Nighttime Stomatal Conductance and Transpiration in C_3 and C_4 Plants[1][W]

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Incomplete stomatal closure during the night is observed in a diverse range of C_3 and C_4 species (Fig. 1; Supplemental Table S1) and can lead to substantial nighttime transpirational water loss. Although water loss is an inevitable consequence of stomatal opening for photosynthetic carbon gain, nighttime stomatal opening is unexpected because carbon gain is not occurring and the need to cool leaves is reduced or absent. Most species have the ability to close stomata more than is commonly observed at night, as demonstrated by reduced nighttime leaf conductance (g_{night}) in response to water stress, abscisic acid (ABA), and other treatments reviewed in this *Update*.

The magnitude of water loss occurring during the night depends on both g_{night} and the vapor pressure difference (VPD) between leaves and the air, as well as canopy structure and atmospheric mixing. While g_{night} has been recorded at up to 90% of daytime conductance, nighttime VPD is typically much lower than daytime. Thus, nighttime transpiration rates (E_{night}) are typically 5% to 15% of daytime rates, although sometimes as high as 30%, based on gas exchange measurements of individual leaves, whole-plant sap flow, and field scale lysimetry (Benyon, 1999; Snyder et al., 2003; Bucci et al., 2004, 2005; Daley and Phillips, 2006; Scholz et al., 2007). While some methods are more accurate and/or have less uncertainty than others, a few studies have compared methods, generally finding agreement even across measurement scales (e.g. leaf versus whole plant; Green et al., 1989). Drawbacks for each method must be recognized, particularly when comparing species or environments. For example, leaf-level gas exchange typically includes cuticular as well as stomatal components of leaf conductance to water vapor, while sap flow methods typically have attendant uncertainties as to the proportion of the measured flux resulting in bole refilling rather than transpiration from the canopy. Nevertheless, there is broad agreement among the methods and scales that stomata of many species remain partially open during the night.

Measurements of minimum leaf conductance induced by ABA application and by drying excised leaves to wilting have been used to separate stomatal ($g_{stomatal}$) and cuticular ($g_{cuticular}$) conductance (Rawson and Clarke, 1988; Howard and Donovan, 2007). Conductance measured at maximal stomatal closure can be functionally defined as $g_{cuticular}$ because it is not under guard cell regulation. For a few species, this would include the effect of dust or stomatal plugs that prevent complete closure (Feild et al., 1998). In general, $g_{cuticular}$ estimates range from 0.004 to 0.020 mol m^{-2} s^{-1} (Rawson and Clarke, 1988; Nobel, 1991; Kerstiens, 1995; Boyer et al., 1997; Burghardt and Riederer, 2003; Howard and Donovan, 2007), far lower than most estimates of g_{night} (Fig. 1; Supplemental Table S1). Thus, most reported values of g_{night} are largely influenced by $g_{stomatal}$.

Although awareness of g_{night} and E_{night} has recently been growing, little is understood about the phenomena. In particular, the costs and benefits of high g_{night} and E_{night} remain largely unknown. However, patterns of occurrence and relationships of these processes with plant physiology are emerging. This *Update* reviews the occurrence of g_{night} in C_3 and C_4 species, plant and environmental factors that affect g_{night}, and both documented and hypothesized implications of g_{night} and E_{night} (Fig. 2).

SOURCES OF VARIATION AND FACTORS AFFECTING g_{night}

Variation Among and Within Species

Species in which g_{night} has been documented include a diverse range of genera and life forms (annuals and perennials; monocots, herbaceous dicots, shrubs, and trees; Fig. 1; Supplemental Table S1) native to a diversity of habitats: e.g. wetland (Loftfield, 1921), desert (Donovan et al., 2003; Snyder et al., 2003; Ludwig et al., 2006), neotropical savanna (Bucci et al., 2004, 2005; Domec et al., 2006; Scholz et al., 2007), temperate deciduous and evergreen forests (Benyon, 1999; Oren

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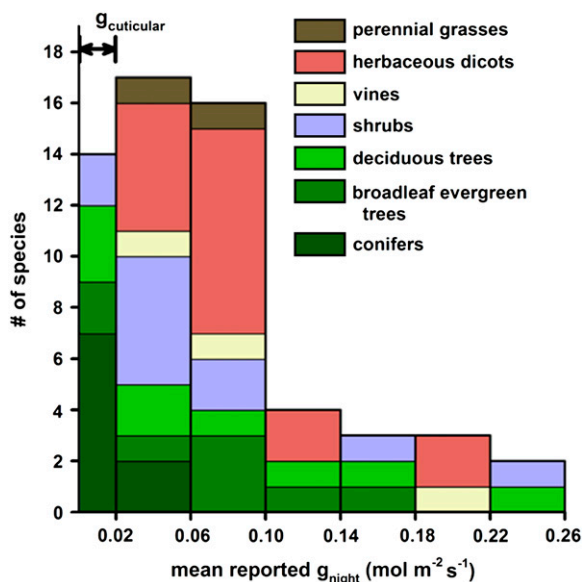
Figure 1. Histogram summarizing reported g_{night} in species among different plant functional groups. For each species, g_{night} was averaged from all reported values with units in mol m^{-2} s^{-1} presented in Supplemental Table S1 and thus represents a mixture of field and greenhouse studies. The black two-headed arrow at the top left of the graph represents the range for reported $g_{cuticular}$ taken from many species, and reported g_{night} within this range may be largely due to $g_{cuticular}$ rather than $g_{stomatal}$. A complete listing of species with references is provided in Supplemental Table S1.

et al., 2001; Barbour et al., 2005; Daley and Phillips, 2006; Kavanagh et al., 2007), and subalpine forest (Herzog et al., 1998). Many horticultural and crop species have substantial g_{night} and/or E_{night} (England, 1963; Rosenberg, 1969; Rawson and Clarke, 1988; Green et al., 1989; Blom-Zandstra et al., 1995; Assaf and Zieslin, 1996; Musselman and Minnick, 2000). Although it has been suggested that sustained nocturnal stomatal opening is not a feature of grasses (Loftfield, 1921), substantial g_{night} has been observed in *Distichlis spicata* (C$_4$; Snyder et al., 2003) and wheat (*Triticum aestivum*; C$_3$; Rawson and Clarke, 1988), among others.

Substantial variation in magnitude of maximum g_{night} has been observed among closely related species (Supplemental Table S1); however, differences among some species are minimal and not biologically significant (see Helianthus species, Supplemental Table S1; Howard and Donovan, 2007). Multiple surveys have shown that g_{night} varies substantially among species within a particular environment or habitat type (Snyder et al., 2003; Bucci et al., 2004; Daley and Phillips, 2006; Kavanagh et al., 2007), and the relationship of species differences to source environment or habitat remains unclear. Additional studies investigating g_{night} in a phylogenetic context in native and common garden locations will be required to determine whether species differences in g_{night} are adaptive.

Many studies have also demonstrated genetic variation in magnitude of g_{night} among cultivars or accessions of single species (Supplemental Table S1). Arabidopsis (*Arabidopsis thaliana*) natural accessions had a 2.5-fold variation in magnitude of g_{night} when grown in a common environment, and the variation was correlated to mean annual VPD of the accessions native environment (M. Caird, unpublished data). Although correlative, this relationship suggests the potential for natural selection to have operated on g_{night}. In addition to genetic variation, there is also evidence for separate genetic control of g_{night} from g_{day}. Three near-isogenic lines of Arabidopsis differed from their parental lines in either g_{night} or g_{day}, but not both, providing evidence that these two traits can be regulated independently due to genetic factors alone (M. Caird, unpublished data). Future studies exploiting natural and mutant genotypes will likely play an important role in discovering the genetic factors that influence g_{night} in plants.

Although recent studies of nighttime water loss generally do not consider differences in stomatal density or adaxial and abaxial surface responses, these factors may contribute to within and among species variation in g_{night}. Not only does stomatal density often differ between adaxial and abaxial leaf surfaces, but the stomata on these surfaces can respond differently to environmental cues such as light. Stomata on the
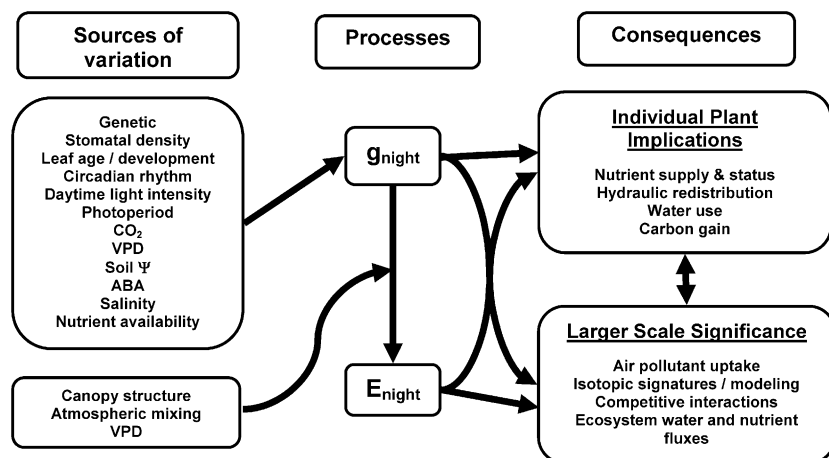
Figure 2. Diagram summarizing sources of variation (internal and external) affecting g_{night} and transpiration (E_{night}), and consequences of g_{night} and E_{night} at the individual plant and larger scales.

abaxial leaf surface, but not the adaxial surface, remained open at night in cotton (*Gossypium hirsutum*; Sharpe, 1973) and fava bean (*Vicia faba*; Aben et al., 1989). Future studies need to consider how these factors may affect g_{night} and E_{night}, particularly with regard to between and within species variation in g_{night}.

Diurnal Patterns for $g_{stomatal}$

For many species, g_{night} is not stable throughout the night period. Endogenous, gradual increases in stomatal opening during predawn hours have been reported in many species under natural field conditions as well as in controlled environments (Schwabe, 1952; Muchow et al., 1980; Anderson, 1982; Lasceve et al., 1997; Leymarie et al., 1998, 1999; Donovan et al., 2003; Bucci et al., 2004; Dodd et al., 2005; Howard and Donovan, 2007). In Arabidopsis accession Columbia, a mean minimum g_{night} of 0.117 mol m^{-2} s^{-1} slowly increased to a predawn mean of 0.161 mol m^{-2} s^{-1}, amounting to a 38% increase in $g_{stomatal}$ during the night (Lasceve et al., 1997). Arabidopsis mutants with disrupted circadian rhythms do not have increased stomatal opening in predawn hours, indicating g_{night} has some component of circadian regulation (Dodd et al., 2004, 2005). Lasceve et al. (1997) also found starch-deficient Arabidopsis mutants do not have the increased endogenous predawn opening observed in wild-type plants, implying that starch metabolism, possibly through the formation of an osmoticant necessary for guard cell osmoregulation, is an important factor affecting stomatal opening during predawn.

Photoperiod length and light intensity can affect the speed and degree to which stomata close in the dark. Incomplete stomatal closure at night resulted from short-day as opposed to long-day photoperiods in Chrysanthemum (Schwabe, 1952). Higher light intensity during the day or longer supplementary lighting intervals (extending light period into the normal night) resulted in faster stomatal closure responses to lights turning off in roses, although closure was still incomplete (Blom-Zandstra et al., 1995). The spectrum of the low intensity supplementary light (25 μmol m^{-2} s^{-1}) also affected g_{night}, with orange and blue supplementary light preventing complete stomatal closure 2.5 h into the night, while white and no (control) supplementary light resulted in g_{night} comparable to previously determined $g_{cuticular}$ (0.01 mol m^{-2} s^{-1}; Blom-Zandstra et al., 1995). This evidence, together with evidence of starch-deficient Arabidopsis mutants having decreased nighttime stomatal opening (Lasceve et al., 1997), suggests that daytime conditions and photosynthetic rates can influence g_{night}. Although the exact mechanism is unclear, it is possible that a byproduct of starch metabolism may affect guard cell osmoregulation at night (Lasceve et al., 1997), causing greater stomatal opening when starch levels are high. Positive correlations have been observed for g_{night} and g_{day} among species in Great Basin habitats (Snyder et al., 2003). Although only correlative data are available, the

relationship may be the result of daytime conditions that allow high photosynthetic rates but also result in high g_{night}. Alternatively, leaf development and stomatal anatomy that affect g_{day} could be a cause for correlation with g_{night}.

Responses to Atmospheric Water Demand

Atmospheric conditions can be important in driving E_{night} when stomata are open, as evidenced by canopy scale measurements of crop water loss on weighing lysimeters (England, 1963; Rosenberg, 1969). Advection was found to create sufficient evaporative demand to cause 20% to 30% of total daily transpiration to occur at night in alfalfa (*Medicago sativa*) in the field (Abdel-Aziz et al., 1964) and kiwifruit (*Actinidia deliciosa*) in orchards (Green et al., 1989). Seginer (1984) extended this concept to show energy requirements and conditions in greenhouses under which E_{night} occurs in roses using a modified version of the Penman model.

In natural systems, increased VPD has been correlated with greater E_{night} at the scale of sap flux for many tree species (Herzog et al., 1998; Benyon, 1999; Oren et al., 2001; Daley and Phillips, 2006; Kavanagh et al., 2007). A trend for lower g_{night} with increasing VPD has been observed in some species (Muchow et al., 1980; Oren et al., 2001; Bucci et al., 2004), yet some data indicate lack of any response (Barbour et al., 2005). However, correlative studies such as these do not control for possible variation due to inherent circadian regulated stomatal opening that might parallel decreasing VPD during the night. Nevertheless, similar correlations have been found when nighttime VPD around plants is experimentally manipulated, providing more direct evidence that some species do close stomata in response to higher VPD during the night just as during the daytime (Bakker, 1991). A more thorough understanding of whether VPD regulates g_{night} in a manner parallel to that of g_{day} will require more studies that manipulate VPD while controlling for other potentially confounding factors, including circadian rhythms.

Responses to Water Availability and ABA

It is expected that at night stomata will be sensitive to decreased water availability, just as during the daytime, to conserve water. Lower g_{night} has been associated with decreased plant water status in *Hibiscus cannabinus* (Muchow et al., 1980), *Pseudostuga menziesii* (Running, 1976; Blake and Ferrell, 1977), and *Helianthus anomalus* (Ludwig et al., 2006). In a field experiment, g_{night} of unirrigated desert shrubs was lower than that of shrubs receiving surface irrigation (Donovan et al., 2003). In greenhouse studies, g_{night} decreased in response to a water stress treatment in wheat (Rawson and Clarke, 1988) and in Helianthus species (Howard and Donovan, 2007). Similar to drought, increased salinity also reduced g_{night} in desert shrubs (Donovan et al., 1999).

The magnitude of g_{night} can additionally vary seasonally. For *Chrysothamnus nauseosus*, g_{night} was reduced at

the end of growing season when soils were dry, while the cooccurring *Sarcobatus vermiculatus* had higher g_{night} (relative to g_{day}) by the end of the season (Donovan et al., 2003). The Sarcobatus response may be related to its capacity to accumulate high concentrations of leaf apoplastic solutes (James et al., 2006), which could in turn affect stomatal regulation. Seasonal changes in g_{night} were also found for *Pinus ponderosa*, with stomata more open during the night in early summer, like Chrysothamnus (Grulke et al., 2004).

ABA can induce stomatal closure during the dark (Rawson and Clarke, 1988; Howard and Donovan, 2007). Similar to responses observed during the daytime, increased concentrations of exogenous ABA resulted in greater stomatal closure at night in Arabidopsis, and stomatal closure in response to ABA was more prominent at higher CO_2 (Leymarie et al., 1998, 1999). In *P. menziesii* seedlings, nighttime leaf resistance was sensitive to the ABA content of leaves (Blake and Ferrell, 1977), indicating ABA induced stomatal closure in response to water stress at night just as during the daytime.

Nutrient Availability

Typically, higher nutrient availability, particularly nitrogen (N), is correlated with higher daytime photosynthesis (Lambers et al., 1998). However, varying results have been found for correlations of nutrient supply and g_{day} (Meinzer et al., 1988; Toft et al., 1989). Similarly, species show different responses of g_{night} to limited nutrient supply. In two field studies with nutrient treatments, high nutrient plants had lower g_{night}, but the experimental designs do not allow unambiguous separation of direct effects due to reduced plant demand for nutrient acquisition regulating g_{night} from indirect effects of plant size or water status (Ludwig et al., 2006; Scholz et al., 2007). Other nutrient response experiments that controlled for plant water status have found differing effects of N supply on g_{night}. For example, reduced g_{night} was observed in N-limited Arabidopsis, but higher g_{night} was found in N-limited *D. spicata* and *Populus balsamifera* subsp. *trichocarpa* (M. Caird and A. Howard, unpublished data). Still other species showed no g_{night} response to soil nutrient limitations (Helianthus species; Howard and Donovan, 2007). The relationship between varying g_{night} responses to nutrients and particular life forms or ecological strategies is unknown and may be related to the underlying causes of nutrient status effects on g_{day}.

IMPLICATIONS OF g_{night} AND E_{night}

Air Pollution Uptake

The occurrence of high g_{night} in many C_3 and C_4 plant species has important implications for air pollutant uptake (Goknur and Tibbitts, 1984; Segschneider et al., 1995; Musselman and Minnick, 2000; Takahashi et al., 2005). $g_{stomatal}$ is a major factor affecting ozone (O_3) uptake in plants (Wieser and Havranek, 1993). Tree

species in areas with high levels of O_3 exposure can have stomata open at night (Wieser and Havranek, 1993; Matyssek et al., 1995), and nocturnal O_3 uptake can be a significant proportion of daily O_3 uptake (up to 9%; Grulke et al., 2004). Stomatal responsiveness may be reduced after exposure to O_3 (Keller and Hasler, 1984; Skarby et al., 1987). Whole-plant production and carbon allocation in *Betula pendula* were also more sensitive to nighttime compared to daytime O_3 exposure (Matyssek et al., 1995). Thus, O_3 damage resulting from nighttime uptake may be an important factor for plants. However, g_{night} may also prove to be useful in areas of high air pollution. For example, *H. cannabinus* may be useful as a phytoremediator of NO_2 because this species has high g_{night} and g_{day} (Takahashi et al., 2005).

Isotopic Signatures and Modeling

Nighttime stomatal opening may influence oxygen isotope signatures of within-canopy CO_2 (Barbour et al., 2005). This has important implications for models describing ecosystem respiratory CO_2 flux and its partitioning into above- and below-ground components. ^{18}O enrichment of leaves will also be affected by g_{night}, complicating the use of such signatures in detecting genetic or environmental effects on transpiration rate. Variation in magnitude of g_{night} among species and the regulation and responses of g_{night} to environmental factors (i.e. VPD) are important considerations in determining how large an impact nighttime stomatal opening will have on oxygen isotope signatures. More research on these topics is required and will need to be incorporated into models.

Potential for Increased Daytime Carbon Gain

Plants may be able to increase their photosynthetic carbon gain by preopening stomata before dawn. This might be especially advantageous in water-limited environments because of a higher potential for early morning carbon gain when temperatures and VPD are lower. Although stomatal responses to light are typically fast, there is some evidence to support the hypothesis that maintaining open stomata at night affects daytime opening. In *Xanthium pennsylvanicum*, the rate of stomatal opening in light was greater when stomata were open during the night (Mansfield and Heath, 1961). However, there is no evidence for an effect of experimentally lowering g_{night} on carbon gain or g_{day} during the subsequent day. Additional research is necessary to directly test whether high g_{night} influences early morning and total daily carbon gain, and if so how much and by what mechanism.

Effects on Water Relations

Plant water potential is expected to equilibrate with the wettest soil layer in the rooting zone overnight. However, substantial E_{night} can prevent equilibration

from occurring, resulting in soil-plant predawn water potential disequilibrium, or predawn disequilibrium (Donovan et al., 2001), which complicates interpretation of soil moisture availability based on plant water potential measurements. E_{night} has been observed to contribute to predawn disequilibrium in many species (Donovan et al., 1999, 2001, 2003; Sellin, 1999; Bucci et al., 2004, 2005; Kavanagh et al., 2007).

Substantial E_{night} may additionally reduce a plant's ability to conduct hydraulic redistribution (HR, also referred to as hydraulic lift; Richards and Caldwell, 1987). HR occurs when some roots are absorbing water from wet soil locations and other roots of the same plant are losing water to relatively dry soil locations. When stomata are open and the atmospheric conditions allow E_{night} to occur, the water loss through the shoot should decrease the amount released to drier soil layers because of impacts on plant water potentials. Plants in natural populations can simultaneously have both HR and high E_{night}, although these two processes may vary in magnitude through the growing season (Donovan et al., 2003; Domec et al., 2006).

Nutrient Supply and Distribution

Significant water loss without simultaneous photosynthetic carbon gain could constitute a major cost to a plant. However, it is possible that E_{night} may provide a benefit that outweighs this cost. Mobile mineral nutrients are moved into the immediate vicinity of plant roots (i.e. the rhizosphere) by transpiration-driven mass flow of the soil solution (Barber, 1995). Thus, the maintenance of a continuous water stream through the plant during both day and night could potentially result in enhanced nutrient availability to the plant. McDonald et al. (2002) showed that CO_2-induced stomatal closure reduced transpiration and N acquisition by *Populus deltoides*.

Using the Barber-Cushman model, the effect of increased water flux on nitrate uptake and nutrient concentration in the rooting zone can be predicted (Barber and Cushman, 1981). The general result is that increasing water flux eliminates or minimizes the depletion zone, which develops in the rhizosphere, by maintaining a supply of nitrate to the root (Barber and Cushman, 1981; Barber, 1995). However, under low nitrate or high root length density conditions, the effect is reduced and total nitrate uptake is not affected dramatically. We are experimentally testing this hypothesis.

In addition to supply of nutrients to roots, the distribution of nutrients within plants, particularly phloem-immobile nutrients such as calcium, depends on the xylem flow rate and duration of transpiration (Marschner, 1995). An increase in the total amount of water flowing through the xylem may improve nutrition when organs are Ca deficient. Daley and Phillips (2006) also suggest that g_{night} may enhance nutrient transport within trees such as paper birch by providing oxygen to sapwood parenchyma cells that function in nutrient transport and storage.

Implications for Growth and Plant Fitness

Implications for plant water and nutrient relations suggest that E_{night} may also impact plant productivity and growth, although experimental evidence on the subject is scarce. It is intuitive that E_{night} poses costs to plants under water-limiting conditions as evidenced by reduction in g_{night} in response to water stress. However, more research is necessary to determine what benefits, if any, may either balance or outweigh these costs.

CONCLUSION

Although research dating back to the late 1800's describes stomata of many C_3 and C_4 plant species as incompletely closing during the night, very little is understood about this phenomenon. We have summarized a growing body of evidence showing that g_{night} is regulated, in many ways similar to daytime stomatal regulation, and that nighttime stomatal opening and transpiration have implications for plant growth and physiology. Nevertheless, more research will be necessary to fully appreciate the significance of g_{night} and E_{night}. Future research on plant regulation of g_{night} and the consequences of substantial E_{night} for water and nutrient relations will be key for understanding the ecological and evolutionary consequences of g_{night} and E_{night} in C_3 and C_4 plants.

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