J. For. 117(1):38–45
doi: 10.1093/jofore/fvy058
Published by Oxford University Press on behalf of the Society of American Foresters 2018.

silviculture

Increasing Atmospheric CO_2 Concentration Stand Development in Trembling Aspen Forests: Are Outdated Density Management Guidelines in Need of Revision for All Species?

Mark E. Kubiske, Christopher W. Woodall, and Christel C. Kern

The effect of rising atmospheric concentrations of carbon dioxide (CO_2) on tree size–density relations has not been thoroughly investigated despite such relations forming the basis of contemporary forest stand stocking metrics. As an initial exploration of the effects of varying CO_2 concentrations on size–density relations, we treated model stands of trembling aspen with increased concentration of CO_2 (560 ppm) for 11 years in northern Wisconsin and found compelling differences in stand development compared with those in ambient atmosphere. Pure and mixed trembling aspen forests grew faster in elevated atmospheric CO_2 and with developmental trajectories of self-thinning communities carrying more stand basal area at equivalent trees per hectare. Comparison of our experimental results with historical stand density data suggests forest developmental characteristics may have changed in response to historical increases in atmospheric CO_2; thus, current stocking guides could underestimate maximum stand carrying capacity. Although our results may be constrained to our study species in a controlled experiment, they still suggest that comprehensive reassessments of stand growth dynamics and size–density relations may be needed across suites of species and spatial extents because of global atmospheric CO_2 increases that have already occurred.

Keywords: aspen, carbon dioxide, stand density, management diagrams, global change

From preindustrial times, the concentration of carbon dioxide (CO_2) in the atmosphere has increased from 270 to >408 ppm (Figure 1) (NOAA 2018). The continuing increase in atmospheric CO_2 has been implicated for contributing to increasing global temperatures and altered climatic patterns (IPCC 2014). Thus, increased CO_2 may have indirect effects on forest dynamics (e.g., growth, mortality, and regeneration) via climatic changes. More important for forest ecosystems, however, are the direct effects of atmospheric CO_2 on forest growth and development, collectively referred to as CO_2 fertilization or enrichment (DeLucia et al. 1999; Ainsworth and Long 2005; Schimel et al. 2015; Miller et al. 2016). Under present conditions, photosynthesis rates for trees and most other forest plants are limited by the availability of atmospheric CO_2 (Norby et al. 2005). Thus, as atmospheric CO_2 increases, photosynthesis, tree growth rates, and ecosystem energy inputs also increase (Curtis and Wang 1998; Norby et al. 2005).

The fertilization effect of increasing CO_2 on plant growth has been well known for several decades (Curtis and Wang 1998; Norby et al. 2005), but those experiments were limited to only short-term (2–3 years) studies on individual plants. However, in the 1990s, researchers at Brookhaven National Laboratory developed free-air CO_2 enrichment (FACE) technology (Hendrey et al. 1999). A number of FACE experiments were established to study intact forest canopies and ecosystems in a CO_2-enriched atmosphere without the need for physical enclosures: loblolly pine (*Pinus taeda*) in North Carolina, sweetgum (*Liquidambar styaciflua*) in Tennessee, three

Received October 2, 2017; accepted October 9, 2018; published online December 3, 2018.

Affiliations: *Mark E. Kubiske (mkubiske@fs.fed.us), USDA Forest Service, Northern Research Station, Rhinelander, WI; Christopher W. Woodall (cwoodall@fs.fed.us), USDA Forest Service, Northern Research Station, Durham, NH; Christel C. Kern (cckern@fs.fed.us), USDA Forest Service, Northern Research Station, Rhinelander, WI.*

Acknowledgments: *We are grateful to Drs. Scott D. Roberts and Thomas J. Dean who provided helpful reviews on an earlier version of the manuscript. The Aspen FACE Experiment was funded by several grants from the US Department of Energy, Office of Science to Michigan Technological University, and by the USDA Forest Service, Northern Research Station. The present study was funded by the USDA Forest Service, Northern Research Station.*

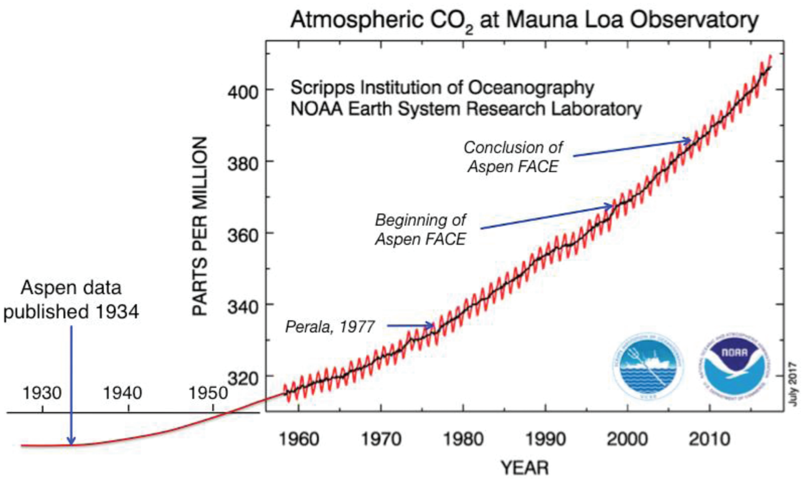

Figure 1. Atmospheric CO_2 concentrations measured at the Mauna Loa Observatory, Hawaii from 1958 to present showing buildup of atmospheric CO_2 (Keeling Curve Figure used with permission of Scripps Institution of Oceanography, doi.org/10.6075/J08W3BHW). The saw-tooth pattern reflects seasonal photosynthetic uptake of CO_2 in the Northern Hemisphere. The backward extrapolation to 1930 is approximated from Etheridge (1998). Reference to Perala (1977) shows publication date of currently used stocking models for Lake States trembling aspen forests using data first published by (Kittredge and Gevorkiantz (1929) and Brown and Gevorkiantz (1934). (cf. Table 1).

aspen (*Populus tremuloides*) communities in Wisconsin, and others around the world, as described by Karnosky et al. (2001). For the first time, it was possible to isolate the effect of CO_2 enrichment on long-term processes in intact, closed-canopy, forest ecosystems.

All three of the North American forest FACE experiments employed elevated CO_2 treatments of 550 ppm (the most conservative emission scenario for the 21st century as reported by the IPCC) so that results could be directly compared across experiments—over the span of those experiments, ambient CO_2 was 370–385 ppm (NOAA 2018). A synthesis of results from those experiments indicated increased biomass production by 23 ± 2 percent in elevated CO_2 across a wide range of site productivity (Norby et al. 2005). The elevated CO_2 treatments also affected reproductive fitness because seeds and fruiting bodies (such as cones) are very strong sinks for photosynthate (Zamski 1995). Compared with controls, paper birch (*Betula papyrifera*) had increased numbers of catkins and numbers of trees bearing flowers in elevated CO_2 (Darbah et al. 2008). In addition, the seeds had 17 percent greater mass, 110 percent greater germination rate, and a lower seedling mortality (Darbah et al. 2007). Similarly, loblolly pine trees in elevated CO_2 increased seed production by threefold (LaDeau and Clark 2001) with the seeds having 265 percent greater lipid content, which acts as both substrate and energy source for developing seedlings (Hussain et al. 2001). Although it is now known that increased CO_2 increases tree growth rate and fecundity, its potential effects on stand development, such as the rate at which stages of stand development progress, maximum potential density (e.g., maximum stand density index), and self-thinning, are not well understood.

The trajectory of self-thinning, i.e., tree mortality related to stand density, is a fundamental process for many silvicultural practices (Reineke 1933). Whether it is initial planting densities or midrotation thinning activities, quantification of self-thinning trajectories for individual stands helps with optimizing tradeoffs between stand productivity and the number of trees on site (i.e., stand density of live trees) (Drew and Flewelling 1979). Thinning is used to remove some proportion of a stand at a prescribed density in order to use trees that would otherwise be lost to density-related mortality (Long 1985, Oliver and Larson 1996). Field studies were conducted, particularly in the first half of the 20th century (e.g., Brown and Gevorkiantz 1934), to establish relations between the number of trees per acre and measures of tree size, such as quadratic mean diameter for the purpose of optimizing stand productivity (Nelson and Bennett 1965). From those data, stocking charts and density management diagrams were developed for most of the commercially important forest types in North America (e.g., Douglas-fir, Drew and Flewelling 1979) to assist managers in determining an optimum stand density for any given management objective (Figure 2). The creators of first-generation stocking charts generally assumed that site quality (e.g., soil type, climate, and atmospheric attributes) had no effect on size–density relations, and so no paradigms were offered for making stocking charts adaptable to changing environmental conditions (e.g., Reineke 1933, Long 1985). This particular aspect of size–density stocking charts was probably exacerbated by the necessary investment of labor for collection of stand size–density field data needed for stocking chart reformulations. Moreover, most of the earlier formulations were developed using temporary field plots that could not be revisited in later years (e.g., Kittredge and Gevorkiantz, 1929). More recent refinements of size–density metrics have included the merger of large-scale forest inventory datasets with tree functional traits (e.g., wood density, Woodall et al. 2005) and climatic information (Ducey et al. 2017; Andrews et al. 2018), which have demonstrated the sensitivity

Management and Policy Implications

Nearly every silvicultural practice is founded upon principles of stand development and size–density relations. However, in many situations, data used to develop currently employed stocking models are in excess of 80 years old, from a time when atmospheric CO_2 was 33 percent lower than the current concentration of >400 ppm. Our study's results suggest that contemporary application of older stocking guides may be under estimating stocking capacity and stand developmental trajectories, especially in light-limited systems as found in northern hardwood systems. A more thorough examination of stocking guides in the context of rising atmospheric CO_2 is recommended across a greater array of species and regional extents.

Table 1. Important forest types in the Upper Great Lakes region.

Forest type	Source	Original data
Spruce–fir (*Picea* spp., *Abies* spp.)	Solomon et al. 1987	1959–1974
Black spruce (*Picea mariana*)	Plonski 1960	NR
Jack pine (*Pinus banksiana*)	Benzie 1977a	Eyre and LeBarron 1944
Red pine (*Pinus resinosa*)	Benzie 1977b	Eyre and Zehngraff 1948
Eastern white pine (*Pinus strobus*)	Philbrook et al. 1973	Frothingham 1914
Northern white cedar (*Thuja occidentalis*)	Johnson 1977	Gevorkiantz and Duerr 1939
Red maple (*Acer rubrum*)	Stout and Nyland 1986	1927–1981
Maple–beech–birch*	Roach 1977	1928–?
Paper birch (*Betula papyrifera*)	Safford 1983	Marquis et al. 1969
Oak–hickory (*Quercus* spp., *Carya* spp.)	Roach and Gingrich 1962	NR
Black walnut (*Juglans nigra*)	Schlesinger and Funk 1977	1928–1930
Aspen (*Populus* spp.)	Perala 1977	Kittredge and Gevorkiantz 1929 Brown and Gevorkiantz 1934
Basswood (*Tilia americana*)	Tubbs 1977	NR
Elm–ash–cottonwood†	Myers and Buchman 1984	Putnam et al. 1960

Note: "Source" refers to the publication in which stand stocking models currently in use by the USFS FIA were referenced by Arner et al. (2001). "Original data" refers to dates or publications that the data were first collected or reported. In some cases, the original publication could not be located, and in other cases no mention was made as to the source of the data (NR).

* (*Acer* spp., *Fagus grandifolia*, *Betula* spp.)

† (*Ulmus* spp., *Fraxinus* spp., *Populus deltoides*)

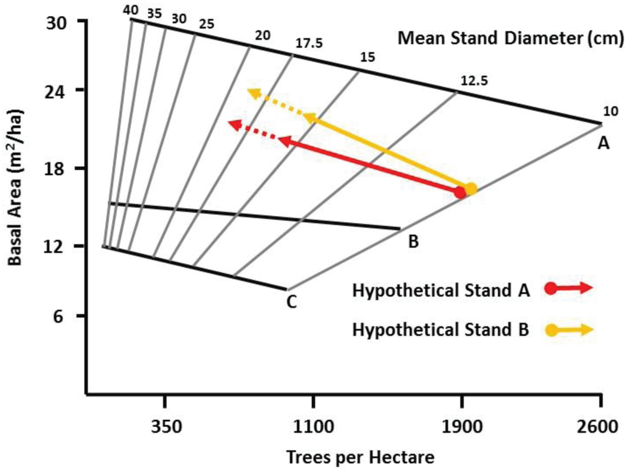

Figure 2. Typical stocking chart for northern hardwoods showing trees per hectare versus stand basal area. The A line shows the self-thinning boundary as stands develop. The B, and C lines delineate target stand conditions for thinning operations. Hypothetical stands represent the trajectories of developing stands under greater concentrations of atmospheric CO_2 resulting in: (A) faster rates of stand development (dashed line) or (B) faster rates of stand development and attaining higher levels of stand stocking (solid and dashed line).

of stand density to site quality (Weiskittel et al. 2009). Various hypotheses can be forwarded regarding the potential influence of rising atmospheric CO_2 on the dynamics of forest stand development with implications for stand density management diagrams. Not only may CO_2 enrichment increase the rates of stand development (e.g., Miller et al. 2016; Figure 2, Stand A) but it may enable higher levels of biomass accumulation (Schimel et al. 2015; Figure 2, Stand B) not withstanding other limitations such as precipitation and nitrogen availability (Hungate et al. 2003). Therefore, a prime opportunity has emerged to evaluate stocking guides derived from datasets collected when the atmosphere was much different than today, while including additional site variables throughout a species' range.

Because stocking indices employed today were most likely derived from forests that developed under environmental conditions substantially different from those of today, we propose that current stocking indices may not adequately apply to the growth and development of contemporary forests. As a means to initially evaluate such a hypothesis, the goal of this study was to estimate stand stocking characteristics of three model trembling aspen (*Polulus tremuloides*; hereafter "aspen") communities grown in elevated atmospheric CO_2 in northern Wisconsin and compare them with historical stand density relations that were used to develop currently employed management guidelines.

Methods

In order to objectively evaluate a selection of stocking indices, we explored stocking models employed by the USDA Forest Service, Forest Inventory and Analysis (FIA) program. The FIA program is mandated by the US Congress to conduct a complete inventory of forests in the US every 5 years, and is the national source of information on status and trends in forest resources (Oswalt et al. 2014). We reviewed the FIA Handbook stocking models (Arner et al. 2001) and traced the literature for the original published data sets used to develop the models. We located publications cited in the FIA Handbook that reported data summaries, and then searched further back in the literature for the original data sets. In some cases, the original data were not referenced, and we used either published stand tables or information derived graphically from published stocking guides.

Detailed descriptions of the Aspen FACE (Free Air CO_2 Enrichment) experiment are given in Dickson et al. (2000) and Kubiske et al. (2015). Briefly, the experiment was initiated in 1997 on a ~32 ha parcel in the USDA Forest Service's Rhinelander Experimental Forest, Oneida Co., Wisconsin (45.6°N, 89.5°W). Six, 30.48-m-diameter, open-air treatment arrays (rings) were constructed to deliver elevated concentrations of atmospheric CO_2 to the interior of the rings. The CO_2 within the rings was regulated by a series of slotted, vertical pipes, and computer-controlled valves to vent supplemental CO_2, which mixed with ambient air and was then carried into the rings by wind. The CO_2 control system proved to be very stable, coming within ±10 percent of the target concentration 90 percent of the time (Kubiske et al. 2015).

The design of the experiment was a complete block design with three replicates: three treatment rings received supplemental CO_2 (+CO_2 treatment, 550 ppm), and three were ambient air controls. In 1997, half of each ring was planted at a 1 × 1 m spacing with rooted cuttings of five naturally occurring aspen clones that had been studied previously for responses to elevated CO_2 (Karnosky et al. 1992; Kubiske et al. 1998). One quarter of each ring was planted with a 1:1 mixture of paper birch (*Betula papyrifera*) and aspen, and the remaining quarter with sugar maple (*Acer saccharum*) and aspen (1:1). The first full year of atmospheric treatments occurred in 1998. Each year, CO_2 fumigation began with bud burst in May and continued through leaf senescence in October.

A central area was identified in each ring where gas concentrations were most stable. The central areas consisted of about 310 trees in each ring and were encircled by five or six rows of trees as a buffer. In October of each year, height (cm; using height poles) and diameter (cm; using diameter tapes or digital calipers) were measured on every tree in the central area of each treatment ring. From 1997 to 2002, diameters were measured at 10.2 cm above the ground. From 2003 to 2005, diameters were measured at both 10.2 cm and 1.37 m (dbh). Thereafter, only dbh was measured until the experiment concluded in 2008. The two sets of diameters measured in 2003–2005 were used to extrapolate diameter at 10.2 cm above ground for the years 2006–2008. Thus, individual tree basal areas (ba_t) were calculated from diameters at 10.2 cm above ground rather than dbh. Total stand basal areas (BA) were calculated as (Σba_t / stand area) and extrapolated to 1 hectare.

For all analyses, the unit of replication was the treatment ring ($n = 3$) for each stand type (pure aspen, aspen–birch, and aspen–maple). Our data comprised repeated size–density measurements through time at 100 percent coverage of each experimental unit, which is a more robust evaluation of stand development than point-in-time measurements across multiple stand conditions (Shaw and Long 2010). We compared the final (2008) heights, diameters, BA, and trees per hectare using a simple, unpaired *t*-test with unequal variance for each stand type. Stand size–density relations were determined with log–log plots of quadratic mean diameter (Dq) versus number of trees per hectare (tph). The quadratic mean diameter was calculated as:

$$\sqrt{\frac{\sum D_i^2}{n}} \qquad \text{Model 1}$$

Maximum stand density index (SDI) was determined as the slope of the log–log regression:

$$\text{tph} = 10^{[a+b(\log \text{Dq})]} \qquad \text{Model 2}$$

where a and b are parameters. Stocking charts were created as BA versus tph throughout the life of the experiment. Linear functions were fit to BA versus tph with least-squares regression. Coefficients for the terms were compared with the ratio of error sums of squares and the appropriate F statistic (Neter et al. 1985).

Results

Our review of the primary reference materials used in development of regional stocking models in the FIA Handbook revealed that data were originally collected up to 80–90 years ago (Table 1). Although many of the models were developed only three or four decades ago, the source data used to develop those models were collected much earlier. For example, the stocking chart and models presently used by FIA for eastern white pine (*Pinus strobus*) were published by Philbrook et al. in 1973, but the principle data set was from a publication by Frothingham in 1914 with data origins potentially even older. Over that same period of time, global atmospheric CO_2 concentration had increased 108 ppm (or 36 percent; Figure 1). Other data sources were first published in the 1920s and 1930s. The average disparity in age (when the age of the stand data is known) between the original stocking data collection and the year 2017 is over 70 years.

An examination of stand growth and size–density relations in the Aspen FACE experiment exhibited a significant and substantial effect of CO_2 enrichment for each stand type (Table 2). After 11 years of growth, aspen and aspen–birch plots in $+CO_2$ had 15 and 20 percent greater (all $P < .05$) height growth, respectively, and 13 and 24 percent larger ($P < .05$) dbh, respectively, than the control. Aspen–maple plots exhibited no significant $+CO_2$ effects on mean height or diameter because of high coefficients of variation (not shown). No community type had significant changes in number of trees per acre because of the $+CO_2$ treatment. Aspen, aspen–birch, and aspen–maple in $+CO_2$ had 23, 49, and 39 percent greater (all $P < .05$) BA, respectively, than the control. Regression models fit to the Aspen FACE data likewise revealed strong $+CO_2$ effects (Figure 3, Table 3). Size–density relations revealed increased slope in all cases, suggesting a significant ($P < .05$) rate of change in maximum SDI (Figures 3A–C), such that stands would support increasingly more tph as Dq continues to increase through time. In addition, the log–log function for pure aspen stands had an increased ($P < .05$) intercept indicating increased maximum SDI at all stand densities. In all cases, the CO_2-enriched stands supported greater ($P < .05$) tph at equivalent BA than the controls (Figures 3D–F).

Discussion

We found stand stocking indices currently used for forest inventory (and regional

Table 2. Stocking of 11-year-old stands in the Aspen FACE experiment.

Species	Treatment	Height (m)	SE (m)	Diameter (cm)	SE (cm)	Trees/ha	SE (#/ha)	Basal area (m²/ha)	SE (m²/ha)
Aspen	Control	8.9	0.1	6.2	0.1	7033	35	34.4	0.5
	$+CO_2$	10.2*	0.2	7.1*	0.3	6790	217	42.2*	1.4
Aspen–birch	Control	7.6	0.2	5.0	0.1	7897	264	38.6	0.7
	$+CO_2$	9.1*	0.3	6.2*	0.3	6845	697	57.4*	2.3
Aspen–maple	Control	6.3	0.2	4.2	0.1	6877	477	38.6	0.9
	$+CO_2$	5.6	0.2	4.0	0.2	7920	376	53.7*	2.1

Note: Means (±standard error [SE]; $n = 3$) of the $+CO_2$ treatment within a stand with * are significantly different from control ($P < .05$). Diameters were measured or extrapolated to 4 cm above ground.

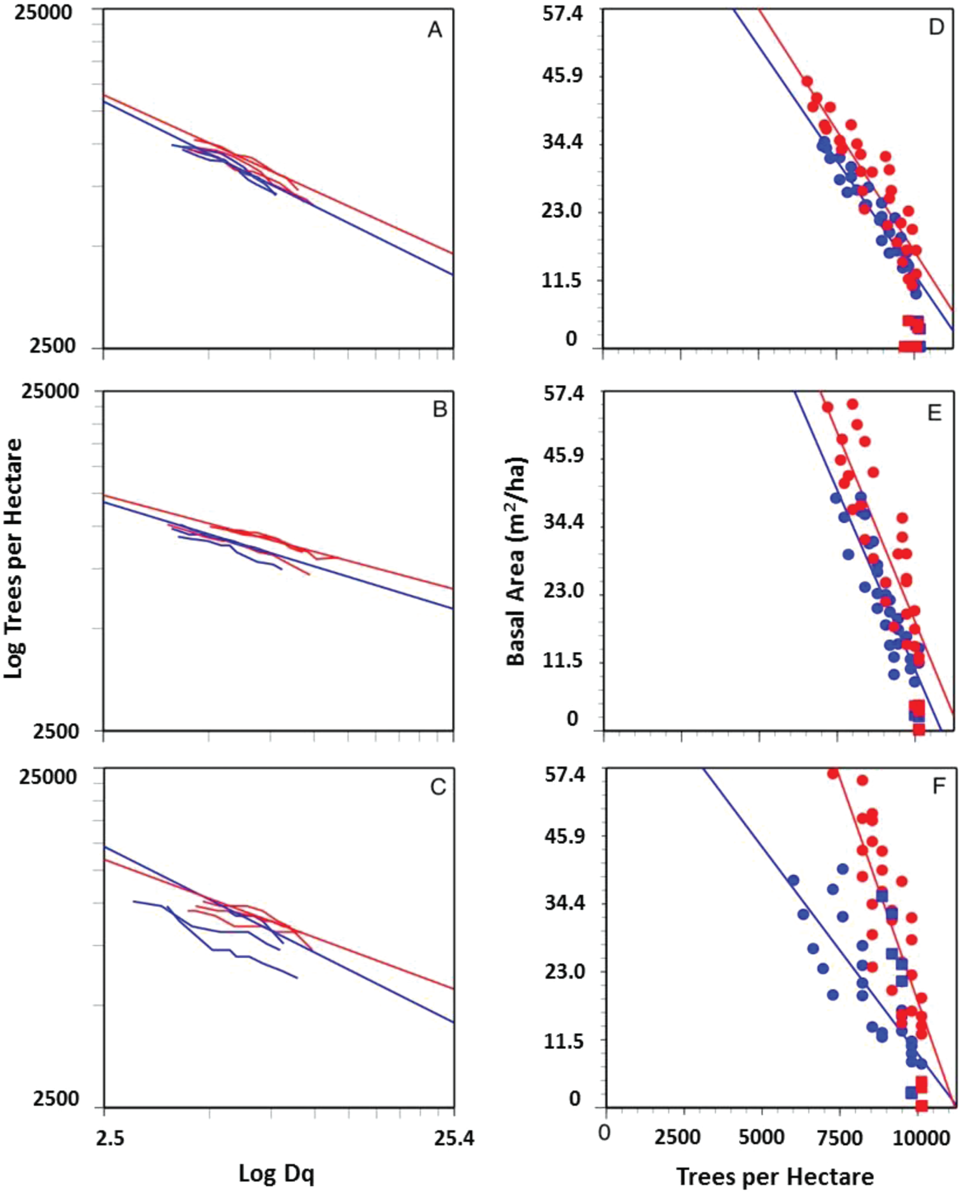

Figure 3. Left column, size–density relations of 11-year-old model aspen stands in the Aspen FACE experiment showing stand progression through time: (A) pure trembling aspen, (B) trembling aspen and paper birch (1:1), (C) trembling aspen and sugar maple (1:1). Blue: control stands; red: grown in elevated CO_2 (each $n = 3$). The log–log slopes of the regression lines are essentially the maximum stand density index for each community. Right column, stocking charts of the stands shown in A—C. Each point represents one treatment replicate from one year. Circles represent the self-thinning condition and were included in the regressions. Squares represent initial stand conditions after planting and were not included in the regressions. Corresponding regression coefficients are shown in Table 3.

Table 3. Regression coefficients of size–density and stand stocking relations of 11-year-old, model aspen stands in the Aspen FACE experiment.

		Species								
		Aspen			Aspen–birch			Aspen–maple		
Model	Treatment	*a*	*b*	r^2	*a*	*b*	r^2	*a*	*b*	r^2
Size–density	Control	3.929	–0.51	0.91	4.188	–0.31	0.95	4.495	–0.82	0.81
	$+CO_2$	4.333*	–0.47*	0.96	4.196	–0.28*	0.90	4.277	–0.38*	0.82
Stocking	Control	89.5	–0.0078	0.93	131.8	–0.0012	0.80	79.0	–0.0070	0.72
	$+CO_2$	98.3*	–0.0083	0.85	146.2*	–0.0013	0.76	168.5*	–0.0015*	0.68

Note: Stands were grown either in ambient air (control) or in air with 550 ppm CO_2 ($+CO_2$), $n = 3$. Size-Density models are: tph = $10^{(a + b\,(\log Dq))}$ where tph is number of trees per hectare, and Dq is the quadratic mean diameter (cm). Stand stocking models are BA = *a* + *b* (tph) where BA is stand basal area (m²/ha). *Significant differences ($P < .05$) between control and $+CO_2$ treatments within species and coefficient on the $+CO_2$ values. Corresponding graphs are shown in Figure 3.

silvicultural activities) may be outdated because the stands from which they were derived grew in atmospheric environments far different from today. For example, Reineke's (1933) model for self-thinning populations and SDI were first published in 1933 based upon loblolly pine data from 1929. Considering that many of the measurements involved timber stands 100–300 years old at the time they were measured (e.g., Brown and Gevorkiantz 1934), the stand models still in use today were built upon some forests that began to develop under preindustrial atmospheric CO_2 (270 ppm). Since that time, CO_2 has increased 50 percent to 408 ppm.

The slopes of our size–density relations changed in the elevated CO_2 plots for all three tree communities. In addition, we found a significantly greater size–density intercept in the pure trembling aspen plots. Our findings are entirely consistent with those of Weiskittel et al. (2009) who reported that site index influenced the slope, and stand purity influenced the intercept of self-thinning boundaries in three western species. We argue that the effects of increased atmospheric CO_2 are tantamount to not only increased site index but also the ability of sites to support biomass (see below for mechanistic descriptions of these phenomena). The upper limits of self-thinning lines largely determine the various limits of prescribed stand density management (Figure 2, for example). Thus, it follows that a shift in the upper limit of self-thinning stand density may necessitate changes in density management prescriptions (see hypothetical stands in Figure 2).

In a review of several models linking stand leaf area with several ecological processes, Long et al. (2004) conceptualized the direct relations of increasing soil resources and light interception with increasing stand leaf area and net primary productivity. Weiskittel et al. (2009) reported that the maximum self-thinning line for three western species increased directly with site quality and other variables. In one noteworthy example, DeBell et al. (1989) compared 25-year-old loblolly pine stands that had similar planting densities across the southeast United States with those in Hawaii. The Hawaiian stands had 19 percent greater survival and supported 108 percent greater volume. The authors did not speculate on what conditions might have accounted for these remarkable differences, but factors such as more nutrient-rich volcanic soils (similar to those in the Pacific Northwest that support highly productive conifer forests), longer year-round photoperiods, and more abundant rainfall in Hawaii than in the Southeast US were most likely influential factors. Whereas increasing evidence indicates that site variables such as soil quality, precipitation, temperature, etc., influence maximum stand density (Andrews et al. 2018), increasing atmospheric CO_2 is superimposed over all other factors contributing to improvements in site quality in many environments.

Efficient resource utilization by leaf area is directly related to productivity (Long et al. 2004). In the Aspen FACE experiment, we found a significantly greater leaf area index (LAI—by 40 percent) in the +CO_2 plots than in the controls (Uddling et al. 2008). In addition, we found that +CO_2 increased stand growth rates in each of the three model aspen communities, a finding that was substantiated by meta-analysis of hundreds of earlier experiments on the effects of elevated CO_2 (Curtis and Wang 1998). Our experimental results of *sustained* increased growth rates with increasing CO_2 were supported by a dendrochonological study of naturally occurring trembling aspen stands up to 50 years old in Wisconsin and Michigan (Cole et al. 2010).

We propose that elevated CO_2 either resource-use efficiency or resource availability, or both, and facilitates improvement in growing conditions (DeLucia et al. 1999, Ainsworth and Long 2005, Norby et al. 2005). The three most limiting factors for forest productivity on a local scale are light, water, and soil N, and there is compelling research demonstrating that all three resources are used more efficiently as CO_2 increases (e.g., Miller et al. 2016). For example, it was suggested that increased CO_2 improves photosynthetic light utilization (Kubiske and Pregitzer 1996). A synthesis of results from four FACE experiments supports that idea (Norby et al. 2005), and was further substantiated by increased leaf area index in the Aspen FACE Experiment (Uddling et al. 2008). Also in that study, despite 40 percent greater transpirational leaf area in the +CO_2 treatments, canopy water use increased by only 18 percent (Uddling et al. 2008) with no attendant decrease in soil water content possibly because increased soil organic matter inputs increase soil water-holding capacity. When examining these limiting factors in terms of stocking index applications, the effects of light versus water-limiting environments arise, because the concept of "stockability" in water-limited environments (e.g., DeBell et al. 1989) may subdue CO_2 enrichment effects. Certainly, this issue of stockability is impactful on stocking index application in a world of rising CO_2 concentrations, but perhaps the larger question relates to how to structure stocking guides so they are dynamic. We conjecture that such dynamic stocking indices would be responsive not only to changing atmospheric conditions (i.e., site quality; Weiskittel et al. 2009, Andrews et al. 2018) but also to shifting species mixtures (Woodall et al. 2005) and their associated functional traits (e.g., shade tolerance; Ducey et al. 2017). Whatever formulation such indexes would assume, they would be an important tool for adaptive management exercises (e.g., Nagel et al. 2017) and should be parsimonious (e.g., Long 1985) for field implementation.

Beyond tree growth physiology, there are other indirect ecosystem effects from increasing CO_2 that should be expected to influence stand dynamics. Studies have shown a clear, positive relation between the magnitude of the CO_2 fertilization effect and site-specific soil N availability (Zak et al. 2000, Reich et al. 2006). In two FACE experiments, CO_2 enrichment stimulated soil N cycling because of increased leaf litter deposition (Zak et al. 2007) and root exudates (Phillips et al. 2011), making more N available to support the CO_2 effect on growth, even on N depauparate sites. More importantly, however, is the likelihood that forests have already undergone considerable changes in developmental characteristics in response to environmental changes, particularly increases in atmospheric CO_2 that have already occurred. From a purely speculative and perhaps theoretical standpoint, the findings of Zak et al. (2007) and Phillips et al. (2011), follow from the fact that photosynthesis is currently limited by CO_2 availability. It is unequivocal that primary productivity of C3 plants, which include trees, increases with increasing atmospheric CO_2, other factors being equal (Curtis and Wang 1998, Norby et al. 2005, Cole et al. 2010). Thus, C3 plants have progressed through evolutionary time with excess capacity to use even contemporary atmospheric CO_2 concentrations. Given that the suite of ecosystem processes dependent upon primary production have coevolved with the primary producers, we argue that ecosystem processes directly related to primary production (such as N cycling) also have the ability to use the increased energetic inputs. Taken together, it can be suggested that the re-examination of stocking indices is needed not only in reaction to rising CO_2 but also to take advantage of potentially more favorable growing conditions, all else being even (i.e., Liebeg's Law of the Minimum).

Conclusions

Based on the results of our study, we call for a re-examination of management guidelines given the likelihood that a changing atmosphere has affected stand development over the last 70–100 years. Forests of today develop and function in an atmosphere enriched with CO_2, sometimes 50 percent higher than when trees used in density quantification started growing. This finding is potentially exacerbated by the likelihood that other environmental factors have also changed, including longer growing seasons and greater inorganic N deposition. The results of our experiment should not serve as the basis for changes in management practices; rather they point to the need for comprehensive field studies and associated analyses to determine the extent to which forest development may already have been affected by increased CO_2. Finally, this study highlights the need for flexible size–density management guides that can incorporate a number of site factors including contemporary atmospheric information and other changing environmental conditions proven to alter self-thinning trajectories.

Literature Cited

Ainsworth, E.A., and S.P. Long. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analysis review of the responses of photosynthesis, canopy properties, and plant production to rising CO_2. *New Phytol.* 165:351–372.

Andrews, C., A. Weiskittel, A.W. D'Amato, and E. Simons-Legaard. 2018. Variation in the maximum stand density index and its linkage to climate in the mixed species forest of the North American Acadian Region. *For. Ecol. Manag.* 417:90–102.

Arner, S.L., et al. 2001. National algorithms for determining stocking class, stand size class, and forest type for forest inventory and analysis plots. Unpublished report of the USDA Forest Service, Forest Inventory and Analysis. Available at http://www.fia.fs.fed.us/library/sampling/docs/supplement4_121704.pdf; last accessed November 1, 2018.

Benzie, J.W. 1977a. Manager's handbook for jack pine in the North Central States. USDA Forest Service General Technical Report NC-32.

Benzie, J.W. 1977b. Manager's handbook for red pine in the North Central States. USDA General Technical Report NC-33.

Brown, R.M. and S.R. Gevorkiantz. 1934. Volume, yield, and stand tables for tree species in the Lake States. USDA Forest Service Technical Bulletin 39.

Cole, C.T. et al. 2010. Rising concentrations of atmospheric CO_2 have increased growth of natural stands of quaking aspen (*Populus tremuloides*). *Global Change Biol.* 16:2186–2197.

Curtis, P.S., and X. Wang. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. *Oecologia* 113:299–313.

Darbah, J.N.T., M.E. Kubiske, N.D. Nelson, E. Oksanen, E. Vaapavuori, and D.F. Karnosky. 2007. Impacts of elevated atmospheric CO_2 and O_3 on paper birch (*Betula papyrifera*): Reproductive fitness. *Sci. World J.* 7(S1):240–246.

Darbah, J.N.T., M.E. Kubiske, N.D. Nelson, E. Oksanen, E. Vaapavuori, and D.F. Karnosky. 2008. Effects of decadal exposure to interacting elevated CO_2 and/or O_3 on paper birch (*Betula papyrifera*) reproduction. *Environ. Pollut.* 155:446–452.

DeBell, D.S., W.R. Harms and C.D. Whitesell. 1989. Stockability: A major factor in productivity differences between *Pinus taeda* plantations in Hawaii and the Southeastern United States. *For. Sci.* 35:708–719.

DeLucia, E.H., J.G. Hamilton, S.L. Naidu, et al. 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science 284*:1177–1179.

Dickson, R.E., K.F. Lewin, J.G. Isebrands, M.D. Coleman, W.E. Heilman, D.E. Riemenschneider, J. Sober, et al. 2000. Forest Atmosphere Carbon Transfer and Storage (FACTS-II) The Aspen Free-air CO_2 and O_3 Enrichment (FACE) Project: An overview. USDA Forest Service General Technical Report NC-214.

Drew, T.J. and J.W. Flewelling. 1979. Stand density management: an alternative approach and its application to Douglas-fir plantations. *For. Sci.* 25:518–522.

Ducey, M.J., Woodall, C.W., and Bravo-Oviedo, A. 2017. Climate and species functional traits influence maximum live tree stocking in the Lake States, USA. *For. Ecol. Manag.* 386:51–61.

Etheridge, D.M., L.P. Steele, R.L. Langenfelds, R.J. Francey, J.-M.Barnola, and V.I. Morgan. 1998. Historical CO_2 record from the Laws Dome, Antarctica. DE08, DE08-2, and DSS Ice Cores. Available at https://data.ess-dive.lbl.gov/#view/ess-dive-c3c4b7bb5b66369-20180704T215529758; last accessed November 1, 2018.

Eyre, F.H. and R.K. LeBarron. 1944. Management of jack pine stands in the Lake States. USDA Forest Service Technical Bulletin 863.

Eyre, F.H. and P. Zehngraff. 1948. Red pine management in Minnesota. USDA Circular No. 778.

Frothingham, E.H. 1914. White pine under forest management. USDA Bulletin No. 18.

Gevorkiantz, S.R. and W.A. Duerr. 1939. Volume and yield of northern white cedar in the Lake States. Unpublished report of the North Central Forest Experiment Station, St. Paul, MN.

Gilbert, A.M. and V.S. Jensen. 1958. *A management guide for northern hardwoods in New England*. USDA Forest Service, Northeast Forest Experiment Station, Station Paper 112. Washington, DC.

Hendrey, G.R., D.S. Ellsworth, K.F. Lewin, and J. Nagy. 1999. A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO_2. *Global Change Biol.* 5:293–309.

Hungate, B.A., J.S. Dukes, M.R. Shaw, Y. Luo, and C.B. Field. 2003. Nitrogen and climate change. *Science* 302:1512–1513.

Hussain, M., M.E. Kubiske, and K.F. Connor. 2001. Germination of CO_2 enriched *Pinus taeda* L. seeds and subsequent seedling growth responses to CO_2 enrichment. *Funct. Ecol.* 15:1–7.

IPCC, 2014. Summary for policymakers. P. 1–32 in *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Field, C.B., V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.). Cambridge University Press, Cambridge.

Johnston, W.F. 1977. Manager's handbook for Northern white cedar in North Central States. USDA Forest Service General Technical Report NC-35.

Karnosky, D.F., Z.E. Gagnon, D.D. Reed, and J.A. Witter. 1992. Effects of genotype on the response of *Populus tremuloides* Michx. to ozone and nitrogen deposition. *Water Air Soil Pollut.* 62:189–199.

Karnosky, D.F., B. Gielen, R. Ceulemans, W.H. Slesinger, R.J. Norby, E. Oksanen, R. Matyssek, G.R. Hendrey, G.E. Scarascia-Mugnozza, and J.L. Innes. 2001. FACE systems for studying the impacts of greenhouse gasses on forest ecosystems. P. 297–324 in *Report No. 3 of the IUFRO Task Force on Environmental Change*.

Kittredge, J. and S.R. Gevorkiantz. 1929. Forest Possibilities of aspen lands in the Lake States. USDA Forest Service Technical Bulletin 60.

Kubiske, M.E., A.J. Burton, A.R. Foss, W.S. Jones, K.F. Lewin, J. Nagy, K.S. Pregitzer, D.R. Zak, and D.F. Karnosky. 2015. Supporting 13 years of global change research: The history, technology, and methods of the Aspen FACE Experiment. *General Technical Report NRS-153*. USDA Forest Service, Northern Research Station, Newtown Square, PA. 50 p.

Kubiske, M.E., and K.S. Pregitzer. 1996. Effects of elevated CO$_2$ and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiol.* 16:351–358.

Kubiske, M.E., K.S. Pregitzer, D.R. Zak, and C.J. Mikan. 1998. Growth and C allocation of *Populus tremuloides* genotypes in response to atmospheric CO$_2$ and soil N availability. *New Phytol.* 140:251–260.

LaDeau, S., and J.S. Clark. 2001. Rising CO$_2$ levels and the fecundity of trees. *Science*, 292:95–98.

Long, J.N. 1985. A practical approach to density management. *For. Chron.* 61:23–27.

Long, J.N., T.J. Dean, and S.D. Roberts. 2004. Linkages between silviculture and ecology: examination of several important conceptual models. *For. Ecol. Manag.* 200: 249–261.

Lou, Y., B. Su, W.S. Currie, J.S. Dukes, A. Finzi, U. Hartwig, B. Hungate, R.E. McMurtrie, R. Oren, W.J. Parton, D.E. Pataki, R.M. Shaw, D.R. Zak, and C.B. Field. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric CO$_2$. *BioScience* 54:731–739.

Marquis, D.A., D.S. Solomon, and J.C. Bjorkbom. 1969. A silvicultural guide for paper birch in the Northeast. USDA Forest Service Research Paper NE-130.

Miller, A.D., M.C., Dietze, E.H. DeLucia, and K.J. Anderson-Teixeira. 2016. Alteration of forest succession and carbon cycling under elevated CO$_2$. *Global Change Biol.* 22:351–363.

Myers, C.C., and R. Buchman. 1984. Manager's handbook for elm–ash–cottonwood in the North Central States. USDA Forest Service General Technical Report NC-98.

Nagel, L.M., B.J. Palik, M.A. Battaglia, A.W. D'Amato, J.M. Guldin, C.W. Swanston, M.K. Janowiak, M.P. Powers, L.A. Joyce, C.I. Millar, D.L. Peterson, L.M. Ganio, C. Kirschbaum, and M.R. Roske. 2017. Adaptive silviculture for climate change: a national experiment in manager-scientist partnerships to apply an adaptation framework. *J. For.* 115:167–178.

Nelson, T.C., and F.A. Bennett. 1965. A critical look at the normality concept. *J. For.* 64:107–109.

Neter, J., W. Wasserman, and M.H. Kutner. 1985. *Applied linear statistical models*. 2nd ed. Irwin, Homewood, IL. P. 861–862.

NOAA. 2018. *National Oceanic and Atmospheric Administration, Earth System Research Laboratory*. Washington, DC. Ed Dlugokencky and Pieter Tans, NOAA/ESRL. www.esrl.noaa.gov/gmd/ccgg/trends/.

Norby, R.J., E.H. DeLucia, B. Gielen, C. Calfapietra, C.P. Giardina, J.S. King, J. Ledford, et al. 2005. Forest response to elevated CO$_2$ is conserved across a broad range of productivity. *Proc. Natl. Acad. Sci.* 102:18052–18056.

Oliver, C.D., and B.C. Larson. 1996. *Forest stand dynamics*. John Wiley & Sons, New York.

Oswalt, S.N., W.B. Smith, P.D. Miles, and S.A. Pugh. 2014. *Forest resources of the United States, 2012. General Technical Report WO-91*. USDA Forest Service, Washington Office, Washington, DC. 218 p.

Perala, D.A. 1977. Manager's Handbook for aspen in the North Central States. USDA Forest Service General Technical Report NC-36.

Plonski, W.L. 1960. Normal yield tables for black spruce, jack pine, tolerant hardwoods, white pine, and red pine. Ontario Department of Lands and Forests Silvicultural Series Bulletin No. 2.

Philbrook, J.S., J.P. Barrett, and W.B. Leak. 1973. A stocking guide for Eastern White Pine. USDA Forest Service Research Note NE-168.

Phillips, R.P., A.C. Finzi and E.S. Bernhardt. 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO$_2$ fumigation. *Ecol. Lett.* 14:187–194.

Putnam, J.A., G.M. Furnival, and J.S. McKnight. 1960. Management and inventory of Southern hardwoods. USDA Forest Service Agriculture Handbook No. 181.

Reich, P.B., S.E. Hobbie, T. Lee, D. Ellsworth, J.B. West, D. Tilman, J.M.H. Knops, S. Naeem, and J. Trost. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO$_2$. *Nature* 440:922–925.

Reineke, L.H. 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 47:627–638.

Roach, B.A. 1977. A stocking guide for Allegheny hardwoods and its use in controlling intermediate cuttings. USDA Forest Service Research Paper NE-373.

Roach, B.A., and S.F. Gingrich. 1962. Timber management guide for upland central hardwoods. USDA Forest Service Central States Forest Experiment Station and North Central Region.

Safford, L.O. 1983. Silvicultural guide for paper birch in the Northeast (revised). USDA Forest Service Research Paper. NE-535.

Schimel, D., B.B. Stephens, and J.B. Fischer. 2015. Effect of increasing CO$_2$ on the terrestrial carbon cycle. *Proc. Natl. Acad. Sci. USA* 112:436–441.

Schlesinger, R.C., and D.T. Funk. 1977. Manager's guide for black walnut. USDA Forest Service General Technical Report NC-38.

Shaw, J.D., and J.N. Long. 2010. Consistent definition and application of Reineke's stand density index in silviculture and stand projection. P. 199–209 in *Integrated management of carbon sequestration and biomass utilization opportunities in a changing climate*. T.B., Jain, R.T. Graham, and J. Sandquist (eds.). Proceedings of the 2009 National Silviculture Workshop, Boise, ID. RMRS-P-61, Fort Collins, CO, USDA Forest Service.

Solomon, D.S. et al. 1987. Fiber handbook: A growth model for spruce-fir and northern hardwood forest types. USDA Forest Service Research Paper NE-602.

Stout, S.L. and R.D. Nyland. 1986. Role of species composition in relative density measurement in Allegheny hardwoods. *Can. J. For. Res.* 16:574–579.

Tubbs, C.H. 1977. Manager's handbook for northern hardwoods in the North Central States. USDA General Technical Report NC-39.

Uddling, J., R.M. Teclaw, M.E. Kubiske, K.S. Pregitzer, and D.E. Ellsworth. 2008. Sap flux in pure aspen and mixed aspen-birch forests exposed to elevated concentrations of carbon dioxide and ozone. *Tree Physiol.* 28:1231–1243.

Weiskittel, A., P. Gould, and H. Temesgen. 2009. Sources of variation in the self thinning boundary line for three species with varying levels of shade tolerance. *For. Sci.* 55, 84–93.

Woodall, C.W., P.D. Miles and J.S. Vissage. 2005. Determining maximum stand density index in mixed species stands for strategic-scale stocking assessments. *For. Ecol. Manag.* 216, 367–377.

Zak, D.R., W.E. Holmes, and K.S. Pregitzer. 2007. Atmospheric CO$_2$ and O$_3$ alter the flow of ^{15}N in developing forest ecosystems. *Ecology* 88:2630–2639.

Zak, D.R., K.S. Pregitzer, P.S. Curtis, C.S. Vogel, W.E. Holmes, and J. Lussenhop. 2000. Atmospheric CO$_2$, soil-N availability, and allocation of biomass and nitrogen by *Populus tremuloides*. *Ecol. Applic.* 10:34–46.

Zamski, E. 1995. Transport and accumulation of carbohydrates in developing seeds: the seed as a sink. P. 25–44 in *The seed, development and germination*, Kigel, J. and G. Galili (eds.). Marcel Dekker, New York.