

## Stomatal numbers, leaf and canopy conductance, and the control of transpiration

De Boer et al. (1) concluded that doubled atmospheric CO<sub>2</sub> concentration ([CO<sub>2</sub>]), by reducing both leaf stomatal density and conductance, would decrease modeled annual transpiration by approximately 60 W m<sup>-2</sup> in Florida's subtropical vegetation. This remarkable result was accompanied by statements that current Floridian annual evapotranspiration (ET) is approximately 120 W m<sup>-2</sup> and that transpiration is approximately 50% of current ET (i.e., ~60 W m<sup>-2</sup>). (The remainder of ET is accounted for by evaporation from soil and interception water.) Because 60 minus 60 W m<sup>-2</sup> equals 0 W m<sup>-2</sup>, modeled transpiration in subtropical Florida would therefore cease with CO<sub>2</sub> doubling, implying significantly increased runoff at constant precipitation. This unlikely scenario may be related to (i) an unrealistically modeled effect of [CO<sub>2</sub>] on stomatal density and conductance and (ii) an exaggerated influence of reduced stomatal conductance on regional transpiration.

Actual stomatal density in more than half the plant species examined was insensitive to [CO<sub>2</sub>] on the time scale of the past 100 y (2). Moreover, comprehensive measurements made on plants grown for several years in subambient, ambient, and elevated [CO<sub>2</sub>] demonstrated little consequence of [CO<sub>2</sub>] on stomatal numbers (3), so we might reasonably assume that stomatal density will be little changed this century by [CO<sub>2</sub>] per se. However, even if stomatal density does decrease this century, that change would not scale to the level of regional transpiration as proposed by de Boer et al. (1).

Transpiration through higher-plant stomata is driven by atmospheric evaporative demand. For a given evaporative demand, actual transpiration is determined by soil water availability, leaf area and stomatal conductance, leaf- and canopy-scale aerodynamic conductance, and overall canopy-atmosphere coupling (references in ref. 4). These factors tend to limit the control of transpiration by stomata. In addition, evaporative demand itself is inversely related to transpiration through regional-scale feedbacks, which further limits the influence of stomata on transpiration (references in ref. 4). One illustrative

result is that the response of native-forest canopy conductance to a 150-ppm CO<sub>2</sub> increase might reduce annual transpiration only approximately 2% (4). Indeed, for annual crops and short-rotation tree plantations, which cover more than 11% of ice-free global land area, increased [CO<sub>2</sub>] might even increase transpiration because of more rapid leaf area development (5).

Despite a well documented effect of stomatal closure on transpiration by isolated leaves, stomatal conductance is expected to have only a modest degree of control over regional transpiration (4). Additionally, evidence that increasing [CO<sub>2</sub>] per se reduces stomatal density, or canopy-scale stomatal conductance, is equivocal. We therefore advocate prudence in applying output from the model of de Boer et al. (1) to issues of regional transpiration or runoff. We also caution against an assumption that transpiration at the global scale is sensitive to a [CO<sub>2</sub>]-induced decrease in stomatal conductance—with or without a reduction in stomatal density—and conclude that projecting effects of increasing [CO<sub>2</sub>] on the hydrologic cycle must account for soil and canopy processes as well as atmospheric feedback mechanisms linking water supply to evaporative demand. In all this, an appropriate treatment of surface conductance is needed.

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1. de Boer HJ, et al. (2011) Climate forcing due to optimization of maximal leaf conductance in subtropical vegetation under rising CO<sub>2</sub>. *Proc Natl Acad Sci USA* 108: 4041–4046.
2. Royer DL (2001) Stomatal density and stomatal index as indicators of paleoatmospheric CO<sub>2</sub> concentration. *Rev Palaeobot Palynol* 114:1–28.
3. Reid CD, et al. (2003) On the relationship between stomatal characters and atmospheric CO<sub>2</sub>. *Geophys Res Lett* 30:1983–1986.
4. Leuzinger S, Körner C (2010) Rainfall distribution is the main driver of runoff under future CO<sub>2</sub>-concentration in a temperate deciduous forest. *Glob Change Biol* 16: 246–254.
5. Tricker PJ, et al. (2009) Water use of a bioenergy plantation increases in a future high CO<sub>2</sub> world. *Biomass Bioenergy* 33:200–208.

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