NOCTURNAL STOMATAL CONDUCTANCE IN C_3 AND C_4 PLANTS: A META-ANALYSIS

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Faqrul Islam CHOWDHURY

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List of symbols and abbreviations

A = Assimilation

Bor = Boreal forest

Cis = Confidence intervals

CWF = Cool white fluorescent lamps

DX = Desert and Xeric species

E_{n} = Nocturnal transpiration

ET = Evapotranspiration

GF = Green fluorescent lamps

g_{n} =Nocturnal stomatal conductance

LEDs = Light Emitting Diodes

MAP = Mean annual precipitation

MAT = Mean annual temperature

Med = Mediterranean

N = Nitrogen

NPK = Nitrogen-Phosphorus-Potassium

O_3 = Ozone

P = Phosphorus

PAR = Photosynthetic active radiation (PAR)

PFTs = Plant functional types

Q= Qualitative review

R= Regression analyses

RGB = Red and blue LEDs (Light Emitting Diodes) with green fluorescent lamps

SC= Step change analyses

SLA = Specific leaf area

Temp = Temperate forest

TOC1 = TIME OF CAB EXPRESSION (TOC1)

Trop = Tropical forest

VPD = Vapour pressure deficit

Ψ_{pd} = Predawn water potential

Abstract

It is currently thought that nocturnal water losses are negligible but recent research indicates that incomplete stomatal closure during night could cause substantial water losses at leaf, plant and ecosystem scales. However, only day time transpiration is currently accounted for in evapotranspiration studies. Under global warming, when water scarcity might increase in some parts of the world, significant nocturnal water losses during a time when photosynthetic carbon gain is absent could potentially impact the global water cycle and, consequently, plant productivity. However there are important uncertainties on the drivers and magnitude of nocturnal water fluxes that hinder its incorporation within modelling frameworks. Here I synthesize studies on nocturnal stomatal conductance (g_n) to find out underlying drivers and whether this process is beneficial in plants through a review of the literature and meta-analysis. In total 62 research articles with 79 unique studies were scanned to obtain data on g_n, and 1097, 589 and 998 data points on early night, late night and daytime stomatal conductance (g_d), respectively, were digitized from those articles. 131 unique C_3 or C_4 plant species were included from 11 plant functional types (PFTs) and 5 biomes around the world. Crop species showed the lowest proportion of night- to day-time stomatal conductance (g_n/g_d) (20.5%) and tropical trees the highest (49.9%). In case of biomes, highest g_n/g_d occurred in the tropics (47%) and Mediterranean ecosystems showed the lowest (19.2%). Interestingly, desert species have the second highest g_n/g_d (37.7%) among the catalogued biomes. I observed how neither vapour pressure deficit nor nutrient status affected significantly g_n across species. These findings indicate that day- and night- time stomatal conductance are driven by different processes, on the one hand, and that enhanced nutrient uptake is not one of the benefits of g_n. Perhaps the clearest trend amongst studies was an increase of g_n from the beginning until the end of the night, indicating significant and widespread endogenous regulation by the circadian clock, potentially enhancing C uptake early in the morning. g_n also tended to decline with water scarcity. Here I quantify the importance of g_n amongst biomes and PFTs, and how circadian rhythms exert the major control in this process at nocturnal time scales.

Keywords: *Nocturnal stomatal conductance, transpiration, evapotranspiration, circadian clock.*

1. Introduction

Evapotranspiration (ET) is responsible for the return of 60% of annual precipitation to the atmosphere, a proportion that increases up to 95% of precipitation in water-limited ecosystems. ET is thus a major driving component of the global hydrological cycle (Hetherington and Woodward 2003, Wilcox and Thurow 2006). Transpiration is considered as the dominant contributor of ET (i.e. evaporation and transpiration) because it accounts for 61% of ET, which is equivalent to approximately 39% of total incoming precipitation (Schlesinger and Jasechko 2014). Transpiration mainly depends on vegetation cover, surface wetness, and the availability of soil water for root transpiration uptake (Wang and Dickinson 2012). For example, in an arid and semiarid olive orchard site, transpiration may account for 100% of the total ET prior to irrigation, but only 69–86% of ET during peak midday fluxes (Williams *et al.* 2004). Besides, transpiration in tropical Amazonian forests accounts for about 70% of ET (Kumagai *et al.* 2005). Surface conductance, a process driven by stomatal conductance, represents another important ET driver.

Indeed, transpirational water losses occur mostly through the stomatal pores. Although these pores comprise only 5% of a leaf surface, the losses of water vapour through stomatal pores can reach up to 95% or more of total leaf water losses. It has traditionally been considered that stomata close during non-photosynthetic periods, causing transpiration to decrease to zero. Hence, most of the hydrological models reduce ET to zero at night in agricultural and Earth science studies (Dawson *et al.* 2007, Fisher *et al.* 2007). However, plant physiological studies have revealed that partial stomatal opening during the night, controlled by guard cell regulation (Howard and Donovan 2010), is leading substantial nocturnal water loss (Caird *et al.* 2007) which may account for more than 12-25% of total transpirational water losses at leaf and plant levels (Resco de Dios *et al.* 2015). Understanding nocturnal stomatal conductance (g_n) is thus essential for assessments of the water balance at leaf to ecosystem scales (Zeppel *et al.* 2014) as it accounts for a substantial fraction of ecosystem water use in different kinds of biomes and ecosystems (Oishi *et al.* 2008, Barbeta *et al.* 2012, Wallace and McJannet 2010). Nocturnal stomatal conductance could additionally impact current discussion on whether there is an acceleration or intensification of the hydrological cycle under global warming scenario, a long-standing paradigm in climate research recently being challenged (Huntington 2006).

g_n has been reported for a wide range of C_3 and C_4 species including grasses, shrubs, trees and crops and for different biomes across the world (Dawson *et al.* 2007, Snyder *et al.* 2003).

However the mechanistic underpinnings of nocturnal transpiration (E_n) and g_n remain poorly understood which consequently impairs model implementation (Caird *et al.* 2007). As water losses through g_n occur during the dark period, when there is no photosynthetic carbon fixation, this process may be a futile or there may be potential benefits derives from E_n and g_n which may include improved oxygen supply to the sapwood (Gansert 2003), increased photosynthetic rates during the early morning hours (Resco de Dios *et al.* 2016a), the prevention of CO_2 build-up during high nocturnal respiration rates (Marks and Lechowicz 2007) or enhanced nutrient uptake via mass flow.

Different drivers affect g_n, implying that is not simply a consequence of “leaky” stomatal closure (Zeppel *et al.* 2014). Drivers of g_n such as vapour pressure deficit (VPD), CO_2 concentration, water availability, temperature etc. have been assessed in many studies, but different results have been obtained. For example, higher g_n in has been observed under nutrient-limiting conditions (Ludwig *et al.* 2006, Scholz *et al.* 2007, Kupper *et al.* 2012), supporting the notion that g_n is beneficial as it enhances nutrient uptake, but g_n reductions under nutrient limitation have also been reported (Howard and Donovan 2007, 2010). Besides, increases in g_n when VPD is lower have been observed in some cases (Muchow *et al.* 1980, Bucci *et al.* 2004), but not in others (Barbour and Buckley 2007, Barbour *et al.* 2005).

Endogenous processes such as circadian rhythms lead to temporal pattern in g_n which result higher rates of g_n in late night time when compared with early night time (Hennessey *et al.* 1993, Easlon and Richards 2009, Resco de Dios *et al.* 2009, 2013a). This regulation of g_n facilitates plants to uptake more C in the early morning (Mansfield and Heath 1961). This process is mainly entrained by the photoperiod, which is a deterministic function of geographic location and time of year (Resco de Dios *et al.* 2013a). However, the role of circadian clock as a driver of nocturnal g_n is still under debate (Resco de Dios *et al.* 2012, 2013a). Although environmental responses of stomata are reasonably fast, stomatal “priming” at predawn may foster responses to morning light, decrease diffusion limitations to photosynthesis and it has sometimes been correlated with enhanced growth (Resco De Dios *et al.* 2016a).

Response of g_n to different drivers is also different from daytime stomatal conductance (g_d). For instance, g_n is often higher under elevated CO_2 than under ambient CO_2 concentrations (Easlon and Richards 2009, Zeppel *et al.* 2012), which is opposite to the typical daytime response of a reduction in g_d under elevated CO_2 (Ainsworth and Rogers 2007). Similarly, g_n response to VPD sometimes differ from g_d, as previously mentioned (Jones 1998). Different g_n vs g_d environmental responses complicate modelling, as they indicate that daytime model processes cannot be applied for predicting nocturnal responses. Inclusion of g_n in modelling is consequently constrained by lack of mechanistic understanding on the drivers of g_n.

In a nutshell, there are still major unknowns on the drivers of g_n and potential benefits that it brings. Moreover, limitations of current techniques make it difficult to access the drivers of nocturnal water loss by plants at ecosystem levels (Resco de Dios *et al.* 2015). However, there is a wealth of studies on g_n in the scientific literature which can be used to synthesize the different drivers as well as the function of g_n. Here I combine these studies through a literature survey in an attempt to find generality of g_n in terms of its drivers, and the potential benefits that the process may bring to the plant. The review is accompanied by some quantitative analyses for those process that had been assessed in different studies and species.

The general objective of this study is to understand the drivers and the potential function of g_n. For that I conducted a broad survey of the literature to understand what aspects of g_n have been assessed. My first goal was to quantify g_n across plant functional types (PFTs) and biomes. Second, I thought to disentangle the effects of environmental drivers on g_n. Third, I will study the effects of biotic drivers on g_n. Fourth, I will discuss the possible functions of g_n, given previous results and, finally, I will present the conclusions. I expected that a wealth of studies would be found and that different processes would influence g_n. My original predictions were that the following drivers would dominate the response:

a. Similar to daytime responses, VPD will have a negative effect on g_n
b. Soils with higher nutrient condition will reduce g_n.
c. Similar to daytime responses, temperature increases g_n.
d. Similar to daytime responses, elevated CO_2 reduces g_n.
e. Similar to daytime responses, higher soil water scarcity will decrease g_n.
f. In the sites with elevated O_3 stomata may remain open overnight.
g. Early night stomatal conductance will be lower than late night g_n due to endogenous circadian regulation.
h. Photosynthates are important drivers of nocturnal opening, by providing osmoticant necessary for opening. Consequently, g_n will be positively affected by photosynthesis.

2. Methods

2.1. Literature search

A thorough search in the Scopus database was performed using the search terms “nocturnal AND stomata*” and “night AND stomata*” which led to 1384 and 2802 documents respectively. To avoid the duplicate the articles a combined search with above search terms was also performed: “nocturnal AND stomata*” OR “night AND stomata*”, and this produced 3736 documents. No filter was applied and such general word combination was used to minimize the number of articles that can be omitted if more stringent filters had been applied. References from each article were also systematically examined to find out other suitable papers that may be left out from the original search in the database. I only considered papers with C_3 or C_4 plants. In the end there were 62 scientific articles containing 79 independent experiments that could be used for this meta-analysis.

2.2. Data collection

Table 1 contains the list of parameters of g_n. In addition, the following data were also collected from each article:

- Experimental data: facility type, age of plants and experiment, PFTs, biomes, species name and period of experiment and solar time for data collection.
- Metrological and geographical data: Mean annual precipitation (MAP), mean annual temperature (MAT) elevation, current precipitation, period of data collection and location.
- Growth condition data such as water availability, nutrient, VPD, CO_2, relative humidity, temperature, photoperiod, photosynthetic active radiation (PAR) were also noted.

Standard deviation or standard error of the mean was also collected when available. Data was converted to SI units if different units were given in the paper. Besides, when start and end of night time was not mentioned in a paper, data from sunset and until 0200h was recorded as early night whereas from 0200h until sunrise it was considered as late night.

Information was obtained from the text and tables for each article to find out the above mentioned data. Data from different graphs was collected by using WebPlotDigitizer-3.8-Desktop software (Rohatgi 2017). In the case of stomatal conductance 1097, 589 and 998 data points on early night g_n, late night g_n and g_d respectively were digitized from the papers.

2.3. Analyses

All analyses and plots were performed with the R (version 3.4.0) statistical software environment (R Development Core Team 2017) using the R-studio interface. The parameters with which g_n data were analysed or reviewed are presented in Table 1. I conducted a qualitative review of the parameters that had been examined in less than 5 species, and a more quantitative assessment or meta-analysis was conducted when in more data-rich parameters.

Table 1: Parameters involved in the analyses (Q= qualitative review, R= regression analyses, SC= Step change analyses)

Drivers		**Analysis type**	**References**
Environmental drivers	Predawn water potential	R	Zeppel *et al.* 2011, Howard and Donovan 2007, Bucchi *et al.* 2004, Scholz *et al.* 2007, Muchow *et al.* 1980, Grulke *et al.* 2004, Turner *et al.* 1978, Dawson and Bliss 1989, Fuentes *et al.* 2014, Donovan *et al.* 2003.
		SC	McNellis and Howard 2015, Scholz *et al.* 2007.
	Vapour pressure deficit	R	Howard and Donovan 2010, Zeppel *et al.* 2011, Howard and Donovan 2007, Escalona *et al.* 2013, Barbour and Buckley 2007, Bucchi *et al.* 2004, Cavender-Bares *et al.* 2007, Moore *et al.* 2007, Daley and Phillips 2006, Phillips *et al.* 2010, Scholz *et al.* 2007, Furukawa *et al.* 1990, Bakker 1991, Muchow *et al.* 1980, Matyssek *et al.* 1995, Goknur and Tibbits 2001, Konarska *et al.* 2016, Pfautsch *et al.* 2011, Mendes and Marenco 2014.
	Air temperature	R	Moore *et al.* 2007, Furukawa *et al.* 1990, Muchow *et al.* 1980, Goknur and Tibbits 2001, Paudel *et al.* 2016, Konarska *et al.* 2016, Barbour and Buckley 2007.
		SC	Resco de Dios *et al.* 2013, Zeppel *et al.* 2011, Konarska *et al.* 2016, Duarte *et al.* 2016.
	Heat wave	Q	Duarte *et al.* 2016.
	Soil temperature	Q	Rogiers and Clarke 2013.

	Salinity	Q	Donovan *et al.* 1999, Christman *et al.* 2009.
	Nutrient	SC	Howard and Donovan 2010, Resco de Dios *et al.* 2013b, Howard and Donovan 2007, Ludwig *et al.* 2006, Scholz *et al.* 2007, Scholz *et al.* 2007, Senbayram *et al.* 2015, Eller *et al.* 2016.
	Ozone	SC	Keller and Hiisler 1984, Skarby *et al.* 1987, Grulke *et al.* 2004, Matyssek *et al.* 1995, Paudel *et al.* 2016, Salvatori *et al.* 2013.
	CO_2	SC	Resco de Dios *et al.* 2013b, Zeppel *et al.* 2011, Shi *et al.* 2016, Easlon and Richards 2009, Costa *et al.* 2015, Resco de Dios *et al.* 2016.
	Light	Q	Blom-Zandstra *et al.* 1995, Easlon and Richards 2009, Konarska *et al.* 2016, Barbour *et al.* 2005, Kim *et al.* 2004.
	Elevation	Q	Habibi and Ajory 2015.
Biotic drivers	Circadian clock	SC	Howard and Donovan 2010, Escalona *et al.* 2013, Barbour and Buckley 2007, Bucchi *et al.* 2004, Takahashi *et al.* 2005, Lewis *et al.* 2011, Moore *et al.* 2007, Daley and Phillips 2006, Donovan *et al.* 2003, Furukawa *et al.* 1990, Easlon and Richards 2009, Lasceve *et al.* 1997, Muchow *et al.* 1980, Zeppel *et al.* 2010, Skarby *et al.* 1987, Turner *et al.* 1978, Matyssek *et al.* 1995, Goknur and Tibbits 2001, Dawson and Bliss 1989, Fuentes *et al.* 2014, Paudel *et al.* 2016, Kim *et al.* 2004, Pfautsch *et al.* 2011, Resco de Dios *et al.* 2016, Rohula *et al.* 2016, Jianhua *et al.* 2015, Ting 1987.
	Assimilation	R	Howard and Donovan 2010, Resco de Dios *et al.* 2013b, Ludwig *et al.* 2006, Rogiers and Clarke 2013, Press *et al.* 1993, Christman *et al.* 2009, Habibi and Ajory 2015, McNellis and Howard 2015, Resco de Dios *et al.* 2016.
	Specific Leaf Area	Q	Ludwig *et al.* 2006, Press *et al.* 1993.
	Stomatal	Q	Cavender-Bares *et al.* 2007, Rogiers and Clarke 2013,

	density		Lasceve *et al.* 1997.
	Leaf Nitrogen	Q	Howard and Donovan 2007, Ludwig *et al.* 2006.
	Genotypic variation	Q	Escalona *et al.* 2013, Blom-Zandstra *et al.* 1995, Lasceve *et al.* 1997, Christman *et al.* 2009, Leymarie et al. 1998, Costa *et al.* 2015, Salvatori *et al.* 2013, Resco de Dios *et al.* 2016.
Others	Sex	Q	Dawson and Bliss 1989.
	ABA	Q	Leymarie *et al.* 1998.
	Starchless mutant	Q	Lasceve *et al.* 1997.
	Plant age	SC	Howard and Donovan 2007 Blom-Zandstra et al. 1995, Grulke et al. 2004, Turner et al. 1978, McNellis and Howard 2015.
	Leaf age	Q	Phillips *et al.* 2010, Zeppel *et al.* 2010, Matyssek *et al.* 1995.

Comparisons across plant PFTs and biomes were conducted using the values under control conditions for species and experiments. PFTs were labelled as in Lin *et al.* (2015). If any species appeared in two or more studies, or if there were multiple genotypes from 1 species, 1 single mean value was taken prior to PFT and biome averaging.

I conducted regression analyses for parameters showing continuous variation and what I will call "step change analyses" for categorical variables. Regression models were performed with the *lm* command in R. Confidence intervals (CIs) for effect-size estimates were calculated and an effect was deemed significant when the interval captured by the CI of the slope did not overlap with zero line. For categorical variables, unweighted analysis was performed by using the percent response ratio (RR) to quantify the response to g_n. This process is followed as it is commonly practiced in ecological meta-analyses (Curtis and Wang 1998, Hedges *et al.* 1999, Wang *et al.* 2012, Resco de Dios *et al.* 2016b). CIs for effect-size estimates were calculated by bootstrapping the unweighted data with a resampling of 10000 iterations. An effect was considered significant when the interval captured by the CI did not overlap the zero line. In case of nutrient treatment, different nutrient concentration such as nitrogen (N), phosphorus (P), and nitrogen-phosphorus-potassium (NPK) were combined to get ample data for meta-analysis.

3. Results and discussion

3.1. Variation of g_n among plants functional types (PFTs) and biomes

I was able to obtain data for 131 individual plant species across 11 PFTs and 5 biomes. Among the different PFTs, the rate of g_n in plants were varied from 18.3 to 123.2 mmolm^{-2}s^{-1} and, in case of biomes, g_n ranged from 39.9 to 145 mmol m^{-2} s^{-1}. Besides, the ratio of g_n/g_d varied from 20.5 to 49.9% in PFTs while the range of the ratio was 19.2 to 47% across the biomes. I did not seek to compile information on cuticular conductance as that has been the topic of other studies, but it is often reported to be below 20 mmol m^{-2} s^{-1}.

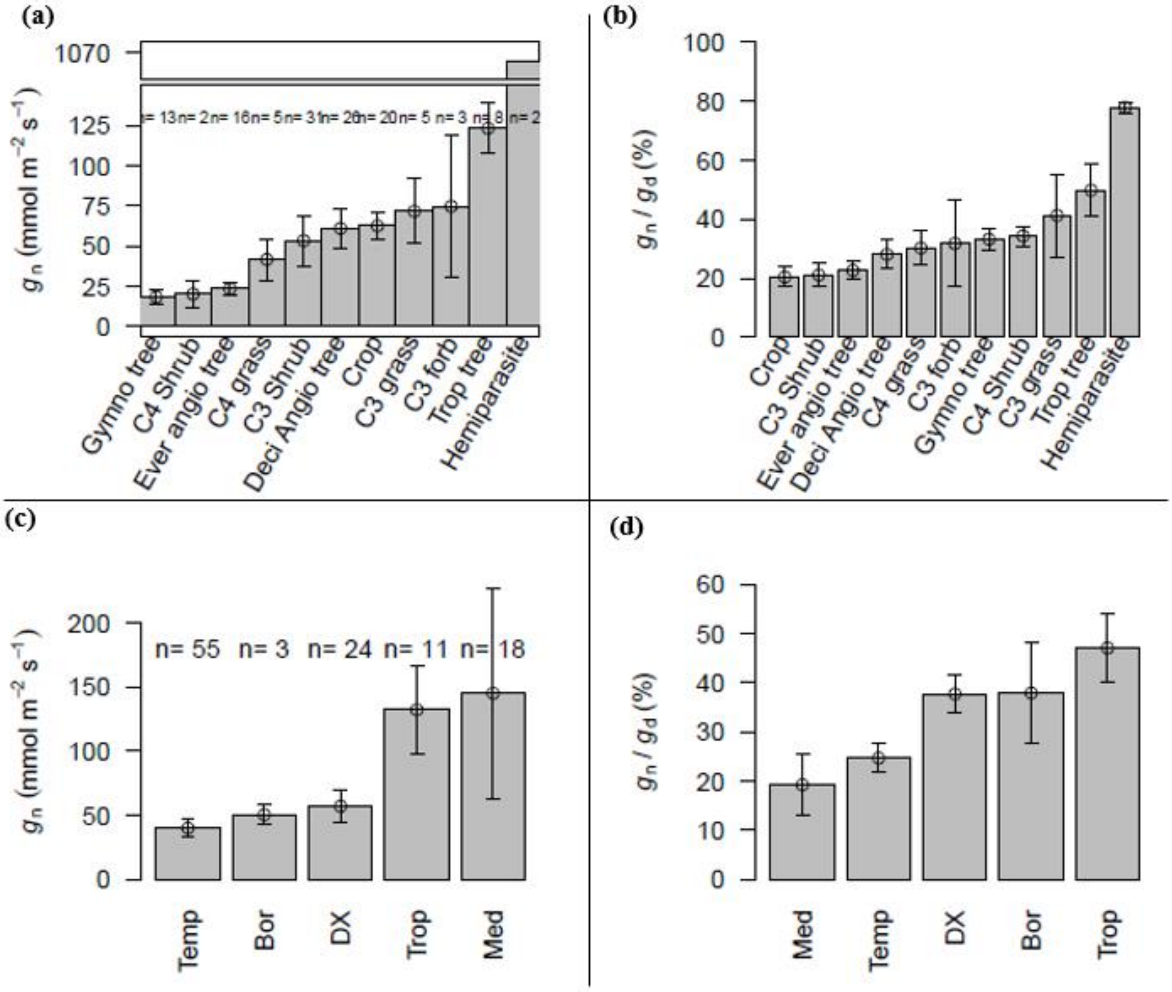

Figure 1: Magnitude of g_n in across PFTs and biomes, (a) g_n vs PFTs, (b) g_n /g_d vs PFTs, (c) g_n vs biomes and (d) g_n /g_d vs biomes (In case of biomes, Med=Mediterranean, Temp=Temperate forest, DX= Desert and Xeric species, Bor= Boreal forest, Trop=Tropical forest). Error bars indicate standard errors. Number of species for each case is indicated by the *n* value.

In case of PFTs the lowest rates of g_n found were for gymnosperm trees (18.3 mmol m^{-2} s^{-1}) whereas tropical trees (123.2 mmol m^{-2} s^{-1}) had the highest g_n rates among trees, with hemiparasitic plants (1064.5 mmol m^{-2} s^{-1}) showing the highest g_n overall. However, when the ratio of g_n over g_d (in %) was considered, crops (20.5%) showed the lowest proportional values of g_n/g_d but tropical trees (49.9%) showed the highest ratio after hemiparasitic plants. Considering previously mentioned thresholds for cuticular conductance, g_n would appear to be insignificant for C_4 shrubs, gymnosperm trees and evergreen angiosperms, as g_n values are only slightly above or below the threshold of 20 mmol m^{-2} s^{-1}.

In the case of biomes, tropical trees have the highest g_n/g_d (47%) and Mediterranean ecosystems the lowest (19.2%). Desert species showed the second highest g_n/g_d (37.7%) among the catalogued biomes, which was higher that the g_n/g_d for sclerophyllous Mediterranean vegetation. The tropics have more soil water availability which may cause the higher stomatal conductance and Mediterranean and desert vegetation try to conserve more water by lower stomatal conductance. The differences in g_n/g_d across two different biomes is therefore intriguing and deserves further analyses.

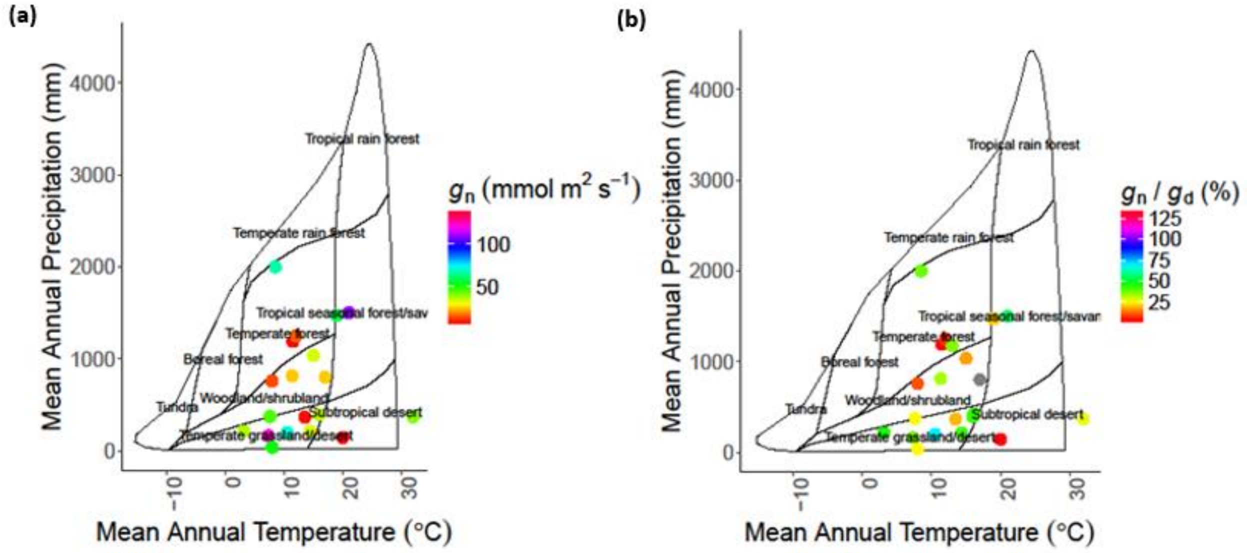

Figure 2: Whittaker biome diagram for g_n

Additionally, I conducted a separate graph to visualize where had g_n been by measured in the field by using a Whittaker biome diagram. This indicates an overall lack of data for tropical rain forest and tundra regions, as well as in boreal regions (figure 2).

3.2. Effects of environmental drivers on nocturnal conductance

Studies on environmental regulation of g_n covered the topics of soil water availability, VPD, temperature, nutrients, O_3, CO_2, light, salinity and elevation.

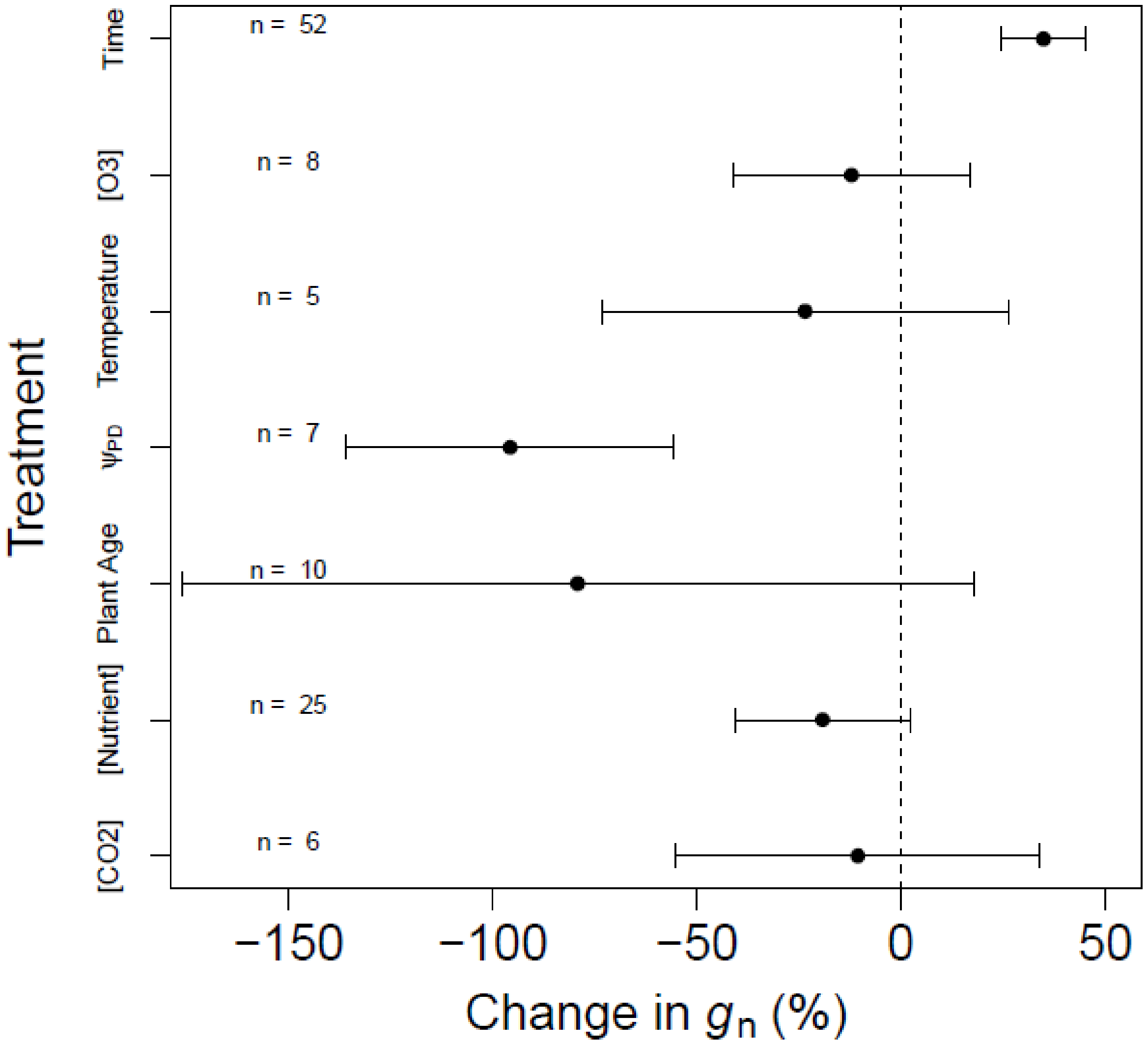

Figure 3: Response of different categorical variables to g_n by step change analyses

3.2.1. Predawn water potential (Ψ_{pd})

Relationships between g_n and Ψ_{pd} were sometimes reported as categorical variables but also continuous variation was reported in other studies. Consequently, I conducted both types of analyses. A step change analyses was performed with 7 studies, and here I observed a significant negative response, meaning that to g_n declined as rhizosphere water scarcity increased (figure 3). However, there was no common significant trend present for the response of PWP to g_n in the 14 additional species for which I could conduct regression analyses. There were 8 species with positive responses, 4 with negative responses, and 2 studies did not show any response. No trend was also apparent across functional types. *Eucalyptus sideroxylon* (Zeppel *et al.* 2011), an evergreen angiosperm, showed positive significant results whereas *Sorghum bicolor* (Muchow *et al.* 1980), a crop species, and *Salix arctica* (Dawson and Bliss 1989), a deciduous angiosperm tree, showed negative significant response to g_n (figure 4).

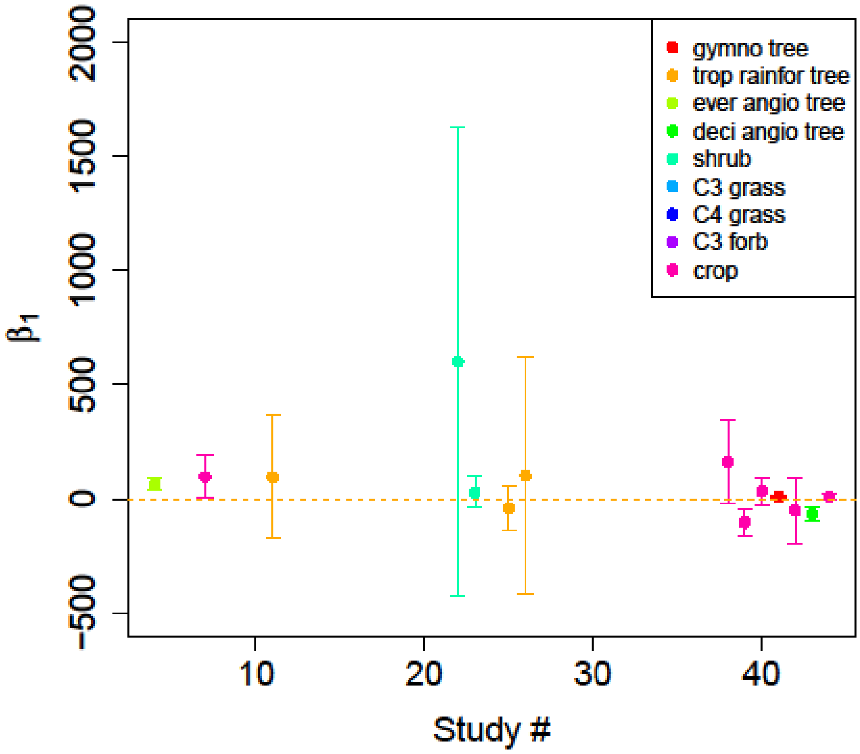

Figure 4: Effect of Ψ_{pd} on g_n across different studies

3.2.2. Vapour pressure deficit (VPD)

VPD was analysed with regression analysis with 37 studies where 4 and 8 of them showed positive and negative responses, respectively with g_n, and rest of them showed no association. Besides, only 8 studies showed significant results where 1 of them was positive and 7 of them were negative. In the case of negative significant responses, 6 of the studies dealt with crops while 2 of them with tropical rain forest trees (figure 5). Among crop species, *Helianthus annuus* (Howard and Donovan 2007) showed a positive significant result, whereas *Vitis vinifera* Tempranillo (Escalona *et al.* 2013), *Solanum melongena*, *Cucumis sativus*, *Capsicum annuum* and *Lycopersicon esculentum* (Bakker 1991) showed negative significant results. Besides, two tropical plants *Ricinus communis* (Barbour and Buckley 2007) and *Styrax* *ferrugineus* (Bucchi *et al*. 2004) also showed negative significant effect to g_n. Although VPD is the major driver of g_d, in this study it is evident that response of VPD to g_n were not significant most of the time. Any potential effects of VPD over g_n are therefore not clear.

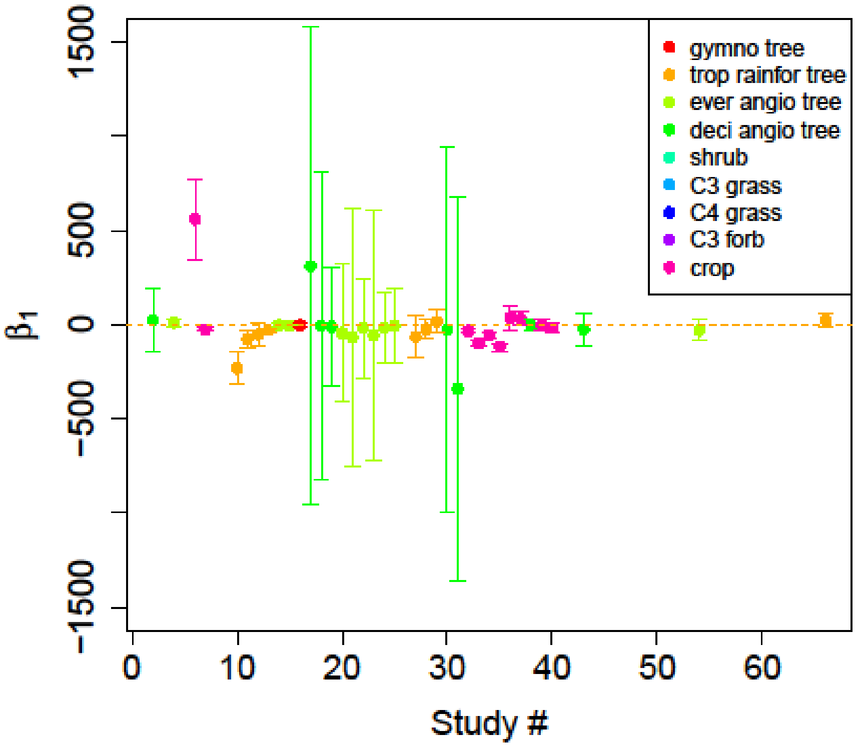

Figure 5: Response of VPD to g_n across different studies

3.2.3. Temperature

3.2.3.1. Air temperature

Temperature was analysed by both step change and regression analyses. In case regression analyses, there were 10 studies analysed where 9 of them showed a tendency towards negative effects and 1 study showed a tendency towards positive effects. However, the tendency was not significant for any studies (figure 6). One tropical rain forest species, *Ricinus communis* (Barbour and Buckley 2007), showed highest negative effect followed by two deciduous angiosperm species, *Populus koreana* and *Populus euramericana* (Furukawa *et al*. 1990) whereas two crop species *Hibiscus cannabinus* and *Sorghum bicolor* (Muchow *et al*. 1980), showed the lowest negative effect. The only positive effect of temperature with g_n is occurred with *Sorghum bicolor* but it was not significant (Muchow *et al*. 1980). On the other hand, similar to regression method, step change also showed an overall negative response (-23.47%), but g_n values were also not significant here. Previous studies showed contrary result in the response of elevated temperature to g_n, i.e. no effect on g_n (Resco De Dios *et al.* 2013b) and decrease of g_n (Zeppel et al. 2011); hence, further studies may be required to further assess the effects of temperature on g_n.

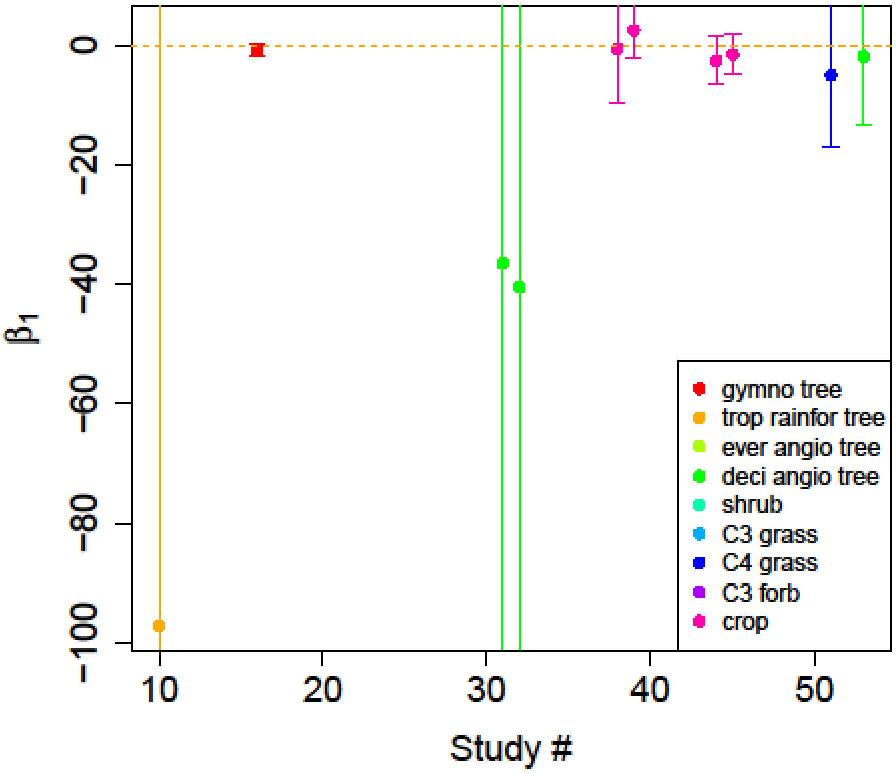

Figure 6: Response of air temperature to g_n across different studies

3.2.3.2. Soil (root-zone) temperature

Cool soil temperatures in *Vitis vinifera* decreased the g_n (31.4 mmol m^{-2} s^{-1}), relative to ambient temperatures where g_n was 36.7 mmol m^{-2} s^{-1}, and the warm temperature treatment results g_n of 39.6 mmol m^{-2} s^{-1} (Rogiers and Clarke 2013). However, lack of studies prevent further generalizations on how soil temperatures affect g_n.

3.2.3.3. Heat waves

There is also an overall lack of studies on heat waves and the only study performed to date (Duarte *et al.* 2016) observed that g_n in *Pseudotsuga menziesii* was negatively affected during and after the heat waves as g_n declined from 26.18 to 13.09 mmol m^{-2} s^{-1} when temperature rose by 12°C above ambient condition in a greenhouse experiment. Heat waves will be more frequent in the in the era of global warming which will impact tree physiological processes including g_n and g_d (Teskey *et al.* 2015). Consequently, further studies should be addressed on impacts of heat wave over g_n.

3.2.4. Nutrients

Effects of increasing soil nutrient availability were analysed in 25 studies with the step change method. The response was overall negative (-19.20%), meaning that nutrient limiting soils will tend to increase g_n (figure 3), but the effect was not significant. In case of nitrogen additions, higher g_n values were found in *Populus angustifolia*, and *Populus balsamifera* (Howard and Donovan, 2010) whereas contrary results were also found in another studies of the same experiment in *Populus balsamifera*, and in *Ulmus laevis* as well as in *Fraxinus excelsior* (Eller *et al.* 2016). In case of P, low concentrations increased the g_n in *E*n. *tereticornis* (Resco de Dios *et al.* 2013b) and in *U. laevis* but decreased g_n in *F. excelsior* (Eller et al. 2016).

Scholz *et al.* (2007) found higher g_n in *Ouratea hexasperma*, *Qualea grandiflora*, and *Blepharocalyx salicifolius* where both N and P treatment were added separately. However, when both nutrients were applied together in the soil, limiting N and P soil decreased the rates of g_n (Eller *et al.* 2016).

From the previous studies it is evident that, the response may vary between N and P treatment; hence, more studies will be needed specially, with the P treatment, as there are few studies using this nutrient (Resco de Dios *et al.* 2013b).

3.2.5. Ozone (O_3)

Responses of g_n to O_3 (-12.162%) were found negative and non-significant in the step change methods in the 8 studies on this topic (figure 3). This suggests that O_3-exposed plants had sometimes lower g_n rates, but not always.

3.2.6. CO_2

Elevated CO_2 showed a negative effect (-10.45%.) when all other parameters remained constant in step change analyses, although the effect was not significant for g_n (figure 3). To measure the effect of CO_2 on g_n 6 studies were analysed. Although some studies report that CO_2 substantially increases the g_n in *Eucalyptus sideroxylon* (Zeppel *et al.* 2011), *Vicia faba* (Easlon and Richards 2009) and *E. camaldulensis* (Resco de Dios *et al.* 2016a), others found different results (Resco de Dios *et al.* (2013b). It has been hypothesized that higher photosynthate production may occurred under elevated CO_2 may cause higher g_n (Easlon and Richards 2009). However, I could not corroborate that the response to CO_2 is always positive.

3.2.7. Dynamics of light

3.2.7.1. Sunlit and shade leaf

Konarska *et al.* (2016) found that g_n/g_d was higher in seven city tree species in case of shading leaves when compared with sunlit leaf. They have reported that on average among seven tree species g_n amounted for 14 mmol m^{-2} s^{-1}, reaching 11 and 23% of midday g_d of sunlit and shaded leaves, respectively.

3.2.7.2. Photoperiod

In two rose cultivars, *Rosa Spp.* Madelon and *Rosa Spp.* Sonia the rates of g_n increased with the decrease of photoperiod (Blom-Zandstra *et al.* 1995). They observed the g_n values of 40.8 mmol m^{-2} s^{-1} and of 25 mmol m^{-2} s^{-1} for *Rosa Spp.* Madelon and *Rosa Spp.* Sonia, respectively, plants maintained in 4 hours of light compared to 19 mmol m^{-2} s^{-1} and 22.2 mmol m^{-2} s^{-1} of g_n respectively after 12 hours. Easlon and Richards (2009) has reported similar findings for *Vicia faba* with g_n decreasing from 32.5 to 24.4 mmol m^{-2} s^{-1} in 8 and 16h photoperiod, respectively.

3.2.7.3. Light quality

The quality of the light that is applied to the trees influenced the magnitude of g_n in *Lactuca sativa* (Kim *et al.* 2004). In their growth chamber experiment, Kim *et al.* (2004) observed that with 18 hour photoperiod, red and blue LEDs (Light Emitting Diodes) with green fluorescent lamps (RGB) had the higher g_n (35.23 mmol m^{-2} s^{-1}) compare to red and blue LEDs (RB), green fluorescent lamps (GF) and cool white fluorescent lamps (CWF), which have g_n value of 35.43, 51.13 and 36.53 mmol m^{-2} s^{-1} respectively and the ratio of g_n/g_d was 24%, 27 %, 39 % and 11 % for RB, RGB, GF and CWF respectively.

3.2.7.4. Canopy position

g_n varied in *Quercus rubra* canopies as the upper canopy leaves with artificial shading showed the highest mean g_n (12.05 mmol m^{-2} s^{-1}), while upper canopy leaves receiving natural sunlight and lower canopy leaves that were naturally shaded showed g_n value of 8.1 and 3.6 mmol m^{-2} s^{-1} respectively (Barbour *et al.* 2005).

3.2.7.5. Daylight shading

After day time shading, g_n in *Vicia faba* increased to 45.58 mmol m^{-2} s^{-1}, much higher g_n (12.08 mmol m^{-2} s^{-1}) than when plants remained unshaded during the day (Easlon and Richards 2009).

3.2.8. Salinity

Soil salinity generally has the potential to reduce the values of g_n in different species. Non-salt tolerant *Chrysothamnus nauseosus* and salt tolerant *Sarcobatus vermiculatus* both decreased g_n after NaCl addition, although the reduction of g_n was much higher in case of *C. nauseosus* (Donovan *et al.* 1999). Besides, NaCl also decreased g_n in different genotypes of *Distichlis spicata* (genotype No. 38, 33, 2, 24, 23, 12), Christman *et al.* (2009) with the exception of one genotype (*D. spicata 23*). Interestingly, g_d increased with NaCl.

3.2.9. Elevation

The magnitude of g_n was increased when elevation increased in case of *Marrubium vulgare* where plants were growing at both low- and high-altitude (i.e. 1100m and 2200m respectively). Low altitude plants had no g_n whereas high altitude plants had shown the g_n of 10 mmol m^{-2} s^{-1} at Payam, Iran (Habibi and Ajory 2015).

3.3. Effects of biotic drivers on plant nocturnal conductance

Studies on biotic drivers on plant nocturnal conductance included the role of endogenous rhythms, morphological and anatomical traits, elemental composition, C assimilation, genotypic variation, sex, ABA, and plant and leaf age.

3.3.1. Endogenous rhythms (time)

Endogenous rhythms had a positive effect on g_n, as reflected by step change analyses, and the CI bars did not cross the zero line meaning response of endogenous rhythms is significant and values of g_n increased late in the night, relative to the early night. The magnitude of the response was a 35% increase (figure 3). This temporal pattern of g_n is predominantly driven by the circadian clock, which leads towards gradual increases in stomatal conductance from the early night to late night period (Hennessey *et al.* 1993; Resco de Dios *et al.* 2013a, 2015). Resco de Dios *et al.* (2013a) has concluded that the circadian clock is the most plausible driver of the increase in g_n between 3 and 12 h after dusk. This meta-analysis is concluding the same finding but with a wide verities of PFTs and biomes.

3.3.2. Morphological and anatomical features

3.3.2.1. Specific leaf area (SLA)

Plants with higher SLA tend to have higher values of g_n. In a field experiment, Ludwig *et al.* (2006) found that *Helianthus anomalus* had a g_n of 57 mmol m^{-2} s^{-1} when SLA was 9.43 m^{2} kg^{-1} whereas g_n decreased to 44 mmol m^{-2} s^{-1} when SLA was 8.9 m^{2} kg^{-1}. Similarly, the C_3 grass *Bartsia trixago* showed similar results as Press *et al.* (1993), where g_n declined from 1095 to 680 mmol m^{-2} s^{-1} when SLA decreased from 11 and 9.4 m^{2} kg^{-1} respectively.

3.3.2.2. Stomatal density

g_n did not show any relation with stomatal density in *Vitis vinifera*. When stomatal density were 127.04, 120.08 and 129.7 stomata mm^{-2}, trends of g_n were 31.4, 36.7 and 39.6 mmol m^{-2} s^{-1} respectively (Rogiers and Clarke 2013). However, g_n increased with stomatal density in starchless mutants of *Arabidopsis thaliana* (127.4 mmol m^{-2} s^{-1}) was lower than in the wild type (155.9 mmol m^{-2} s^{-1}), where the mutant plant had higher 348 stomata mm^{-2} while the wild-type had 290 stomata mm^{-2}. It refers variation in g_n could be explained by genetic variation in stomatal density and size (Lasceve *et al.* 1997). Normally, higher pore density causes greater g_d (Nobel 1999). Here, I have found the similar response of stomatal density to g_n and g_d.

3.3.3. Elemental composition (Leaf Nitrogen)

In optimum conditions, with high nitrogen and water availability, *Helianthus anomalus* showed higher leaf Nitrogen (N) (31 mg g^{-1}) and had higher rates of g_n of 57 mmol m^{-2} s^{-1}, while it decrease to 44 mg g^{-1} when the rate of g_n was 44 mmol m^{-2} s^{-1} (Ludwig *et al.* 2006). However, ambiguous result in case of *Helianthus annuus* have been found where both increasing and decreasing trends of g_n magnitudes for different leaf N level (Howard and Donovan 2007).

3.3.4. Carbon assimilation and carbohydrates

Assimilation (*A*) often showed a positive association with g_n, but responses were generally not significant (figure 7). Resco de Dios (2016) reported that relationships between nocturnal stomatal responses and carbon metabolism were only apparent for conductance at predawn but not at early night. However, contrary results were also found in 3 studies and one of them is significant with a C_4 grass species *Distichlis spicata* clone No. 33 (Christman *et al.* 2009) which means higher g_n during the night may decrease the photosynthesis in the following day. Further studies will be necessary to find out the causes of reduction of A when g_n is higher.

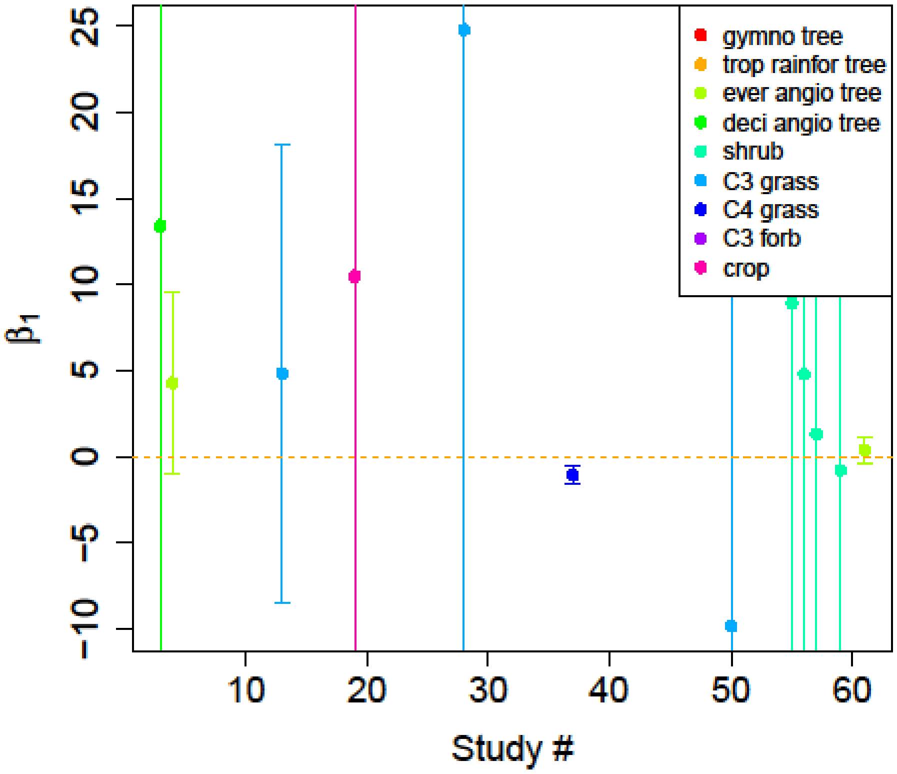

Figure 7: Response of next day photosynthesis to g_n across different studies

3.3.5. Genotypic variation

In this study there were 8 studies that addressed with genotype variation, and all of the studies found variation of g_n across genotype. Resco de Dios *et al.* (2016) observed genetic correlations between nocturnal stomatal conductance and genotype in *E. camaldulensis*. Similar findings were also reported for wide range of PFTs, for example in crop species, *Vitis vinifera* (Escalona *et al.* 2013), *Phaseolus vulgaris* (Salvatori *et al.* 2013) and *Rose spp.* (Blom-Zandstra *et al.* 1995), shrub *Distichlis spicata* (Christman *et al.* 2009), and C_3 grass *Arabidopsis thaliana* (Leymarie *et al.* 1998, Costa *et al.* 2015). It may represent g_n is an heritable traits among offspring.

3.3.6. Others

3.3.6.1. Sex

Magnitudes of g_n varied with the sex of plants. Female (45.1 mmol m^{-2} s^{-1}) plants of *Salix arctica* have shown higher g_n than male (32.5 mmol m^{-2} s^{-1}) where male plants tends to had lower leaf potential at the artic habitat of Canadian Arctic Archipelago (Dawson and Bliss 1989).

3.3.6.2. ABA

Application of higher dosage ABA (50 µM) increased the g_n and g_d of different genotypes of *Arabidopsis thaliana* species. However, in lower dosage of ABA (10 µM) have showed decrease of g_n than control plants except *A. thalian*a Ler genotype (Leymarie *et al.* 1998).

3.3.6.3. Starchless mutant

Starch deficient mutant of *A. thaiana* shows lower late g_n, which is 127.4 mmol m^{-2} s^{-1}, than the wild type plant (155.7 mmol m^{-2} s^{-1}) with 63.74% of g_n in relation to g_d (Lasceve *et al.* 1997). This temporal pattern may be involved due to the endogenous regulation of circadian clock.

3.3.6.4. Plant age

Responses of plant age (-79.16%) to g_n were found negative which means that young trees had higher g_n than mature trees. Most of the studies follow this trend including *Helianthus annuus* (Howard and Donovan, 2007), *Rosa spp*. Rosa Spp. (Madelon and Sonia cultivar) (Blom-Zandstra *et al.* 1995), *Pinus ponderosa* (Grulke *et al.* 2004), and *Rubus spectabilis*, *Rubus laciniatus* and *Rubus armeniacus* (McNellis and Howard 2015) except for *Glycine max* (Turner et al. 1978) and *Rubus ursinus* (McNellis and Howard 2015) where mature trees had a higher rate of g_n. Young trees need more water and nutrients for their development and growth as well as to maintain fitness, thus having higher magnitude of g_n.

3.3.6.5. Leaf age

Newly expanded leaves of *Eucalyptus saligna* and *E. grandis* tress, irrespective of different periods of the year, were shown more than twice g_n values than adjacent mature leaves (Phillips *et al.* 2010). In case of *E. grandis,* average g_n for old leaves was 8.8 mmol m^{-2} s^{-1} while young leaves from the same tree had g_n of 31 mmol m^{-2} s^{-1}. Similar significant results also observed for *E. saligna* with g_n of 2.4 and 10.1 mmol m^{-2} s^{-1} for mature and young leaves respectively. Zeppel *et al.* (2010) also reported similar results in two different species namely *Angophora bakeri* and *E. parramattensis* in early night g_n. However, in late night g_n mature leaves had little higher g_n than young leaves.

4. Implications of nocturnal conductance

4.1. Function of nocturnal conductance

My data allows to discard the idea that g_n is beneficial as it enhances nutrient uptake. There were no clear association between nutrient uptake and g_n, and there was a positive association between leaf N and g_n. However, this study supports that g_n may support higher C assimilation rates. This is because g_n was consistently higher late in the night than early, and also because of the positive association between g_n and A and with leaf N. Thus, it would appear that g_n is part of the trait syndrome that allows a plant to show high A and, consequently, elevated growth rates.

Mechanisms explaining why circadian regulation enhance g_n later in the night are relatively well understood, and they involve interactions between the canonical clock gene TIME OF CAB EXPRESSION (TOC1) with ABA related genes (Pokhilko *et al.* 2013).

An alternative function of nocturnal conductance that yet remains to be evaluated is its potential contribution to respiration in parenchyma cells by the delivery of O_2. I could not test this hypothesis with my dataset, but it remains as another potential explanation on the function of g_n. Increasing O_2 delivery to the parenchyma would imply that higher rates of respiration occur late at night, when g_n is maximal. Indeed, some studies have also reported higher predawn respiration rates (Gessler *et al.* 2017), consistent with this hypothesis.

4.4. Relationships with hydraulic lift and growth

E_n and g_n reduces the hydraulic lift where a competing sink is created for water movement towards plant canopies (Donovan *et al.* 2001, 2003, Kavanagh *et al.* 2007, Scholz *et al.* 2008, Howard *et al.* 2009). In this study it is evident circadian clock is a major drivers of g_n and this mechanism helps plants to anticipate transitions from dawn to dusk; hence, without circadian resonance plants would show low efficiency in photosynthesis which, in turn, would result in lower plant growth (Smith and Stitt 2007). Besides, it has been experimentally and repeatedly observed that plants with impaired clock function show reduced fitness (Highkin and Hanson 1954, Green *et al.* 2002, Dodd *et al.* 2005).

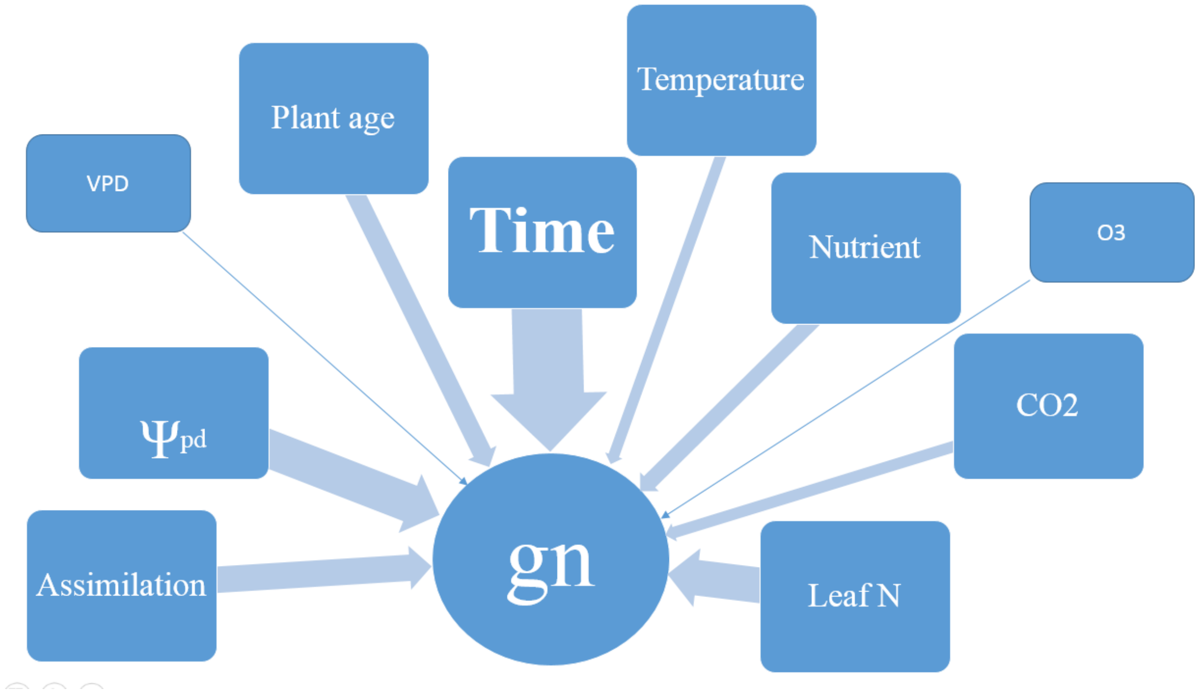

Figure 8: Important drivers of g_n process, drivers with the wider the arrow and closer to g_n has the higher impact

5. Conclusion

It is evident that due to g_n substantial water losses occur during the nocturnal period, and this does not seem to be just a case of partially open stomatal pores. Different factors affect this process (figure 8), which is very different from g_d. VPD, which is a major driver of g_d, has no effect on g_n. Although there were some positive or negative effects found on temperature, nutrients availability, CO_2 etc. none of them showed significant association with g_n. It was found for a wide range of PTFs and biomes around the world that substantial portions of water losses occur through g_n, and the circadian clock was one of the major drivers. The association between g_n, A and leaf N indicates that g_n is part of a syndrome of high growth or that late night g_n directly increases A by reducing response times in the morning. Hence, g_n and circadian regulation of plants can no longer be ignored as meaningful drivers of evapotranspiration.

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