

Offsetting changes in biomass allocation and photosynthesis in ponderosa pine (*Pinus ponderosa*) in response to climate change

EVAN H. DELUCIA,^{1,3} RAGAN M. CALLAWAY¹ and
WILLIAM H. SCHLESINGER²

¹ Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA

² Departments of Botany and Geology, Duke University, Durham, NC 27708, USA

³ Author to whom correspondence should be addressed

Received October 7, 1993

Summary

We examined the effect of climate on aboveground biomass allocation of ponderosa pine (*Pinus ponderosa*) by measuring trees in disjunct forest stands growing on the same substrate at high-elevation montane sites and low-elevation desert sites. Climatic differences between the sites were comparable to the difference between present and future climates of interior North America that is expected to result from a doubling of atmospheric CO₂ concentration. Relative to the montane populations, the desert populations allocated a greater proportion of biomass to sapwood (functional xylem) at the expense of foliage. The leaf/sapwood area ratio and percent of aboveground biomass in sapwood for trees of the same height were 0.201 m² cm⁻² and 58% for montane trees and 0.104 m² cm⁻² and 71% for desert trees.

In a phytotron experiment, increases in net photosynthesis and net assimilation rate for seedlings grown under future conditions of high CO₂ and temperature were offset by a decrease in leaf area ratio. As was observed for large trees at different elevations, increased temperatures caused an increase in biomass allocation to stem in the phytotron seedlings. Thus, CO₂- and temperature-driven shifts in biomass allocation negated the effect on growth of the CO₂-driven increase in carbon assimilation rate. Our data from the controlled growth chamber and field experiments suggest that future climate conditions, including elevated atmospheric CO₂, may not stimulate growth and productivity of ponderosa pine.

Keywords: elevated CO₂, global warming, growth, productivity.

Introduction

The ability of terrestrial ecosystems to sequester carbon is a key determinant of future increases in atmospheric CO₂ and thus of future climatic conditions. Forests provide the critical link in the transfer of carbon from atmospheric to terrestrial pools. Of ecosystems worldwide, forests contribute approximately 64% of total continental productivity and 43% of global productivity (calculated from Whittaker 1975); yet our understanding of the response of forests to future climatic conditions is limited (Eamus and Jarvis 1989). Two long-term studies of the response of trees to future atmospheric CO₂ concentrations have yielded conflicting results. In a study conducted with open-top field chambers and optimal nutrient and water availability, the growth of sour orange trees was more than doubled by a doubling of atmospheric CO₂ (Idso et al. 1991). In contrast, there was no increase in the carbon storage of yellow-poplar trees grown in native soil for three seasons under twice-ambient CO₂,

but with no supplemental water or fertilizer (Norby et al. 1992). Effects of increased temperatures were not investigated in either of these experiments.

General circulation models (GCMs) indicate that a doubling of atmospheric CO₂ during the next century could increase mean annual temperature by 1.5–4.5 °C and decrease precipitation in interior North America (Manabe and Wetherald 1987, Rind et al. 1990, Houghton et al. 1991). We have used unique open-forest communities growing on the same soil type, but at different elevations, on the east slope of the Sierra Nevada to examine the effect of climate on aboveground biomass allocation of ponderosa pine (*Pinus ponderosa* Laws.). The montane stands are in the matrix of the Sierra Nevada coniferous forest or high elevation pinyon–juniper woodland, and the disjunct desert stands are in the midst of Great Basin sagebrush vegetation. The desert stands are relicts of a more extensive conifer forest from the late Pleistocene (Billings 1950, DeLucia et al. 1988, Schlesinger et al. 1989). Climatic conditions at the montane and desert stands differ in temperature and precipitation to a degree comparable with the difference, at a particular location, predicted by the GCMs to arise over the next 50–100 years. It is important to recognize, however, that these stands have evolved under different climatic regimes without concurrent changes in atmospheric CO₂, and that these geographic differences in climate may not precisely mimic changes occurring over time. To examine ecotypic differences among elevational populations and potential interactions between elevated CO₂ and temperature, we also conducted a short-term experiment with seedlings under controlled growth conditions.

In addition to direct effects on photosynthetic and respiratory physiology, climate-driven shifts in biomass allocation will have a major impact on tree growth (Jarvis and Jarvis 1964, Poorter et al. 1990). We hypothesize that in warm, dry conditions, investment in stem and root growth (*heterotrophic tissues*) rather than foliage (*autotrophic tissue*) may decrease growth rate and compensate for CO₂-stimulation of photosynthesis. Thus under future climatic conditions, forest productivity may decrease and the ability of forest ecosystems to sequester atmospheric carbon may be reduced.

Methods

Field experiment

Aboveground biomass allocation was measured in three desert and two montane stands of trees growing on soils derived from hydrothermally altered andesite. The sites and their mean May air temperature and mean annual precipitation were: Alpine County, 950 mm, 11.5 °C; Virginia Mountains, 450 mm, 11.5 °C; Peavine Mountain, 242 mm, 13.1 °C; Desert Research Institute, 230 mm, 13.8 °C; and Ramsey Mine, 200 mm, 14.0 °C. Among sites, soils were not significantly different ($P > 0.05$) in pH, and soils and foliage did not differ among sites in N, P, or Ca⁺ content (Schlesinger et al. 1989). These sites are described further by DeLucia et al. (1988) and Schlesinger et al. (1989). To minimize destructive sampling, trees were com-

bined into a desert group (Peavine Mt., DRI, and Ramsey Mine; $n = 17$) and a montane group (Alpine County and Virginia Mountains; $n = 17$). Because the differences in climatic conditions at the montane and desert sites are comparable to the differences predicted by GCMs to arise at a single site in the next 100 years, we compared the desert and montane stands as a basis for assessing the impact of climate change on the productivity of ponderosa pine stands.

At each site, five to seven trees ranging in diameter from less than 6 to more than 50 cm (measured at a height of 1.4 m) were felled and divided into components: sapwood (functional xylem), heartwood (occluded xylem), bark, and leaves. Total bole height and basal diameter of all branches on each bole were measured on trees cut above the basal swell. Thin (3–5 cm) disk sections were cut at 1-m intervals from each bole and an additional section was cut at the base of the live crown. Disks were stained with bromocresol green to delineate sapwood from heartwood (Kutscha and Sachs 1962), and the cross-sectional areas of sapwood, heartwood and bark on each disk were measured. The area of each component in each section was used to calculate the volume per tissue per section and these values were summed to calculate the volume per bole. Specific gravity was determined in order to convert tissue volumes to masses. A similar approach was used to calculate the components of branches.

All leaves were removed from 5–6 branches per tree, dried at 60 °C, and weighed to the nearest gram. Fresh 5–10 g subsamples were collected from one randomly chosen branch from each of the 17 trees in each climate group and measured for one-sided leaf area with a Li-Cor LI 3100 area meter. Specific leaf areas (SLA) of the subsamples were used to convert leaf mass to leaf area.

Using logarithmic ($\log y = a + b \log x$) or linear regression models, the mass (or areas) of each component was regressed against tree diameter, measured at 1.4 m (DBH), and the slopes of the regression models for desert and montane populations were compared by covariance analysis (Steele and Torrie 1980). The individual regression equations are presented in Callaway et al. (1993a). These regression models were used to calculate the expected patterns of aboveground biomass allocation for desert and montane trees of the same height or diameter.

Phytotron experiment

Seeds were collected from four isolated populations of ponderosa pine growing along an elevation-related water and temperature gradient (two desert and two montane populations) on soils derived from hydrothermally altered andesite, near Reno, Nevada. The seed collection sites were Alpine County, Alum Creek, Peavine Mountain, and Ramsey Mine, as described in DeLucia et al. (1988) and Schlesinger et al. (1989).

Ponderosa pine seedlings were grown in a 2×2 factorial design ($\text{CO}_2 \times \text{temperature}$), in 1.8-liter PVC tubes (35-cm deep). Initially, seedlings were grown for 30 days in a greenhouse. They were then separated into four groups (32 seedlings per population per treatment), moved into four growth chambers, and grown for 30 days before the first harvest. The remaining plants were harvested after an additional 30

days. Within each treatment, seedlings were ranked by size and placed in 16 pairs. One of each pair was taken at each harvest.

The treatment conditions were: low CO₂/low temperature (350 μl l⁻¹ and 25/15 °C), low CO₂/high temperature (30/15 °C), high CO₂/low temperature (700 μl l⁻¹), and high CO₂/high temperature, the difference between the first and the last combination representing the difference between present conditions at a particular location and anticipated conditions at the same location following an increase in atmospheric CO₂ and temperature. Irradiance in the growth chambers was 1000 μmol m⁻² s⁻¹ (PAR) measured at mid-shoot height. Environmental conditions in the chambers were measured continuously. Pots were watered twice daily with a dilute nutrient solution (Downs and Hellmers 1979).

Growth analysis variables were calculated from the change in biomass and leaf area between harvests (Hunt 1990). Above- and belowground CO₂ exchange rates were measured with an infrared gas-analysis system (Callaway et al. 1993b). The attached intact shoot or the entire pot (without the shoot) was enclosed in an assimilation chamber, and CO₂-exchange rates were measured under the growth environmental conditions. Shoot respiration was measured at night and root (pot) respiration was measured at day and at night.

Three-way analysis of variance was used to compare population, CO₂, and temperature effects on all dependent variables (shoot and root biomass, leaf area, gas-exchange, etc.), and two-way analysis of variance and Tukey's multiple range test were used to compare temperature and CO₂ effects on seedling characteristics after populations were combined within treatments (SYSTAT, Evanston, IL). Dependent variables were normally distributed and did not require transformation.

Results and discussion

The difference in temperature and humidity between the desert and montane sites caused a divergence between ponderosa pine populations in the relationship between leaf area and sapwood area (Figure 1). Leaf/sapwood area ratios, measured as the slopes of the regression lines, were 0.201 and 0.104 m² cm⁻² for montane and desert species, respectively. In an extremely moist forest of western Oregon, this ratio for ponderosa pine increases to 0.25 m² cm⁻² (Waring et al. 1982). Sapwood supplies water to support transpiration from foliage, and previous studies have shown a strong species-specific relationship between leaf and sapwood area (Waring and Schlesinger 1985). It is unclear whether temperature, humidity or site water balance is the dominant factor affecting aboveground biomass allocation in ponderosa pine at different elevations. Whitehead and Jarvis (1981) hypothesized that investment in sapwood should vary directly with increased transpirational demand and thus atmospheric vapor pressure deficit.

When allometric relationships were used to calculate the proportion of mass in different compartments, for a desert and a montane tree of the same height or diameter, we found that the desert tree invested considerably more dry matter in sapwood than the montane tree (Figure 2). The proportionate allocation on a volume

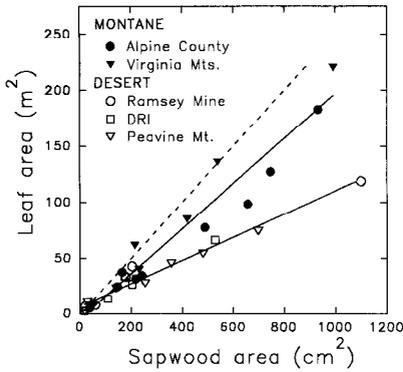


Figure 1. Leaf area (one-sided) per tree as a function of cross-sectional sapwood area measured at the base of the live crown (SA) for ponderosa pine in montane and desert climates. For montane trees: $LA = 3.839 + 0.201SA$, $r^2 = 0.94$; for desert trees: $LA = 6.646 + 0.104SA$, $r^2 = 0.96$. Slopes differed significantly ($P < 0.001$, ANOVA). The dashed line is for ponderosa pine growing in a more mesic climate, measured by Waring et al. (1982).

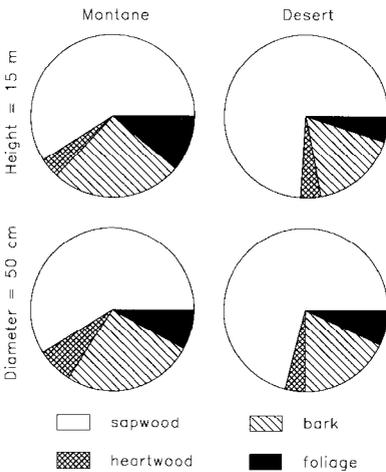


Figure 2. Aboveground biomass allocation calculated for a montane and desert ponderosa pine of equal height or equal diameter. Allocation patterns were calculated from site-specific regression equations relating aboveground dimensions to bole diameter at 1.4 m above the soil surface (equations from Callaway et al. 1993a). Montane trees were significantly taller than desert trees of comparable diameter. Total mass and diameter for montane and desert trees of the same height were 329 kg and 34 cm, and 1242 kg and 60 cm, respectively. For trees of the same diameter, total mass and height for montane and desert trees were 848 kg and 17.7 m, and 723 kg and 12.1 m, respectively. The percent sapwood for desert and montane trees of the same height was 74 and 59%, respectively, and 71 and 59%, respectively, for trees of the same diameter.

basis was similar to the allocation on a dry mass basis (data not shown). The relationships between leaf and sapwood area and between leaf and sapwood mass are functionally based—large sapwood area and volume facilitate water flux during episodes of rapid transpiration, provide water storage during drought, and may

provide protection from embolisms (Tyree and Dixon 1986). Sapwood, though primarily composed of dead tracheids, contains approximately 6% (v/v) living parenchyma cells (Panshin and De Zeeuw 1970, Ryan 1990). These cells contribute to carbohydrate storage in the bole of large trees, which supports respiration during extended drought (Waring and Running 1978). Growth rate, however, is directly proportional to biomass invested in foliage (Tilman 1988, Poorter et al. 1990). Thus the relatively low productivity of trees in warm, dry climates may be due to the temperature- and water stress-driven shifts in biomass allocation from foliage to sapwood as well as from above- to belowground growth.

In the phytotron experiment, differences in growth variables among populations of ponderosa pine were statistically significant ($P < 0.01$); however, there were no consistent differences between desert and montane populations. Root/shoot ratio, for example, was similar among seedlings from one of the desert and montane seed sources, yet seedlings from these sites were significantly different from the other montane and desert seedlings (data not shown). Seed sources were combined for further statistical analysis of temperature and CO₂ effects. A complete statistical analysis of population differences is presented in Callaway et al. (1993b).

Increased CO₂ concentration and temperature caused significant increases in seedling biomass at the first harvest (Table 1), and these differences were maintained to the second harvest. The high CO₂ and temperature treatments, therefore, had no long-term effect on relative growth rate (RGR; Table 1). The high CO₂/high temperature treatment stimulated growth only during the very early stages of the experiment, and once climate-driven allocation shifts occurred, plants in all treatments converged on the same growth trajectory.

For seedlings grown under controlled conditions, the direct effects of elevated CO₂ concentration and temperature on photosynthesis were offset by corresponding shifts in biomass allocation. Net assimilation rate (NAR) represents the 24-h integral of leaf photosynthesis minus the summation of root and shoot respiration (a small component of NAR is mineral accumulation), and leaf area ratio (LAR) represents the relative investment in leaf area per mass of the whole plant. Qualitatively, mean relative growth rate (RGR) is defined as the product of mean NAR and mean LAR (Hunt 1990). In the elevated CO₂ treatments, there was a shift in biomass allocation from leaves to roots and stems causing a significant decrease in LAR. Net photosynthesis was stimulated by CO₂ enrichment (Table 1). Elevated CO₂ concentration also decreased root respiration. Several recent reports have observed depressions in mitochondrial respiration in plants grown in elevated atmospheric CO₂ (Amthor et al. 1992, Wullschleger and Norby 1992). This response is not universal (Thomas et al. 1993) and the mechanisms for inhibition remain obscure. In response to CO₂ enrichment, increased photosynthesis and decreased root respiration together caused an almost significant increase in NAR ($P = 0.105$, $F = 2.65$). This increase was offset by the pronounced decrease in LAR, and, as a result, CO₂ enrichment had no effect on RGR of ponderosa pine seedlings grown under controlled conditions.

Recent studies with *Liriodendron tulipifera* and with an assemblage of tropical forest species suggest that allocation to root growth and fine-root turnover may

Table 1. The effect of temperature and atmospheric CO₂ concentration on growth and gas exchange of ponderosa pine seedlings. Plants were grown at low CO₂/low temperature (350 µl l⁻¹ and 25/15 °C; representing current climatic conditions); low CO₂/high temperature (30/15 °C); high CO₂/low temperature; and high CO₂/high temperature (700 µl l⁻¹; representing future climatic conditions). Mean values were compared with an ANOVA followed by a multiple range test, and values that were statistically different ($P < 0.05$) are designated by different superscripts. Significant treatment effects (C = CO₂; T = temperature; C × T = CO₂ × temperature interaction; $P < 0.05$; ns = not significant) are also indicated.

Measured characteristics	Low CO ₂ /low temp.	Low CO ₂ /high temp.	High CO ₂ /low temp.	High CO ₂ /high temp.	Significant treatment effects
<i>Seedling biomass (g)</i>					
1st Harvest	0.265a	0.265a	0.286a	0.343b	C, T, C × T
2nd Harvest	1.66a	1.70a	1.76a	2.15b	C, T, C × T
<i>Allocation (at 2nd harvest)</i>					
Root/shoot ratio	0.825a	0.795a	0.884b	0.878b	C
% Stem	5.32ac	6.03b	4.96a	5.53ab	C, T
% Leaf	49.78a	49.88a	48.50a	48.09a	C
<i>Growth analysis</i>					
RGR (g g ⁻¹ day ⁻¹)	0.052a	0.053a	0.052a	0.052a	ns
NAR (g m ⁻² day ⁻¹)	5.91a	5.83a	6.18a	6.48a	ns
LAR (m ² g ⁻¹)	0.0094a	0.0098a	0.0089a	0.0085a	C
<i>Gas exchange</i>					
Photosynthesis (mmol g ⁻¹ s ⁻¹) ¹	0.041a	0.037b	0.044a	0.040a	C, T
Shoot respiration (mmol g ⁻¹ s ⁻¹) ²	0.0035ac	0.0040b	0.0033a	0.0038bc	T
Root respiration, day (mmol g ⁻¹ s ⁻¹)	0.016ab	0.017a	0.011b	0.012bc	C
Root respiration, night (mmol g ⁻¹ s ⁻¹)	0.027a	0.026a	0.019b	0.018b	C

¹ Net CO₂ flux per mass of whole shoot.

² Whole-shoot respiration measured at night.

increase under elevated atmospheric CO₂ (Norby et al. 1992, Korner and Arnone III 1992). These shifts in allocation reduce growth and productivity, and because most belowground carbon is released back to the atmosphere by microbial respiration, CO₂ enrichment does not stimulate carbon storage in these systems. By means of field and growth-chamber experiments, we have demonstrated that CO₂- and temperature-driven shifts in biomass allocation may negate the positive effects of a stimulation of photosynthesis and a depression of respiration, and result in no net increase in growth of ponderosa pine under future increased CO₂ concentration and temperature conditions. These data support increasing evidence that future climate conditions, including elevated atmospheric CO₂, may decrease forest productivity.

Acknowledgments

The authors are grateful to Dr. Robert Nowak at the University of Nevada, Reno, for laboratory space and logistical support. We thank Darrin Moore, Will Pyle and Beth Thomas for technical assistance, and the Desert Research Institute, US Forest Service and Bureau of Land Management for permission to harvest trees. The thoughtful review of an earlier draft of this manuscript by Scott Heckathorn, Shawn Naidu, Eileen Carey, Michele Arntz and Hafiz Maherali was appreciated. This project was funded by a grant from USDA/NRI (91-37101-6724; Forest Biology), and an NSF grant to the Duke University

Phytotron (BSR 87-06429). The final revision of this manuscript was completed while EHD was supported by a Bullard Fellowship from Harvard University.

References

- Amthor, J.S., G.W. Koch and A.J. Bloom. 1992. CO₂ inhibits respiration in leaves of *Rumex crispus* L. *Plant Physiol.* 98:757–760.
- Billings, W.D. 1950. Vegetation and plant growth as affected by chemically altered rocks in the Great Basin. *Ecology* 31:62–74.
- Callaway, R.M., E.H. DeLucia and W.H. Schlesinger. 1993a. Aboveground biomass allocation of ponderosa pine under different climate regimes: an analog for response to climate change. *Ecology*. In press.
- Callaway, R.M., E.H. DeLucia and W.H. Schlesinger. 1993b. Compensatory responses of CO₂-exchange and biomass allocation and their effects on the relative growth rate of ponderosa pine in different CO₂ and temperature regimes. *Oecologia*. In press.
- DeLucia, E.H., W.H. Schlesinger and W.D. Billings. 1988. Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. *Ecology* 69:303–311.
- Downs, R.J. and H. Hellmers. 1978. Controlled climate and plant research. Academic Press, NY, 145 p.
- Eamus, D. and P.G. Jarvis. 1989. The direct effects of increase in the global atmospheric CO₂ concentration on natural and commercial temperate trees and forests. *Adv. Ecol. Res.* 19:1–55.
- Hunt, R. 1990. Basic growth analysis. Unwin Hyman, London, 248 p.
- Houghton, J.T., G.J. Jenkins and J.J. Ephraums. 1991. Climate change, the IPCC scientific assessment. Cambridge University Press, NY, 364 p.
- Idso, S.B., B.A. Kimball and S.G. Allen. 1991. CO₂ enrichment of sour orange trees: 2.5 years into a long-term experiment. *Plant Cell Environ.* 14:351–353.
- Jarvis, P.G. and M.S. Jarvis. 1964. Growth rates of woody plants. *Physiol. Plant.* 17:654–666.
- Korner, C. and J.A. Arnone III. 1992. Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science* 257:1672–1675.
- Kutscha, N.P. and I.B. Sachs. 1962. Color tests for differentiating heartwood and sapwood in certain softwood species. US Forestry Products Laboratory Report No. 2246, 15 p.
- Manabe, S. and R.T. Wetherald. 1987. Large-scale changes in soil wetness induced by an increase in atmospheric carbon dioxide. *J. Atmos. Sci.* 44:1211–1235.
- Norby, R.J., C.A. Gunderson, S.D. Wullschleger, E.G. O'Neil, and M.K. McCracken. 1992. Productivity and compensatory responses of yellow-poplar trees in elevated CO₂. *Nature* 357:322–324.
- Panshin, A.J. and C. De Zeeuw. 1970. Textbook of wood technology. Vol. 1. McGraw-Hill, NY, 223 p.
- Poorter, H., C. Remkes and H. Lambers. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.* 94:621–627.
- Rind, D., R. Goldberg, J. Hansen, C. Rosenzweig and R. Ruedy. 1990. Potential evapotranspiration and the likelihood of future drought. *J. Geophys. Res.* 95:9983–10004.
- Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Can. J. For Res.* 30:48–57.
- Schlesinger, W.H., E.H. DeLucia and W.D. Billings. 1989. Nutrient-use efficiency of woody plants on contrasting soils in the western Great Basin, Nevada. *Ecology* 70:105–113.
- Steele, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics—a biometrical approach. McGraw-Hill, NY, 633 p.
- Thomas, R.B., C.D. Reid, R. Ybema and B.R. Strain. 1993. Growth and maintenance components of leaf respiration of cotton grown in elevated carbon dioxide partial pressure. *Plant Cell Environ.* 16:539–546.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, NJ, 360 p.
- Tyree, M.T. and M.A. Dixon. 1986. Water stress induced cavitation and embolism in some woody plants. *Physiol. Plant.* 66:397–405.
- Waring, R.H. and S.W. Running. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant Cell Environ.* 1:131–140.

- Waring, R.H. and W.H. Schlesinger. 1985. Forest ecosystems—concepts and management. Academic Press, NY, 31 p.
- Waring, R.H., P.E. Schroeder and R. Oren. 1982. Application of the pipe model theory to predict canopy leaf area. *Can. J. For. Res.* 12:556–560.
- Whitehead, D. and P.G. Jarvis. 1981. Coniferous forests and plantations. *In* Water Deficits and Plant Growth, Vol. VI. Ed. T.T. Kozlowski. Academic Press, NY, pp 50–132.
- Whittaker, R.H. 1975. Communities and ecosystems. 2nd Edn. Macmillan Publishing Co., NY, 385 p.
- Wullschleger, S.D. and R.J. Norby. 1992. Respiratory cost of leaf growth and maintenance in white oak saplings exposed to atmospheric CO₂ enrichment. *Can. J. For. Res.* 22:1717–1721.

