CO_2 trees compared with those in ambient CO_2 in a study involving free-air CO_2 enrichment (FACE) on a midrotation loblolly pine stand on the North Carolina piedmont (Ellsworth 1999).

The effects of elevated CO_2 on physiological processes are summarized in *figure* 2.

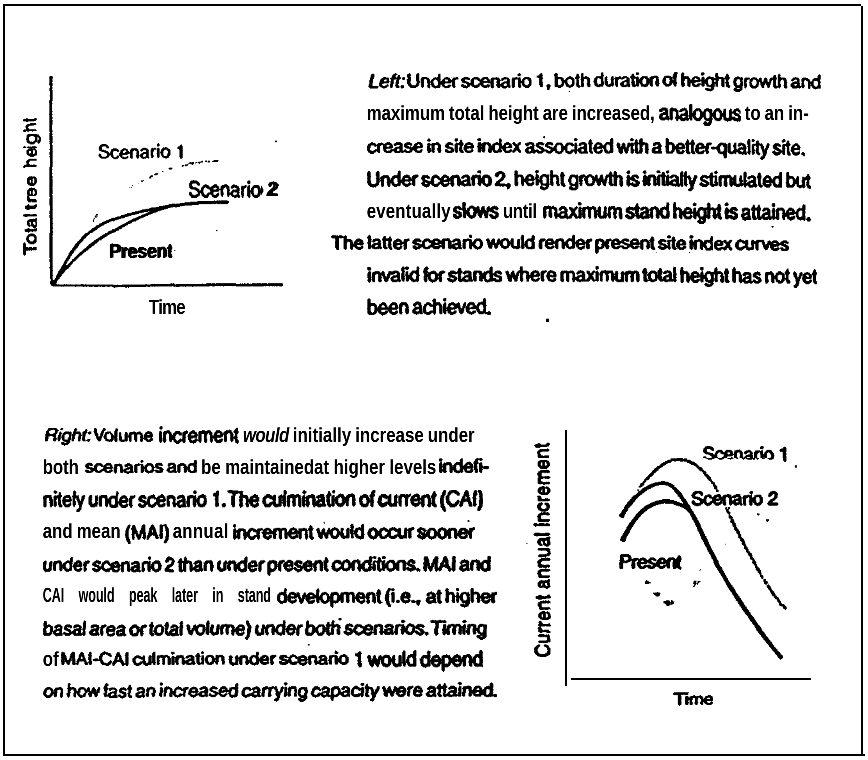


figure 3. Two scenarios for loblolly plantation growth dynamics under elevated CO_2 for a hypothetical site where no other management or environmental changes have taken place. Total height growth and height growth rate are reflected in site index curves.

Stand Productivity

At the very least, increasing atmospheric CO_2 concentrations will accelerate early stand growth and dynamics. This phenomenon has been observed in seedlings and seedling stands grown under elevated CO_2 since stand initiation (Groninger et al. 1995, 1996; Burdick 1996; Tissue et al. 1996). Branches of trees grown under present-day CO_2 concentrations, then exposed to projected CO_2 conditions, demonstrated increased growth and photosynthetic rates (Teskey 1995; Kress and Johnsen, unpubl. data). Increased efficiency in the use of water and nitrogen may translate into production of more wood fiber before net growth slows or stops as these resources are depleted. The most critical remaining questions about forest production are what determines the actual duration of this accelerated growth, and what is the long-term significance of increased efficiency in nitrogen use. Given what we now know about the direct impact of elevated CO_2 on stand development, two scenarios appear plausible *(fig. 3):*

Scenario I. Tree growth will occur at a faster rate and continue beyond present-day carrying capacity, thereby increasing achievable total stand volume.

Scenario 2. Growth will occur at a faster rate but carrying capacity will not change. Growth rates will eventually slow as site resources are depleted until the stand reaches present-day carrying capacity, resulting in accelerated culmination of growth but little or no net increase in total volume.

Researchers will not be able to determine which scenario better describes the growth response of forest ecosystems to elevated CO_2 without at least a decade of observations in a variety of management situations. In an uncontrolled study in Europe, *Quercus ilex* stand development was accelerated by high CO_2 concentrations from natural CO_2 springs (Hättenschwiler et al. 1997). However, this growth enhancement declined in a manner consistent with scenario 2. Whether silvicultural treatments could have altered the results is not known.

In both scenarios, annual increment initially increases, as has been observed in the free-air CO_2 enrichment study in North Carolina, Scenario 2 may also necessitate revising site index equations to reflect an initially steeper growth curve. Maintaining higher productivity levels and capitalizing on potentially higher site-carrying capacity will likely mean providing additional resources through silvicultural treatments. However, because the fundamental resources that make loblolly pine grow will not change, the relative productivity of sites and site selection criteria will be unaffected. For practical purposes, short- and long-term growth increases associated with scenario 1 are perhaps analogous to application of phosphorus to a severely P-deficient site. The short-term gain associated with scenario 2 might be likened to early control of aggressive herbaceous vegetation.

Faster growth raises the possibility that sites with insufficient moisture may become commercially viable as CO_2 concentrations increase. This phenomenon might be observable most readily near the western edge of the range in Oklahoma and Texas and on dry soils throughout the current natural and naturalized range of loblolly pine. A change in precipitation

Management

Likely changes in loblolly pine plantation management in response to atmospheric CO2 increases include the following.

- **Shorter rotations.**
- **Reduced time until first commercial thinning and subsequent thinnings.**
- **increased optimal planting density.**
- **Increased need for pruning to maintain current product quality standards.**
- **Increased need for site nutrition management.**
- **Similar or reduced weed control intensity.**
- **Increased wildfire intensity.**

patterns could alter or negate the positive effects of increased CO_2 on commercial range or site expansion.

Northward extension of the ranges of tree species has been a widely suggested response to increases in mean temperature induced by elevated CO_2 (Pastor and Post 1988). Although warmer winters might suggest a northward extension of the commercial range of loblolly pine, the effects of elevated CO;? and climate changes on winter hardening of leaf and bud tissues in this species are not known. The recent extension 6f the commercial range of loblolly pine into Pennsylvania might indicate a favorable winter hardiness response to increasing CO_2 concentrations or simply be attributable to several consecutive years of Favorable winters or the selection of appropriate genotypes.

Silvicultural Strategies

With elevated CO_2, slower growth rates may follow accelerated early stand growth if limitations are encountered sooner than under present conditions. Intensively managed stands-where resource needs are well understood and supplied as needed—will therefore be best suited to take advantage of *a* high-CO_2 world. Unmanaged stands may still grow faster but not to the same extent as those under intensive management. How can managers take advantage of accelerated early stand growth?

Stocking. In stands where incremental harvesting is planned, accelerated growth may shorten the time before first thinning and between subsequent thinnings or final harvest. However, if denser canopies were sustainable, elevated CO_2 might permit acceptable growth rates to be maintained at higher stand densities., If so, higher stocking levels could be maintained before &inning or harvest becomes necessary. Higher planting densities may also be considered under this scenario. Where product quality is a concern, pruning may become an increasingly valuable tool to compensate for delayed self-pruning in more light-efficient lower branches.

Fertilization. Rapid growth associated with elevated CO_2 may accelerate deficiencies of some mineral nutrients while potentially decreasing optimal application rates of others (Lewis et al. 1994). For example, although more fiber may be produced per unit N taken up, for other nutrients, where efficiency per unit fiber produced is unchanged, more fertilizer applications may be needed. This would compensate for removal of nutrients due to frequent or high-volume harvests. Further, higher growth rates will tie up more nutrients in standing biomass and litter. This will increase the need for fertilization even if harvesting intensity does-not change. Researchers evaluating the long-term sustainability of pine plantation management should take into account the impacts of CO_2 concentration on nutrient cycling.

Weed control. Early research indicated that some species showed *a* stronger growth response to CO_2 enhancement than others, raising the possibility that changes in competitive fitness will change competitive dynamics and increase the need for intensive vegetation control. However, studies of elevated CO_2 and common hardwood and herbaceous weed competitors have suggested that the intensity of competition with pines is not likely to increase (Gmninger et al. 1995; Burdick 1996; Gavazzi 1998). Rather, increases in the efficacy of herbicidal competition control, concomitant with increasing atmospheric CO_2 concentrations, are reducing the number and vigor of hardwoods where these species have been controlled repeatedly, suggesting that at least some forms of weed control may become less important in the future.

***Genetically* improved stock.** Most loblolly pine planting stock is now "genetically improved." Will improved stock maintain its growth advantage in a high-CO2 world? We are unaware of any research that has specifically. addressed this question for loblolly pine. However, studies with other species have generally indicated that fast-

Photorespiration

Perhaps the world's most important biochemical reaction is that catalyzed by ribulose bisphosphate carboxylase (rubisco). By some estimates, this enzyme is responsible for the fixation of some 200 billion tons of CO_2 every year as it catalyzes the first step of photosynthetic carbon reduction—photosynthesis (Taiz and Zeiger 1991).

Interestingly, rubisco fixes not only CO_2 (carboxylation) but also oxygen (O_2) (oxygenation). This oxygenation reaction is the first step in photorespiration. Both processes, carboxylation and oxygenation, occur simultaneously in plants; however, the oxygenation reactions (photorespiration) result in the loss of CO_2 from plant cells. In other words, there is a competition between CO_2 and O_2 for rubisco. At current levels of CO_2 and O_2, it is believed that 20 to 50 percent of fixed carbon is lost to plants as a result of photorespiration (Larcher 1995).

Researchers have demonstrated the antagonistic relationship between O_2 and CO_2 by experimentally manipulating the concentrations of these gases in the air. For example, lowering the O_2 level to 2 percent while leaving CO, concentrations unchanged Increased photosynthesis in loblolly pine by 16 to 30 percent (Samuelson and Teskey 1991). Similarly, photorespiration was decreased by raising CO_2 levels. As levels of CO, rise in the atmosphere, rates of photorespiration will fall, resulting in higher rates of net photosynthesis for trees.

growing provenances and families retain their advantages under elevated CO_2 (Johnsen and Major 1998). Similarly, results after four years in a large-scale genotype x nutrition trial clearly indicate that faster-growing loblolly pine families are taking better advantage of additional resources via fertilization (McKeand, pers. commun.), suggesting that they may also be able to capitalize on CO_2 fertilization. At the clonal level, genotypic variation in the magnitude of growth response to elevated CO_2 has been observed in black spruce (Major and Johnsen, unpubl. data); if it exists, similar variation might be used advantageously as loblolly pine clonal technology develops. However, for now it appears that genetically improved stock remains a valid investment under continuously changing atmospheric CO_2 concentrations (Saxe et al: 1998).

Furl loads. Projected increases in biomass production and increased branchiness (Tissue et al. 1996) could lead to increased fuel load after harvest if residue recovery is not intensified. This, combined with the trend away from prescribed fire in pine plantations in the Southeast, could increase the frequency and intensity of wildfire. In some cases, litter decomposition rates may be slowed because of a higher C:N ratio in dead foliage-a common finding in seedling studies-further increasing the combustibility of lobiolly pine stands, especially following harvest. However, early results from the free-air CO_2 enrichment study indicate no impact of elevated CO_2 on the C:N ratio of litter (Finzi et al. 1998).

Pest control. Changes in insect and disease cycles and outbreak severity could determine the relative cost or benefit of increasing CO_2 on managed loblolly pine productivity. Most research in this area has focused on examining the response of secondary compounds considered important in defense against insect attack. These studies indicate a large range in responses, from negative to benign to positive (see Saxe et al. 1998). Wilkens et al. (1998) presented a model describing susceptibility of loblolly pine to bark beetles as a function of resource availability. In their model, moderate stress *decreases bark beetle susceptibility* as photosynthesis is affected less than growth, allowing excess photosynchates to be shunted into defensive compounds. Under higher resource levels, their model predicts a higher percentage of photosynthate used for growth, and thus less available for defensive compounds. This is consistent with the observation that stands on productive sites are most vulnerable to bark beetle damage. In elevated CO_2 studies, photosynthetic rate usually increases much more than growth rate, suggesting that tree investment in defensive compounds may be increased.

Acclimation

Acclimation is a change in the capacity of physiological processes in response to alterations in physical environment resource availability. Short-term exposure of C_3 plants to CO_2 enrichment increases the rate of photosynthesis. However, long-term CO_2 enrichment sometimes decreases photosynthetic capacity such that plants exposed to enriched CO_2 concentrations have photosynthetic rates similar to plants exposed to ambient CO_2. In a few of the studies involving loblolly pine and CO_2, long-term CO_2 enrichment affected rubsico activity (Tissue et al. 1993; Lewis et al. 1994; Thomas et al. 1994; Lewis et al. 1996), rubisco content (Tissue et al. 1993; Lewis et al. 1996; Ellsworth et al. 1998), and chlorophyll content (Tissue et al. 1993; Lewis et al. 1996) such that photosynthetic capacity decreased slightly. However, in these studies and all others involving loblolly pine and CO_2, plants grown and measured in elevated CO_2 had significantly higher photosynthetic rates than plants grown and measured in ambient CO_2. Thi photosynthetic enhancement was maintained over a wide range of available water and nutrients for seedlings exposed to elevated CO_2 in growth chambers (Fetcher et al. 1988; Groninger et al. 1996; Will and Teskey 1997), field-grown trees exposed to elevated CO_2 using branch chambers (Liu and Teskey 1995; Teskey 1995; Murthy et al. 1996, 1997; Teskey 1997), trees exposed to elevated CO_2 in open-top chambers (Tissue et al. 1996, 1997; Lewis et al. 1996), and trees exposed to elevated CO_2 using FACE technology (Ellsworth et al. 1995, 1998). The only time the photosynthetic enhancement associated with CO_2 enrichment dii appeared was when nitrogen or phosphonts was manipulated to achieve extremely low foliar concentrations in pot-grown seedlings (Tissue et al. 1993; Lewis et al 1994; Thomas et al. 1994). Accelerated photosynthetic rates do not directly translate to increased growth. However, all else equal, accelerated rates of carbon gain increase the substrate available for growth.

Sustainability Issues

Observations of accelerated growth in the short term should in no way be interpreted as a rationale to decrease the current emphasis on implementing sustainable management practices. Although increased resilience may result from greater tree vigor, problems associated with a fixed level of resource depletion during stand development may appear or cause damage sooner than is currently recognized. The onset of micronutrient deficiencies or shoot blight (terminal leader mortality associated with very rapidly growing saplings in intensively managed plantations) may exemplify this phenomenon. In other cases, more rapid growth may shorten the response time to appropriate silvicultural treatments, magnifying the value of successful practices toward the sustainability of timber management.

Conclusions

It cannot be categorically stated that the productivity of managed Ioblolly pine forests will. benefit from all changes in environmental conditions.' However, the experimental evidence to date suggests that photosynthesis, tree carbohydrates, and stem growth will be enhanced over several growing seasons. The preponderance of forestry research suggests that coincidental trends of increasing CO_2 and more intensive forest management are complementary, at least in enhancing short-term forest productivity. Whether elevated CO_2 concentrations will interact with stresses associated with intensively managed loblolly pine, such as fusiform rust and pitch canker, is not known. Managers must be ready to capitalize on these conditions if the potential benefits of elevated CO_2 concentrations are to be realized.

Increasing atmospheric carbon dioxide concentrations will most likely occur in conjunction with cyclical or linear changes in such other climatic factors as temperature, precipitation patterns, and storm frequency and severity. Further, environmental changes may interact with insect and disease stresses, perhaps dampening or precluding growth gains discussed here, although for now such effects remain speculative. It is also possible that reduced specific gravity and lower fiber quality associated with rapid growth may dampen the merchantable gain associated with higher stand-level productivity. From an economic standpoint, forest managers may need to reinvest some or all of the profit associated with the growth increases to counteract potentially greater pressure from damaging agents.

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