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Comment on "Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees"

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Zani *et al*. (Research Articles, 27 November 2020, p. 1066) propose that enhancement of deciduous tree photosynthesis in a CO_2-enriched atmosphere will advance autumn leaf senescence. This premise is not supported by consistent observations from free-air CO_2 enrichment (FACE) experiments. In most FACE experiments, leaf senescence or abscission was not altered or was delayed in trees exposed to elevated CO_2.

Zani *et al.* (*1*) relied on long-term observations of temperate deciduous trees and a short-term manipulative experiment to conclude that increases in spring and summer productivity due to elevated CO_2, temperature, or light levels will lead to earlier autumn senescence, thereby creating an important constraint on future growing-season length and carbon uptake of trees. They rightly assert that evaluating this scenario and the implications for future autumn trajectories requires quantitative, empirical evidence "from a combination of controlled experiments and long-term in situ observations on mature trees exposed to real-world environmental changes." Despite this assertion, they ignored a wealth of evidence on autumn senescence provided by free-air CO_2 enrichment (FACE) experiments—evidence that largely contradicts their main findings.

The FACE experiments are controlled experiments of trees (including mature trees) exposed in situ for multiple years to future atmospheric CO_2 concentrations under real-world environmental conditions. Although there may be compelling evidence that earlier spring leaf-out influences autumn senescence through growing-season productivity or other mechanisms, the evidence from FACE experiments (Table 1) does not support the authors' conclusion that senescence will come earlier in trees in a warming, CO_2-enriched world.

Autumn senescence or abscission (leaffall) was observed in at least seven species of temperate deciduous trees for up to 12 years in six FACE experiments in the United States and Europe. In most cases there was no observed effect of elevated CO_2. Leaffall of *Betula pendula* trees occurred later in elevated CO_2 relative to control plots in two of four years in the BangorFACE experiment (*2*) and was 4 to 5 days later in mature *Carpinus betulus* and *Fagus sylvatica* trees in the WebFACE experiment (*3*). Only the *Quercus petraea* trees at WebFACE exhibited earlier abscission in response to elevated CO_2 (*3*). The longest record comes from the Oak Ridge National Laboratory (ORNL) FACE experiment with *Liquidambar styraciflua* trees (*4*, *5*). The average time of 50% leaffall over 12 years was day-of-year 283 ± 2.4 in both ambient and elevated CO_2 (Fig. 1A). In 9 of 12 years, there was no effect of CO_2 on the timing of abscission (Fig. 1B), with differences in timing usually two or fewer days. In two years (2004 and 2008), abscission occurred 5 to 6 days later in elevated CO_2. Only in 2002 did abscission occur appreciably earlier in elevated CO_2, and this was in response to a late-season drought (*5*). Additional evidence comes from two experiments in which trees or intact ecosystems were exposed to a combination of elevated CO_2 and elevated air temperatures within outdoor, open-top enclosures. With both *Acer saccharum* and *A. rubrum* saplings in the TACIT experiment (*6*) and the mature, deciduous *Larix laricina* trees in the SPRUCE experiment (*7*), senescence or abscission was delayed in warmer temperatures, in contrast to the lack of response to warming reported by Zani *et al.*, and there was no effect of elevated CO_2.

These FACE and outdoor chamber experiments are far more realistic tests of CO_2 and warming effects on autumn canopy dynamics than the experiment described by Zani *et al.*, in which 2-year-old trees from a nursery in 3-liter pots of artificial soil and compromised by a foliar fungal infection were exposed to elevated CO_2 in unreplicated closed chambers over one simulated and shortened growing season. Their hypothesis is based on the premise that stimulation of photosynthesis earlier in the growing season creates a sink limitation that subsequently causes earlier senescence. Hence, it is noteworthy that photosynthesis and productivity were enhanced in these FACE experiments. An exception was ORNL FACE, where N limitation toward the end of the experiment precluded photosynthetic enhancement (*8*), but the response of timing of leaffall to elevated CO_2 was nonetheless the same early in the experiment when photosynthesis and primary productivity were stimulated and later in the experiment when they were not. The absence of a negative relationship between seasonal productivity and senescence date in PopFACE (*9*) (actually a positive relationship was reported) was not considered by Zani *et al.* to be at odds with their premise because productivity in the fertilized and irrigated PopFACE experiment was very high and there presumably was no sink limitation. Were the trees in other experiments in Table 1 sink-limited? It is difficult to evaluate sink limitation in these experiments in the context of the analysis by Zani *et al.* because the metrics for sink limitation are not clear, and their example from monocarpic barley plants in which senescence is strongly linked to reproductive output probably is not relevant to forest trees. DukeFACE, ORNL FACE, and the SPRUCE experiment were demonstrably N-limited, which is expected to influence sink activity (*10*). No feedback inhibition of photosynthesis in elevated CO_2 was observed in the mature forest trees in the webFACE experiment, which suggests that active sinks were maintained, most likely below ground (*11*), as was also the case at ORNL FACE (*8*). In contrast, it is well known that sink limitation is a frequent artifact of elevated CO_2 experiments with potted plants because CO_2 stimulation of growth can cause a plant to outgrow its pot and resource supply, creating feedback inhibition on photosynthesis (*12*) and accelerating leaf senescence. This dynamic cannot be considered relevant to the real world or to the hypothesis they were testing.

The development and operation of large-scale FACE experiments involved considerable investment of financial and scientific resources, and FACE results have supported important advances in ecosystem modeling of CO_2 responses (*13*) and global-scale evaluation of the future trajectory of the terrestrial carbon sink (*14*). They provide the best available data for testing hypotheses about ecosystem responses to future atmospheric CO_2 conditions. Future projections of autumn phenology have little credibility when FACE results that contradict them are ignored.

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Table 1. Autumn senescence and abscission responses of temperate deciduous trees in FACE and field chamber experiments.

Experiment	Genus	Years (treatment, observations)	Response to elevated CO_2	Source
BangorFACE	*Betula*, *Alnus*	4, 4	Abscission delayed 2–3 weeks in *Betula* in 2 years; no effect in *Alnus*	(*2*)
PopFACE	*Populus*	2, 2	Delayed senescence	(*9*)
RhinelanderFACE	*Populus*	8, 2	Delayed senescence	(*9*)
WebFACE	*Carpinus*, *Fagus*, *Quercus*	4, 4	Abscission 4–5 days later (*Carpinus*, *Fagus*); abscission 5 days earlier (*Quercus*)	(*3*)
DukeFACE	*Liquidambar*	2, 1	No effect on abscission date	(*15*)
ORNL FACE	*Liquidambar*	12, 12	No effect on abscission (most years, Fig. 1); earlier abscission (drought year)	(*4*, *5*)
SPRUCE, CO_2 × temperature	*Larix*, shrubs (also *Picea*)	2, 1	No effect of elevated CO_2; delayed senescence with warming	(*7*)
TACIT, CO_2 × temperature	*Acer*	3, 3	No effect on abscission of elevated CO_2; delayed abscission with warming	(*6*)

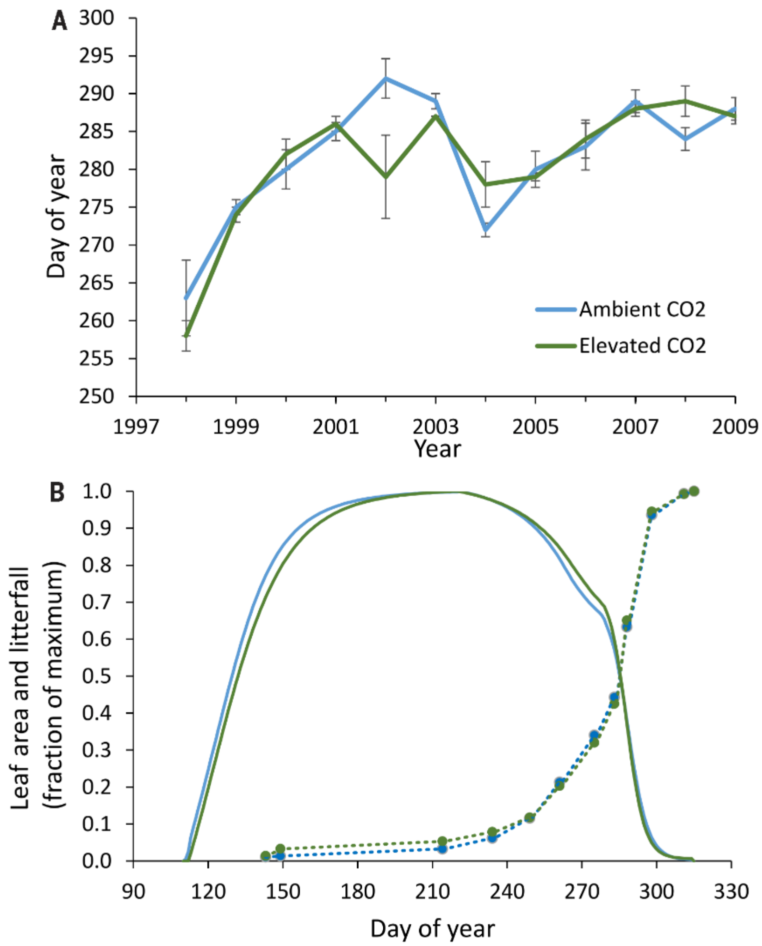

Fig. 1. Leaffall of *Liquidambar styraciflua* trees in the ORNL FACE experiment. (A) Day of year when 50% of leaf area had abscised. Data are means (±SE) of three plots in ambient CO_2 and two plots in elevated CO_2. (B) Daily relative leaf area index (solid lines) and litterfall (dotted lines) in 2001. [Data source: (*4*) and https://facedata.ornl.gov/ornl/ornl_data_plantresponse.html]

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