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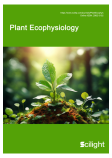

Review

Stomatal Density and Index Are More Responsive to Light Intensity than to [CO_2]: A Meta-Analysis and Implications for Paleo-CO_2Reconstruction

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Abstract: Stomatal density is one of the plant traits influencing leaf gas exchange and is known to be affected by the plant's environment. Understanding its degree of plasticity to various abiotic factors is therefore important. We conducted a meta-analysis of a wide range of experiments in which plants were grown under different levels of CO_2, light, temperature, and water availability, and derived generalized dose-response curves. Although both stomatal density and stomatal index showed a significant negative correlation with CO_2 levels, these relationships were weak and only marginally consistent across the analyzed experiments. In contrast, the effect of growth light intensity was positive, highly consistent, and substantially stronger than the impact of atmospheric CO_2. Temperature also positively influenced stomatal density, while water availability showed no consistent effects. Based on these dose-response curves, we highlight several caveats when using stomatal density or stomatal index for paleo-CO_2 reconstruction. The weak CO_2 response, coupled with the strong confounding impact of light intensity, poses significant limitations to the accuracy of such estimates.

Keywords: CO_2; daily light integral; light intensity; meta-analysis; paleoclimatology; stomatal density; stomatal index

1. Introduction

There are probably more stomata on Earth than grains of sand on all the world's beaches. A single leaf can contain hundreds of thousands of stomata (Ciha & Brun, 1975), making the total number of stomatal pores on a single tree - or across an entire forest - staggeringly immense. Stomata act as critical gateways for carbon dioxide uptake while limiting water loss, thus playing a central role in Earth's carbon and water cycles (Berry, Beerling, & Franks, 2010). At the leaf level, gas and water fluxes are co-regulated by various stomatal characteristics. One extensively studied trait is stomatal conductance, which can respond relatively quickly (within minutes to hours) to changes in light intensity, CO_2 concentration, or the leaf's water status (Lawson & Vialet-Chabrand, 2019). Over longer time frames (days to months), plants can further adjust their gas and water fluxes by producing new leaves with different stomatal sizes, or by altering the number of stomata per unit leaf area. This latter trait, known as 'stomatal density', forms the central focus of this paper.

Stomatal density (SD) is known to vary systematically within a plant. Typically, SD is higher on the abaxial (lower) side of a leaf than on the adaxial (upper) side, and it increases from the base to the tip of the leaf, as well as from the midrib toward the leaf margin (Salisbury, 1927). SD may also increase with a leaf's position on the plant, and can vary with genotype or species (Wall et al., 2023). These factors must be considered when examining how SD responds to environmental conditions (Körner, 1988; Woodward, 1993; Roth-Nebelsick, 2005). Our study investigates how SD is influenced by four important abiotic factors: ambient [CO_2], light intensity, temperature and water availability. To this end, we conducted a meta-analysis focusing on the longer-term effects of these factors on SD. A few years ago, Yan, Zhong, and Shangguan (2017) conducted a similar analysis and found that the response ratio of SD between high and low CO_2 levels was not significantly different from 1.0, suggesting no overall effect of ambient [CO_2]. They also found that both higher temperature and lower water availability increased SD. However, their analysis did not consider the effects of light intensity, a gap that we aim to address in this study.

A standard meta-analysis typically categorizes the levels of an environmental factor or treatment in each experiment as 'high' and 'low', and then calculates the relative response by comparing the ratio of the phenotypic variable of interest between these two categories (Gurevitch et al., 2018). However, the observed response can also depend on the specific levels of the environmental factor applied, and may saturate within certain ranges. To gain more comprehensive and generalizable insights, it is beneficial to derive dose-response curves, which describe the response of a phenotypic variable across a broad range of levels for the environmental factor of interest (Poorter et al., 2022a). In this study, we adopt this approach to derive dose-response curves for the four environmental factors under consideration. Since plants typically respond more to the cumulative light flux received over time rather than the instantaneous light intensity present at a given moment in time (Kelly et al., 2020), we represent light availability in our analysis using the Daily Light Integral (DLI). DLI quantifies the total number of quanta in the photosynthetically active range (400–700 nm) received per unit ground area per day. This metric generally provides a more biologically relevant measure of light availability for plants (Poorter et al., 2019).

The application of dose-response curves for SD has proven significant in paleoclimatology. As atmospheric CO_2 concentrations continue to rise, understanding Earth's climate sensitivity to CO_2 is of critical importance. Examining past variations in atmospheric CO_2 and the corresponding climate changes can provide valuable insights (Hönisch et al., 2023). CO_2 levels from the past 800,000 years can be measured directly from air trapped in Antarctic ice (Higgins et al., 2015). However, for periods prior to 800,000 years ago, direct measurements are not possible, making it necessary to rely on proxy estimates (Royer, 2001). One such method of reconstruction involves comparing the SD of well-preserved fossilized leaves to that of the same or closely related species growing today (e.g., McElwain & Chaloner, 1996; Kürschner, 1997; Rundgren & Beerling, 1999; Kürschner, Kvaček, & Dilcher, 2008). This approach was pioneered by Woodward (1987), who showed that SDs sampled in the 1980s were generally lower than those of herbarium specimens collected 200 years earlier. A functional explanation for the observed negative relationship between SD and atmospheric [CO_2] is that higher CO_2 levels allow plants to maintain sufficient CO_2 uptake, while decreasing water loss through transpiration by decreasing the number of stomata per unit area (Royer, 2001). Assuming that the sensitivity of these plants to CO_2 has remained constant over time, SD in fossilized leaves offers a proxy for estimating atmospheric CO_2 levels in past eras.

Not all findings have been unequivocal, though. Herbarium material of various species collected over an 80–110 year span did not reveal any consistent trends over time (e.g., Hu et al., 2015; Ydenberg et al., 2021). Over a span of 70–90 years, Körner (1988) observed *increases* in SD rather than decreases, be it that there was considerable variation among species and the overall response was not statistically significant. Experimentally, the negative relationship between SD and [CO_2] has also been inconsistent, with various studies failing to replicate it (e.g., Apel, 1989; Reid et al., 2003). A complication that soon became apparent, is that SD not only depends on the number of stomatal cells initiated, but also on the degree of expansion of the surrounding epidermal cells. This issue has prompted researchers to adopt the stomatal index (SI) as an alternative proxy. SI represents the percentage of stomata relative to the total number of stomata and epidermal cells (Salisbury, 1927). In the paleobotanic literature it is generally assumed that SI is more strongly influenced by ambient [CO_2] than by other environmental factors, such as water availability or light intensity (Royer, 2001), making it a potentially more reliable indicator for ancient CO_2 levels than SD. As a result, SI has become the more dominant metric in this field (see compilation by Hönisch et al., 2023), although its underlying premise is still not well constrained. To address this, we also have derived dose-response curves for SI in relation to environmental variation, as far as data were available.

In this paper, we examine the effects of CO_2 concentration, daily light integral, temperature, and water availability on both stomatal density (SD) and stomatal index (SI). Using a meta-analysis of studies in which plants were experimentally exposed to varying levels of these environmental factors, we derive generalized dose-response curves wherever possible. We evaluate the consistency of the data, determine the form of the dose-response curve that best represents the generalized relationships, and quantify the overall plasticity. Finally, we assess the generalizability of the CO_2 dose-response curve and compare our results with functions currently used to estimate past CO_2 concentrations based on fossil SD and SI.

2. Materials & Methods

We analyzed compiled data from experimental treatments where plants were grown for a minimum of two weeks and at least one-third of their actual lifespan, under varying levels of CO_2, light intensity, temperature, or water availability, and where stomatal density (SD) and/or stomatal index (SI) was reported for leaves that had developed under these conditions. These experiments were conducted in growth chambers, glasshouses, open-top chambers or free-air CO_2 enrichment (FACE) facilities, provided that the plants were grown individually or in mono-specific stands. Unlike the meta-analysis by Yan et al. (2017), we excluded data from herbarium specimens and from field-grown plants in CO_2 springs or along natural gradients of light, temperature, water availability or altitude, as other environmental factors may have co-varied with the factor of interest.

Stomatal density exhibits significant variation across plant species. Many tree species lack stomata on the adaxial (upper) surface of their leaves, while numerous herbaceous species exhibit higher stomatal densities on the abaxial (lower) side compared to the adaxial side (Salisbury, 1927; Körner, 1988). However, in some cases, stomata are more abundant or exclusively present on the adaxial surface (Kaul, 1976). When SD data were reported for both leaf surfaces, we summed the values from the abaxial and adaxial sides, as this provides the most comprehensive measure relevant to gas exchange. For SI, we averaged the values from both surfaces. If data for only one side was reported (typically the abaxial side), we used that value as SD or SI estimate, assuming that researchers considered that to be the most relevant surface for their species of interest. To standardize the data, phenotypic values in a given experiment and species were subsequently scaled to the values observed at a reference [CO_2] of 450 ppm, a Daily Light Integral (DLI) of 8 mol m^{-2} d^{-1}, an average temperature level over the full diurnal cycle of 20 °C. For water availability, drought severity was estimated by scaling the biomass or leaf area of drought-stressed plants relative to control plants grown under optimal water conditions. We therefore excluded papers where no quantification of plant size was made. For [CO_2] and DLI we expanded the datasets reported by Poorter et al. (2019, 2022a, 2022b), incorporating approximately 50% more data to the compilation.

After scaling the phenotypic responses for each species and each individual experiment separately, we fitted four types of curves describing different potential relationships in the data: (a) no relationship, (b) linear regression, (c) a saturating curve and (d) a quadratic polynomial. To determine the best-fitting curve, we applied the Akaike Information Criteria (AIC). Although an assessment across different environmental factors to some extent is a comparison between different entities, we used the data and the resulting curve fits to summarize all observations through three key indices.

(a) A **Plasticity Index (PI)**: This index represents the ratio of SD or SI derived from the fitted relationships at CO_2 concentrations of 1200 and 200 ppm, a DLI of 50 and 1 mol m^{-2} day^{-1}, or temperatures of 35 and 5 °C, respectively. For drought stress, we considered SD and SI values under optimal watering conditions relative to those at 10% of the optimal plant biomass. In cases of negative responses, we calculated the inverse of the ratio and denoted this with a minus sign, to maintain comparable scales.

(b) A **Consistency Index (CI)**: This index reflects the percentage of experiments in which plants treated with the highest levels of CO_2, light, temperature or water exhibited higher SD or SI compared to those treated with the lowest levels. A value of 100% indicates fully consistent increases across experiments, while 0% indicates fully consistent decreases. A value of 50% suggests either random variability, or strong contrasting responses between species.

(c) A **Reliability Index (RI)**: This index assesses the robustness of the selected form of the dose-response curve, the PI and the CI, on a scale from 0 to 9. It accounts for the number of experiments, the number of species studied, the variability between observations, and the range of the environmental factors over which experimental data are available. A higher value indicates a lower likelihood of changes in results with the addition of new data. While this index is particularly useful for comparing different plant traits in response to the same environmental variable, it can also be used - albeit with caution - to compare the reliability of PI and CI across different environmental factors.

For a more detailed description of the analysis, readers are referred to Poorter et al. (2022a) and Supporting Info S1.

3. Results & Discussion

3.1. Stomatal density

In total, we compiled data from 245 papers, with references listed in Supporting Info S2. The analysis of these data reveals a significant and overall negative response of stomatal density (SD) to ambient CO_2 levels: as CO_2 concentration increases, SD decreases (Figure 1A). Median values calculated for each subsequent 10% of the data suggest a steeper slope in the low-CO_2 range compared to the high-CO_2 range, consistent with the 'ceiling' discussed by Roth-Nebelsick (2005), where SD becomes less responsive to further increases in [CO_2]. However, the data show considerable variability, and the Akaike Information Criterion identified a linear relationship as the simplest model to describe the trend. The slope of this regression line is very modest, with a Plasticity Index (PI) of -1.07 (Table 1), indicating a marginal decrease of 7% in SD across the CO_2 range of 200–1200 ppm. Moreover, the consistency of the response across the compiled experiments is relatively low: when comparing the treatments with the highest and lowest CO_2 levels within each experiment and for each species, 40% of the studies report increases in SD, while 60% report decreases (Table 1). This distribution is close to what would be expected by chance, where increases and decreases would occur in approximately 50% of the experiments.

What might cause such large variability? Firstly, methodology may play a role, as SD can vary substantially within a single leaf, between different leaves, and even between the adaxial and abaxial sides (Salisbury, 1927; Körner, 1988; Poole et al., 1996; Yan et al., 2017). Therefore, care must be taken to sample the same part of the same leaf in the analysis (Woodward, 1993), or, ideally, to systematically sample various parts of the leaf to account for spatial variability. Secondly, intrinsic differences among species, functional groups or phylogenetic clades may contribute to the observed variability. The results suggest that herbaceous C_4 species, in general, show no response to [CO_2], whereas both herbaceous and woody C_3 species exhibit a slightly negative response (Table 2). However, none of these species contrasts is statistically significant. Thirdly, strong interactions between [CO_2] and other environmental conditions could lead to variations among experiments. Currently, however, there are too few data in our dataset to derive dose-response surfaces, which would enable quantification of the strength of these interactions and offer a more detailed understanding. Finally, maternal effects may also influence SD (Vráblová et al., 2018). However, nearly all experiments in our compilation used seeds from plants grown at control CO_2 levels, likely limiting this source of variation.

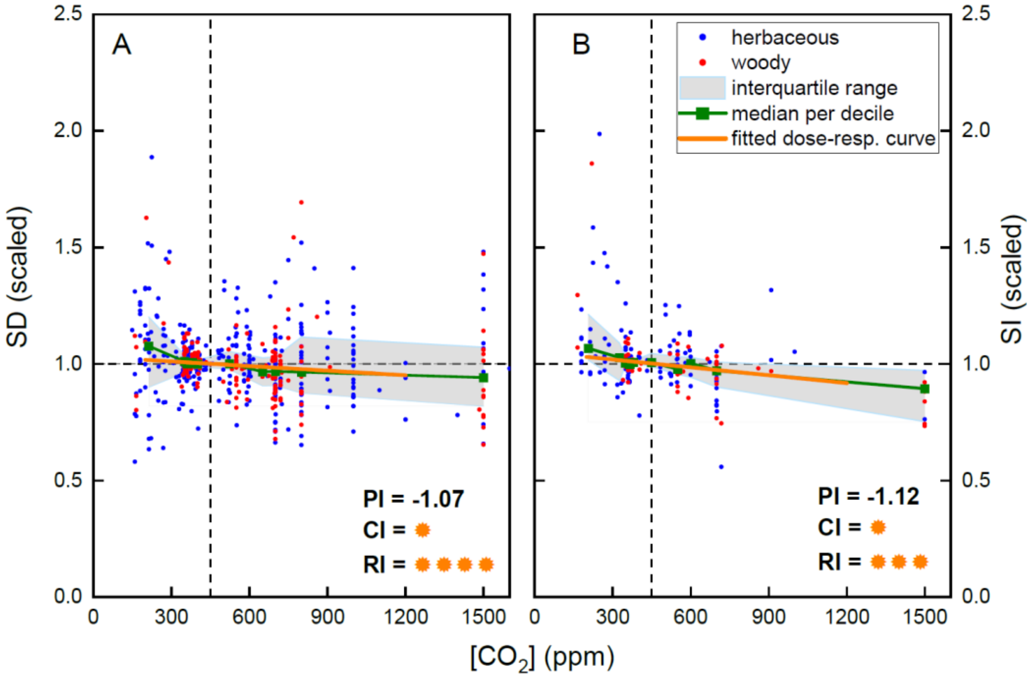

Figure 1. Dose-response curves for (**A**) Stomatal Density (SD) and (**B**) Stomatal Index (SI) as functions of ambient CO_2 concentration. Data points represent scaled mean values per species and experiment, relative to a reference [CO_2] of 450 ppm. Data for herbaceous plants are in blue, for woody species in red. Green squares indicate the median scaled trait value and [CO_2] per decile of observations, or per group of 10 observations when fewer than 100 observations are available. The shaded area represents the interquartile range (25th and 75th percentiles). The thick orange line shows the fitted relationship across all data points. Calculated Plasticity Indices (PI) are provided, along with a visual indication of the Consistency index (CI) and Reliability Index (RI). The strength of the Consistency Index is indicated by the number of orange symbols: none: % increases in the trait value with an increase in the abiotic environmental factor: 40–60%; ✸: 30–40% or 60–70%; ✸✸: 20–30% or 70–80%; ✸✸✸: 10–20% or 80–90%; ✸✸✸✸: 0–10% or 90–100%. The strength of the Reliability Index: no symbol: 0–1; ✸: 2–3; ✸✸: 4–5; ✸✸✸: 6–7; ✸✸✸✸: 8–9. For more detail see Tables 1 and 2 and Supporting Info S3 (Figures S1–S8).

Table 1. Summary of the dose-response curve analysis for Stomatal Density (SD) and Stomatal Index (SI) in relation to four environmental factors: (1) ambient CO2 concentration (2) Daily Light Integral (DLI), (3) average daily temperature and (4) water availability during growth.

Env. Factor	**Trait**	**Range in Env. Factor**	**# of Observations**	**# of Species**	**Fit**	**Pseudo r^2**	**Plasticity (PI)**	**Consistency (CI)**	**Reliability (RI)**	***p***	**a**	**b**	**c**
[CO_2] (ppm)	SD	150–3200	660	180	L***	0.02	−1.07	40	8	ns	1.031	-6.53×10^{-5}	
	SI	165–2000	220	80	L***	0.14	−1.12	32	7		1.053	-1.12×10^{-4}	
DLI (mol m^{-2} day^{-1})	SD	0.4–72	360	100	S***	0.51	**1.93**	**94**	7	ns	1.477	0.526	6.69×10^{-2}
	SI	0.9–64	130	30	S***	0.31	**1.96**	**92**	4		1.285	0.553	0.1147
Temp. (°C)	SD	5–38	150	35	L***	0.31	**1.54**	68	4		0.710	1.40×10^{-2}	
	SI	13–30	10	5	nd	nd	nd	57	1				
Water (Rel. units)	SD	0.15–1	110	35	-	0.00	1.14	47	3		0.8709	0.1291	
	SI	0.25–1	30	10	nd	nd	nd	62	2				

Columns 1 and 2 indicate the environmental factor under consideration and the traits analyzed. For temperature, the average temperature over the full day/night cycle during active growth was used. Water stress was assessed as the relative biomass of water-stressed plants compared to well-watered plants in the same experiment. Columns 3 and 4 show the range of the environmental factor for which data are available in the database, as well as the total number of observations (i.e., number of mean values per species and level of the environmental factor of interest; rounded to the nearest 10). Column 5 indicates the number of species for which observations are available for the various traits. Column 6 refers to the form of the dose-response curve. Fitted equations were categorized as follows: no relationship (-; Y = a where Y is the scaled value of the phenotypic trait and a is the overall average of Y values); linear (L; $Y = a + bX$ where X is the environmental factor), or saturating (S; $Y = a\,(1 - b \cdot e(-c^X))$). No fit was determined (nd) with fewer than 30 datapoints, Column 7 shows the fraction of variability explained by the fitted curve. Column 8 lists the Plasticity Index (PI) calculated as the fitted value at [CO_2] = 1200 divided by the fitted value at [CO_2] = 200; or the fitted value at DLI = 50 divided by the fitted value at DLI = 1. Positive values indicating positive trends with the environmental factor of interest, while negative PI values indicate decreasing trends; bold numbers indicate a $|PI| \geq 1.5$. The Consistency Index (column 9) represents the percentage of cases (species x experiment combinations) where the phenotypic value at the highest level of the experimental factor considered was greater than at the lowest level. Values lower than 15 or larger than 85 signify highly-consistent positive or negative responses and are indicated in bold. Column 10 shows the Reliability Index (RI), based on the number of records in the database for that trait, the number of different species, the range of levels for the environmental factor, and the average deviation from the median response. The RI is on a relative scale from 0 (low) to 9 (high reliability level). Column 11 shows the significance of a bootstrap test comparing differences in PI for stomatal density and stomatal index. The last 3 columns provide the values for parameters a, b and, if relevant, c for the equations mentioned above.

Table 2. Variation in Plasticity Index (PI) for Stomatal Density (SD) and Stomatal Index (SI) among functional groups, for four environmental factors.

Env. Factor	Trait	C_3 Woody			C_3 Herb.		C_4 Herb.		
		PI	n	*p*	PI	n	PI	n	*p*
[CO_2]	SD	−1.14	220	ns	−1.06	320	−1.01	90	ns
	SI	−1.13	60	ns	−1.04	100	−1.01	30	ns
DLI	SD	1.95	170	ns	2.27	150	-	20	-
	SI	2.54	30	ns	1.79	80	-	0	-
Temperature	SD	1.88	50	ns	1.41	70	-	0	-
	SI	-	0	-	-	0	-	0	-
Water	SD	1.32	40	ns	1.09	50	-	0	-
	SI	-	10	-	-	10	-	0	-

PI data were analyzed based on dose-response curves for three distinct functional groups: C_3 woody species, C_3 herbaceous species, and C_4 herbaceous species. The number of data points available for each group is also provided, rounded down to the nearest 10 (n). Each data point represents the average value per treatment for each experiment and species or genotype. PI's and significance values were not calculated for groups with fewer than 30 data points. To assess statistical significance, we tested whether the PI of C_3 woody species and C_4 herbaceous species differed significantly from that of C_3 herbaceous species, by means of bootstrapping (5000 repetitions). None of the contrasts between functional groups showed significant differences.

The results for light intensity contrast sharply with those for CO_2, as light exerts a strong influence on SD (Table 1). Numerous studies have reported positive responses to higher light intensity (e.g., Cooper & Qualls, 1967; Valladares et al., 2002; Wang et al., 2020b), a trend that is evident in our meta-analysis as well (Figure 2A). The response of SD is most pronounced at low DLI levels, and saturates above 35 mol m^{-2} d^{-1}. When considering the range of 1–50 mol quanta m^{-2} d^{-1}, which encompasses DLI's from the shaded forest floors to low-latitude deserts exposed mostly to full sunlight, the Plasticity Index is 1.93, indicating nearly a doubling of SD over this range. This value is intermediate compared to the responses of 85 ecophysiological traits to DLI, but comparable in size to the well-known increases in leaf thickness and photosynthetic capacity (Poorter et al., 2019; Poorter et al., 2022b). The increase in SD is highly consistent, with a Consistency Index of 94%, indicating that nearly all experiments and species exhibit increases in SD with higher light levels. The Reliability Index indicates an intermediate level of confidence. As with [CO_2], we analyzed whether responses to light intensity varied among species groups. While herbaceous C_3 species may exhibit slightly stronger responses than woody C_3 species, these differences are small and statistically non-significant (Table 2). For each of the groups, the effect of light on SD is markedly stronger than CO_2.

Information on SD responses to temperature and water availability is much scarcer compared to responses to CO_2 and light. The dose-response curve for temperature indicates a positive association, best described by a linear relationship (Figure 3A). The Plasticity Index for temperature is 1.54 over the 5–35 °C range, with a Consistency Index of 68%. While the Plasticity Index is higher for woody C_3 species compared to herbaceous C_3 species (Table 2), also this species contrast is not significant. Water availability or stress was quantified by comparing the size of water-stressed plants to control plants, assuming that control plants in the compiled experiments were adequately watered. No significant relationship was found (Figure 1B), which aligns with a low Consistency Index of 47% (Table 1). Further separations in species subgroups are given in supporting Info S4. We did not analyze responses to varying levels of nutrient availability or relative humidity. However, small data compilations conducted so far indicate that responses to these factors are also mixed (Bertolino, Caine, & Gray, 2019; Fanourakis et al., 2020).

3.2. Stomatal index

While SD is functionally linked to gas exchange, stomatal index (SI) provides greater insight into the developmental process of stomatal initiation (Royer, 2003). Similar to SD, SI generally exhibits a negative correlation with [CO_2], but with a slightly steeper slope, indicating greater plasticity (more negative PI; Figure 1B). Unlike SD, however, the median values for each consecutive 10% of the data do not indicate saturation at higher CO_2 levels. Therefore, these experimental data do not support the concept of a 'ceiling' in SI at CO_2 concentrations above current levels, as proposed by Woodward (1987) and Roth-Nebelsick (2005). The Consistency Index for SI deviates further from the neutral 50% than that for SD, suggesting a slightly more consistent relationship with [CO_2]. Nevertheless, with a Consistency Index of 32%, this relationship remains weak and far from universal. On average, herbaceous C_3 and C_4 species, as well as young woody plants, exhibit similar Plasticity Indices (Table 2).

Information on the effect of light on SI is less abundant. However, similar to SD, the response of SI to daily light integral (DLI) contrasts sharply with its response to [CO_2], both in direction and strength. The dose-response curve for DLI is positive, and follows a saturating pattern (Figure 2B). The Plasticity Index for SI is 1.96, and the results exhibit high consistency (>90%). Intriguingly, these findings contrast with earlier studies by Salisbury (1927) and Poole et al. (1996), which were not included in our dataset because they compared sun and shade leaves within individual trees. Those studies observed differences in SD that largely diminished or disappeared when SI was analyzed. We have no clear explanation for this discrepancy, but it is possible that the regulation of SI at the whole-plant level differs from that within a single plant. Additional independent research on this contrast would be valuable.

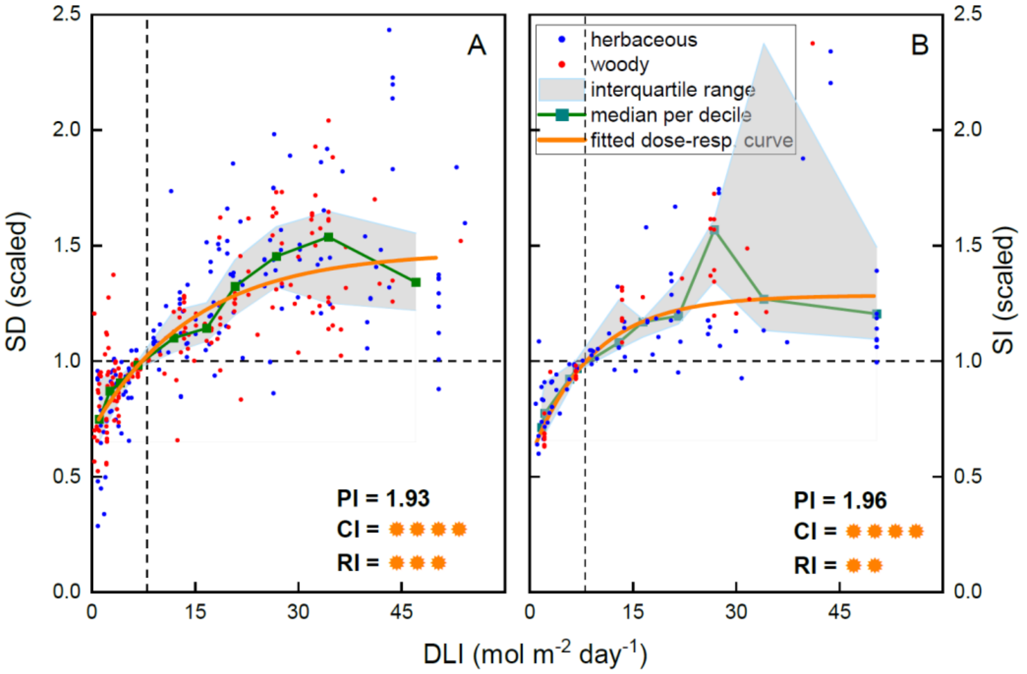

Figure 2. Dose-response curves for (**A**) Stomatal Density (SD) and (**B**) Stomatal Index (SI) as functions of Daily Light Integral (DLI). Data points represent scaled mean values per species and experiment, relative to a reference DLI of 8 mol m^{-2} d^{-1}. Two and four datapoints, respectively, with values exceeding 2.5 are not shown in this graph, but can be inspected in Figs. S03 and S04. For further details on data scaling, symbols, and indices, see the legend of Figure 1.

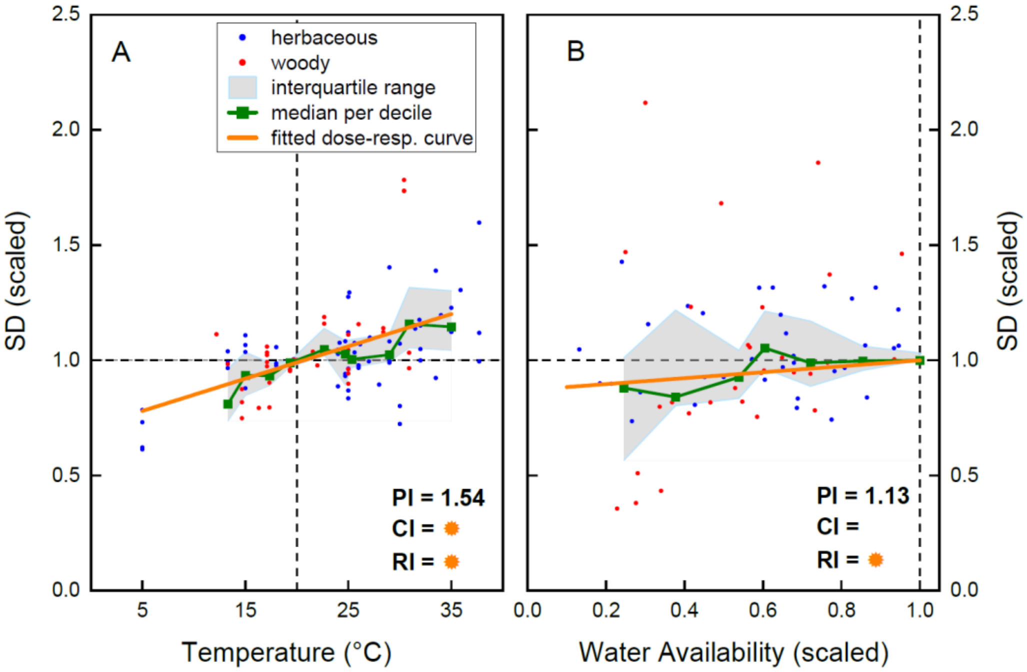

Figure 3. Dose-response curves for Stomatal Density (SD) in relation to (**A**) Temperature and (**B**) Water Availability. In (**A**), data points represent scaled mean values per species and experiment, normalized to values at a mean daily temperature of 20 °C. In (**B**), SD values are scaled relative to control plants grown under optimal water availability, with drought stress severity inferred from the biomass or leaf area of plants of drought-stressed plants compared to controls. For more information see the legend of Figure 1.

Another potential explanation is that one or more of our assumptions may not (fully) hold. Our approach aims to integrate as much information as possible, often combining data from different subfields of plant biology (Poorter et al., 2022a). Unfortunately, this information is highly scattered, and we rely on the assumption that compiling sufficient data for all species or subgroups thereof will allow to establish the proper dose-response curves. However, the available data remain limited, and to some extent reflect experiments where SD was measured for species A and B, whereas others focused only on SI for species C and D, rather than determining both traits for all species. We therefore also analyzed data for those literature sources where both SD and SI were determined for leaves exposed to different light intensities. For those cases, we found a PI of 2.39 for SD, and 1.78 for SI, indicating a weaker response for SI. This aligns with the general observation that the size of stomatal complexes and pavement cells decreases under higher light intensities (Rahim & Fordham, 1991; Thomas, Woodward, & Quick, 2004; Oh & Kim 2010). Consequently, SD tends to increase with light intensity not only because there are relatively more stomatal complexes formed at high light, but also because the epidermal cells are smaller in size. Regardless of which data are included, the overarching conclusion remains that both SI and SD are far more sensitive to prevailing light conditions than to ambient CO_2 concentration.

We found insufficient data to construct dose-response curves for SI in response to temperature and water availability. The limited experimental data available showed no significant differences in SI between high-temperature and low-temperature treatments, nor between plants exposed to low and high water-availability. In both cases the Consistency Index was close to 50% (Table 1), indicating no clear pattern. Although these findings are based on limited data, they align with Royer's (2003) proposition that SI is largely independent of temperature and water availability. However, the results also highlight that light intensity is a far more significant modulator of SI than previously recognized.

3.3. The value of SD and SI for paleo-reconstruction

Stomatal density (SD) and stomatal index (SI) can both be measured from fossil leaves with a well-preserved cuticle. Of these two traits, SI is currently preferred to estimate CO_2 concentrations over geological timescales (Royer, 2003). However, based on the results of the meta-analyses discussed above, we would like to highlight several areas of caution regarding the use of either of these proxies.

1. Canopy position of leaves. Across the environmental ranges analyzed, the response of SD to [CO_2] is relatively modest compared to its response to temperature, and only slightly greater than its response to water availability (Table 1). Both SD and SI show weak responses to [CO_2] when compared to their much stronger responses to variations in light intensity. Given the high sensitivity of both traits to daily light integral (DLI), it is essential to account for the canopy position of fossilized leaves when interpreting stomatal data (Poole et al., 1996). In paleo-botanical studies, it is often assumed that most leaves in fossil assemblages are canopy leaves from light-saturated environments. This assumption is based on the idea that upper canopy leaves are more abundant, and more likely to be transported by wind to the actual deposition sites (Ferguson, 1985; Greenwood, 1991). However, light levels in a tree canopy can easily decrease by half within the top 4 m of a tree crown (Fauset et al., 2017). Assuming a DLI of 30 mol m^{-2} d^{-1} above the canopy, and that sun and shade leaves of trees follow the same trends as the fitted curve in Figure 2B, we calculate that leaves 4 m below the top of the tree canopy would have approximately 6% lower SI. This reduction represents half the 12% variation in SI observed across the CO_2 range of 200–1200 ppm range (Table 1), underscoring the importance of light gradients within the canopy (Poole et al., 1996).

Several proxies can help distinguish sun leaves from shade leaves in fossil specimens. Sun leaves typically have smaller epidermal cells, less undulated cell walls and greater ^{13}C discrimination compared to shade leaves (Kürschner, 1997; Graham et al., 2014; Šantrůček et al., 2014; Dunn et al., 2015; Poorter et al., 2022a). Although some studies indicate that the majority of fossil leaves were likely exposed to high-light conditions (Ferguson, 1985; Greenwood, 1991; Kürschner, 1997), others indicate considerable variation in the light environments experienced by fossil leaves (Bush et al., 2017). Therefore, it is prudent to infer the original canopy position of fossil leaves when using them for paleo-CO_2 reconstructions. For example, Reichgelt et al. (2020) estimated CO_2 levels from early Miocene fossil leaves by selecting those with relatively high cell density, minimal cell undulation and high leaf ð^{13}C. Since cell density and leaf ð^{13}C values are already key input parameters in current gas-exchange models for CO_2 estimation (Franks et al., 2014), incorporating these criteria does not require much additional analytical work. Consequently, this approach should be considered standard protocol when interpreting fossil leaves for CO_2 reconstructions.

The above analysis relies on the assumption that the dose-response curve for SD and SI, as determined for whole plants grown at different DLIs, is also applicable to leaves that experience varying light availability within a tree. While this assumption holds for a range of leaf-level traits (cf. Niinemets, Keenan, & Hallik, 2015; Poorter et al., 2019), the few studies comparing the SI of sun and shade leaves in individual trees have reported much larger differences in SD than in SI (Salisbury, 1927; Poole et al., 1996; Kürschner, 1997). As noted earlier, this aspect warrants further investigation.

2. Above-canopy light availability. The issue of DLI related to canopy position extends to broader above-canopy light conditions. Assuming a fixed level of DLI for canopy leaves across geological eras overlooks uncertainties introduced by variables such as cloud cover, which can vary and affect above-canopy light availability (Stephens, 2005). Based on the saturation observed in the dose-response curves (Figure 2A,B), we would expect the SD or SI of plants in locations with minimal cloud cover, such as desert areas at low latitudes, to be relatively unaffected. However, fossil leaves are often better preserved in wetter areas, where cloud cover can substantially influence DLI, and consequently SD and SI. Of particular interest are environments with few or no modern analogues, such as temperate polar forests during the hothouse climates of the Cretaceous and Eocene (e.g., Herman & Spicer, 2010; West, Greenwood, & Basinger, 2019). The above-canopy light conditions in these environments are difficult to reconstruct and the associated ecophysiological adaptions are challenging to constrain

(Brentnall et al., 2005; Konrad, Roth-Nebelsick, & Traiser, 2023). Nonetheless, fossil leaves from these environments do get used in paleo-CO_2 reconstructions (Wolfe et al., 2017; Wang et al., 2020c).

3. *Between and within-species specificity.* We established generalized dose-response curves based on the compiled data, showing consistent positive responses to light, but variable responses to [CO_2] (Table 1). This variability poses a challenge for accurately estimating paleo-CO_2 levels. A key question is whether this variation stems from between or within species differences in stomatal responses. Although we found slightly stronger responses to [CO_2] in C_3 herbaceous and woody species compared to C_4 species, these differences were not statistically significant. Similarly, there were no significant differences in plasticity between C_3 herbs and woody species (Table 2). We also tested whether SD responses were different between deciduous and evergreen tree species. For CO_2, PI was marginally and non-significantly different (−1.05 and −1.14, respectively), but for light intensity, evergreens showed higher plasticity than deciduous species (2.20 and 1.56, respectively, respectively), with $0.05 < p < 0.10$. Since most fossilized leaves stem from woody species, and have a better chance to be preserved when the leaves are sturdy and therefore of evergreen nature, this may aggravate the problems with interpretation mentioned above.

In paleobotany, researchers calibrate absolute values of SD and SI in fossil leaves with those of their nearest-living relatives growing under known CO_2 concentrations (McElwain & Steinthorsdottir (2017). However, substantial species-level differences in SD and SI, as well as variations between genotypes, have been reported (e.g., Christophel & Rowett, 1996; Hovenden & Schimanski, 2000; Wall et al., 2023). Consequently, selecting a genotype from a nearest-living relative introduces additional uncertainty into CO_2 estimates. Another source of uncertainty stems from within-species variability in the relative CO_2-response observed across experiments. In our compilation, such repetition was available for only a few species, and primarily in sufficient numbers for SD. In Figure 4, we show the responses for the most-frequently studied species, *Triticum aestivum*, and the 'living fossil' *Ginkgo biloba*. For both species, studies report both positive and negative responses to increasing [CO_2]. However, the overall pattern is not very different from the generalized dose-response curve shown in Figure 2A. This suggests that relying on data for a given species from only one or two experiments may not produce a robust calibration curve. To better capture these species-specific or genotypic responses, more comprehensive datasets are required. Nonetheless, given the within and across species variation of SI and SD in response to [CO_2], it is unlikely that modern living species, such as *Ginkgo biloba*, can be used to estimate CO_2 concentrations in deep time, as the genetic and ecophysiological variability cannot be constrained.

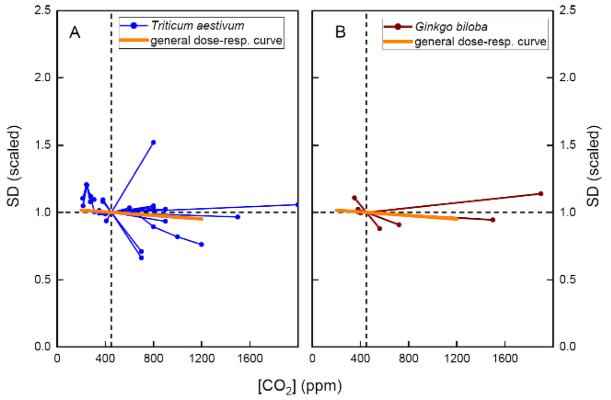

Figure 4. Effect of ambient CO2 on Stomatal Density (SD) as reported in different experiments for (A) *Triticum aestivum*, and (B) *Ginkgo biloba*. The orange line represents the overall fit from Figure 1A. Data points connected by a line are mean values per experiment. All data are scaled relative to the phenotypic values at a reference [CO_2] of 450 ppm.

4. *Experimental data vs using historical leaves.* To estimate paleo-CO_2 levels, transfer functions can be established between CO_2 concentration and SI or SD. These functions are analogues to the dose-response curves we previously discussed, but with inverted axes. Several approaches have been used to derive these transfer functions. These include, from shorter to longer timespans: (1) plants grown experimentally under various CO_2 concentrations, (2) herbarium leaves collected during periods with known CO_2 levels, and (3) leaves from sub-recent sediments calibrated against CO_2 data from ice-core records. We compared five transfer functions derived from herbarium records and sedimentary leaves, converting them into CO_2 dose-response curves and scaling them similarly as our general dose-response curve (Figure 5). The difference in slope between the generalized dose-response curve on the one hand and those derived from the published transfer functions on the other is striking. The latter exhibit much steeper slopes compared to the curve based on controlled experiments. This was previously noted by Beerling & Chaloner (1992) and Royer (2001). They postulated that long-term genetic pressures on stomatal initiation may outweigh the more immediate, modest plastic response. They further suggested that it might take 100–1000 years for plants to fully adjust to new atmospheric CO_2 levels. For trees this would imply adaptation over 2–10 generations. From an ecophysiological perspective, reduced stomatal density under elevated CO_2 seems plausible, as a lower SD could maintain sufficient conductance for CO_2 diffusion. It is not easy to experimentally substantiate this thesis, but the scarcely-available evidence is not supportive. Yang et al. (2023) conducted an experiment where rice was grown over five consecutive generations under either control or elevated CO_2. They found a marginal *increase* in SD due to [CO_2], in both the 1st and 5th generation, rather than the anticipated decrease. Their study, the first of its kind to assess SD across so many generations, offers little support for a substantial and negative generational effect.

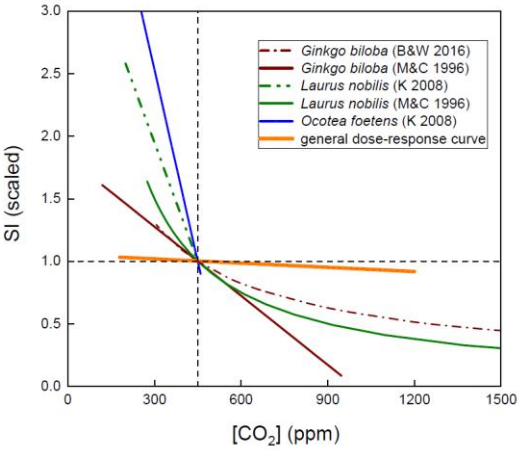

Figure 5. Comparison of the generalized dose-response curve for Stomatal Index (SI) with respect to [CO_2] (shown in Figure 1B) with transfer functions derived for *Ocotea foetens* and *Laurus nobilis* (Kürschner, Kvaček, & Dilcher, 2008), *Laurus nobilis* and *Ginkgo biloba* (McElwain & Chaloner, 1996), and *Ginkgo biloba* (Barclay & Wing, 2016).

Alternatively, the marginal change observed in experimental plants (Figure 5) could be attributed to the fact that they all originated from seeds of plants grown under present-day CO_2 levels, and were often pre-grown under control CO_2 levels during seedling establishment. Studies show that older leaves signal their growth conditions to younger leaves, influencing SD and SI in newly-developing leaves in response to both CO_2 concentration (Lake et al., 2001) and light intensity (Thomas, Woodward, & Quick, 2004). This suggests that a temporary carry-over effect from past CO_2 conditions might lead to an underestimation of the CO_2 effect in experimental approaches. However, the median duration of CO_2 experiments in our compilation was 98 days. For comparison, even a single day of exposure to different light conditions already affects the final SD (Schoch et al., 1980). Thus, assuming similar dynamics, we expect 98 days of CO_2 exposure to be sufficient to eliminate legacy effects. Another possible explanation for the observed discrepancy is that stomatal development in field-collected plants over extended time periods may be influenced by co-varying environmental factors, such as cooler temperatures during periods of lower [CO_2] (Figure 3A). Finally, publication bias could play a role, with studies reporting transfer functions with shallow slopes being less likely to be submitted or accepted for publication. In any case, understanding the mechanisms driving the difference in sensitivity between contemporary experimental data and field-collected historical measurements would be helpful to improve confidence in transfer functions based on field data.

5. Extrapolating transfer functions. A final consideration is that transfer functions derived from herbarium or sediment leaves, and calibrated using CO_2 concentrations from ice cores, are only validated within the range of 280–400 ppm, as these are the data for which we have independent CO_2 measurements. Any values beyond this range represent extrapolations, which complicates the use of these transfer functions for periods when CO_2 levels exceeded current values.

The toolbox available to paleobotanist is limited, and their methodologies cannot be as refined as those employed by ecophysiologists studying living plants. Nonetheless, the questions paleobotanists address are crucial, and reliable proxies for past CO_2 concentrations are indispensable for understanding system Earth. Unfortunately, stomatal density and stomatal index responses to CO_2 suffer from considerable variability and inconsistency. New approaches that integrate (eco)physiological and morphological traits with modeling techniques (Franks et al., 2014; Konrad et al., 2017) hold greater promise. These methods are increasingly replacing SD- and SI-based approaches due to their improved reliability. Despite this progress, it remains prudent to base paleo-CO_2 reconstructions on a diverse array of proxies. As demonstrated effectively by Hönisch et al. (2023), combining multiple lines of evidence enhances confidence in estimates and provides a more comprehensive understanding of past atmospheric conditions.

4. Conclusions

We developed generalized dose-response curves for stomatal density (SD) and stomatal index (SI) in response to [CO_2] and light intensity, along with additional curves for SD as dependent on temperature and water availability. Although both SD and SI exhibited negative correlations with [CO_2], these responses were relatively small and inconsistent. In contrast, their responses to changes in Daily Light Integral (DLI) were significantly stronger and more consistent, emphasizing the dominant influence of light in shaping SD and SI. Consequently, the position of leaves within the canopy or variations in light availability across different eras introduces significant complexity, further challenging the reliability of fossil leaf stomata as robust paleoproxies for reconstructing past atmospheric CO_2 concentrations.

Supplementary Materials

The following supporting information can be downloaded at: https://www.sciltp.com/journals/PlantEcophys/2025/1/514/s1. S1. Extended Materials & Methods. S2. References used for the meta-analyses, listed per environmental factor. S3. Detailed figures of the responses of stomatal density and index to [CO2], Daily Light Integral, Temperature and Water availability. S4. Responses of various functional groups of species.

Author Contributions

H.P. and T.L.P. conceptualized the idea and carried out the data collection. H.P. calculated and analyzed the data. H.P. TL.P. and T.R. wrote the ms, with H.P. and T.L.P. covering the ecophysiological aspects, and TR the paleobotanical aspects.

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Data Availability Statement

Data are available upon request from Hendrik Poorter.

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Conflicts of Interest

The authors have no conflict of interest.

Peer Review Statement

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Abbreviations: CI, Consistency Index; DLI, Daily Light Integral; PI, Plasticity Index; RI, Reliability Index; SD, Stomatal Density; SI, Stomatal Index

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References marked with an asterisk indicate studies included in the meta-analysis.

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