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Soil nitrogen limitation does not impact nighttime water loss in *Populus*

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Summary Nighttime transpirational water loss from C_3 trees occurs without carbon gain and is both common and substantial. However, the magnitude of this water loss varies and a better understanding of the environmental factors driving this variation is needed. We investigated the response of nighttime conductance (g_{night}) and transpiration (E_{night}) to soil nitrogen limitation. We used instantaneous gas exchange measurements in greenhouse studies of *Populus angustifolia* James (narrow-leaf cottonwood) and *Populus balsamifera* L. spp. *trichocarpa* (Torr. & A. Gray ex Hook.) Brayshaw (black cottonwood). g_{night} for sufficiently watered plants ranged from 0.045 to 0.308 mol m⁻² s⁻¹ for *P. balsamifera* and 0.037 to 0.188 mol m⁻² s⁻¹ for *P. angustifolia*, which was much larger than minimum leaf conductance (g_{min} ; up to 0.005 mol m⁻² s⁻¹ in the dark). Long-term nitrogen limitation sufficient to substantially reduce biomass did not affect g_{night} or E_{night} when potentially confounding water stress effects were eliminated. We conclude that nighttime water loss from two *Populus* species is large and although it is under stomatal control is not regulated at night in response to soil nitrogen availability.

Keywords: drought, fertilization, nitrate, nocturnal, stomatal conductance, transpiration, water relations.

Introduction

Water availability is considered a major limiter of plant productivity in natural and agricultural systems (Lambers et al. 2008). Yet, transpirational water loss without concomitant carbon gain occurs at night in a wide range of C_3 plant species (Musselman and Minnick 2000, Caird et al. 2007, Dawson et al. 2007). Many of these species are woody plants (Caird et al. 2007 and references therein, Cavender-Bares et al. 2007, Dawson et al. 2007, Kobayashi et al. 2007, Scholz et al. 2007, Seibt et al. 2007, Goldstein et al. 2008, Mitchell et al. 2009) with reported rates of nighttime conductance (g_{night}) ranging from 0.001 to 0.450 mol m⁻² s⁻¹. Although low compared to daytime rates, these nighttime rates are often considerably higher than estimates of conductance through the cuticle and stomata at maximal closure (mini-

mum leaf conductance; g_{min} ; Rawson and Clarke 1988, Howard and Donovan 2007, Marks and Lechowicz 2007). This suggests that reported rates of high g_{night} are largely due to stomatal opening and should be under guard cell regulation.

Most studies quantify nighttime water loss in natural populations and report correlations with environmental and other physiological variables, such as leaf nitrogen content, soil moisture, air temperature and vapor pressure deficit (Benyon 1999, Oren et al. 2001, Bucci et al. 2004, Grulke et al. 2004, Dawson et al. 2007, Hubbart et al. 2007, Kavanagh et al. 2007, Marks and Lechowicz 2007, Christman et al. 2008, Moore et al. 2008, Mitchell et al. 2009). Some manipulative experiments, mostly with herbaceous species, have been performed to test these correlations (Rawson and Clarke 1988, Ludwig et al. 2006, Barbour and Buckley 2007, Cavender-Bares et al. 2007, Howard and Donovan 2007, Scholz et al. 2007, Christman et al. 2009, Chu et al. 2009, Easlon and Richards 2009, Christman et al. 2009). However, additional controlled tests are needed for woody species and to resolve recent contradictory results in the literature.

It has been suggested that nighttime water loss may be regulated in response to soil nitrogen availability with E_{night} potentially providing a nitrogen uptake benefit (Snyder et al. 2003, Caird et al. 2007, Scholz et al. 2007, Cramer et al. 2009). If maintaining a flux of water towards roots at night can decrease the formation of nutrient depletion zones, then increased E_{night} could be beneficial when water is plentiful and mobile nutrients such as nitrate are scarce. This idea is theoretically supported by the Barber Cushman model of root nutrient uptake which predicts that increased water flux to the root rhizoplane will decrease nitrate depletion zones around roots (Barber and Cushman 1981, Barber 1995). No consensus has been found among studies assessing the effect of E_{night} manipulations on plant nitrogen uptake (McDonald et al. 2002, Snyder et al. 2008, Christman et al. 2009).

A complementary approach is to test whether nutrient limitations result in up-regulation of g_{night} to promote higher E_{night} when nutrients are limiting. However, results for this in the literature are contradictory. No regulation of g_{night} in response to long-term nitrogen limitation was found for *Helianthus* and *Arabidopsis* in controlled environment experiments (Howard and Donovan 2007, Christman et al. 2009). Although applica-