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Response to Comment on “Increased growing-season productivity drives earlier autumn leaf senescence in temperate trees”

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Our study showed that increases in seasonal productivity drive earlier autumn senescence of temperate trees. Norby argues that this finding is contradicted by observations from free-air CO₂ enrichment (FACE) experiments, where elevated CO₂ has been found to delay senescence in some cases. We provide a detailed answer showing that the results from FACE studies are in agreement with our conclusions.

Using experimental and observational data, Zani *et al.* (1) showed that increases in spring and summer productivity correlate with earlier autumn senescence of temperate trees, and that this process may counteract the expected long-term delays in leaf senescence under autumn warming. In his Comment (2), Norby argues that this finding is contradicted by observations from FACE experiments where leaf senescence was not altered or was delayed in trees exposed to elevated CO₂. However, although we agree that FACE experiments are critical to study the responses of plants to a CO₂-enriched environment, we believe that results from these experiments do not contradict the findings of our study. Indeed, the results from FACE studies lend additional empirical support for the proposed sink-driven mechanism.

Our model does not predict that increased CO₂ will generally lead to advanced senescence. The autumn phenology model developed in our study is based on the empirical evidence that earlier spring leaf-out, elevated spring and summer temperatures, and higher irradiation all independently counteract the expected delays in senescence under warmer autumns. Our predictions therefore do not depend on CO₂ levels, as can be seen from the similar performance of the photosynthesis-driven model, which accounts for CO₂, and the growing-season index model, which does not account for atmospheric CO₂ levels [figure 3 of (1)]. The effect of rising atmospheric CO₂ levels over recent decades on Central European autumn senescence dates thus appears to be negligible relative to the effects of rising temperatures. In fact, because of the interactive effects of growing-season productivity and autumn

temperatures, our model predicts continuing delays in senescence over the coming three decades with strongly increasing CO₂ levels under the RCP8.5 scenario.

The sink limitation paradigm predicts that elevated CO₂ will cause advanced leaf senescence only if (i) high CO₂ leads to increased spring/summer photosynthesis, (ii) these increases in photosynthesis (source strength) outweigh CO₂-driven increases in sink strength, (iii) the respective individual is limited in its carbon sink capacity (e.g., through limited nutrient supply), and (iv) autumn warming does not counteract these trends. The FACE studies cited by Norby (2) do not disagree with these predictions, as we explain below.

Asshoff *et al.* (3), Godbold *et al.* (4), and Richardson *et al.* (5) did not measure photosynthesis, and their data therefore cannot be used to directly test the relationship between spring/summer productivity and leaf senescence. Asshoff *et al.*, however, measured growth responses and found that only *Fagus sylvatica* showed a small response under elevated CO₂, whereas “none of the other dominant species (*Quercus petraea*, *Carpinus betulus*) showed a growth response to CO₂ in any of the 4 years or for all years together” [(3), p. 848]. This “nonresponsiveness” of growth to elevated CO₂ and the observation that leaf senescence was only marginally affected by elevated CO₂ (4- and 5-day delays, respectively, in *Carpinus* and *Fagus*; 5-day advance in *Quercus*) agree with the sink limitation hypothesis.

The FACE experiment of Godbold *et al.* [(4), p. 839] showed that “an increase in fine root growth is a common feature in trees under elevated CO₂ and [may] be due to

high C allocation to roots, but also as a mechanism to increase nutrient uptake to meet the demand of increased aboveground growth.” Root tip numbers in *Betula pendula* increased by 31% and 41% under elevated CO₂ in 2 years, likely resulting in an increased nutrient supply and sink strength that may explain the species’ delayed autumn phenology under elevated CO₂ in these 2 years. In agreement with this, Taylor *et al.* (6) emphasized that only in the absence of sink limitation can there be a positive effect of CO₂ on autumn growth, which aligns well with our sink-driven framework of autumn senescence. They “hypothesized that, with no sink limitation, photosynthesis and canopy greenness would be maintained for longer in elevated CO₂ [...]” [(6), p. 271]. The absence of a sink limitation can likely be explained by the high nutrient availability at the FACE study site. In addition, *Populus* is associated with nitrogen-fixing bacteria (7), which may reduce nutrient limitation. The role of soil nutrient supply is also clear from a 3-year CO₂-enrichment study on *Populus trichocarpa* (8), showing that elevated CO₂ strongly advanced leaf senescence at low (natural) nutrient availability, but much less under high nutrient availability.

Norby (2) suggests that “with both *Acer saccharum* and *A. rubrum* saplings in the TACIT experiment [(9)] and the mature, deciduous *Larix laricina* trees in the SPRUCE experiment [(5)], 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 CO₂.” Instead, we reported that both autumn temperatures and spring/summer productivity had strong, interacting effects on autumn leaf senescence, which matched the observations in the aforementioned studies. Despite the counteracting effect of spring and summer productivity, autumn warming still delayed senescence dates [figure 1 of (1)]. The finding in the SPRUCE experiment (5) that year-round warming of up to 9°C leads to a delay in senescence also does not contradict our results. Although a 9°C warming probably is well above the photosynthetic optimum of boreal species, such high autumn warming likely outweighed sink limitation effects in this study.

In conclusion, we think that there is no disagreement between the results of FACE experiments and our broad-scale analysis. As Norby (2) argues, studies that found advanced autumn phenology in response to elevated CO₂ were characterized by sink limitation, which is in full agreement with our proposed mechanism, and we certainly agree that elevated CO₂ should not drive earlier leaf senescence if the balance between carbon source and sink strength is maintained. Given the feedback loops between carbon source processes (photosynthesis) and sink processes (the most important of which is nitrogen availability) (10)

and the inherent difficulties in quantifying sink versus source strength (11), the effect of CO₂ fertilization on autumn phenology remains difficult to predict. The continued combination of experimental and observational approaches will be necessary to generate robust predictions about future changes in autumn senescence, and FACE experiments provide important data for this. Obtaining a global picture of the sink limitation effect will require tests of the relative effects of source and sink activities on leaf senescence in a variety of species from different biogeographic and phylogenetic backgrounds and in different root and soil systems.

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