Title:

**Unraveling the neglected role of UV radiation on stomata: a meta-analysis with implications for modeling ecosystem-climate interactions**

Running title:

**UV radiation and stomata**

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**Abstract**

Stomata play a pivotal role in regulating gas exchange between terrestrial plants and the atmosphere controlling water and carbon cycles at organismal, ecosystem and global levels. Accordingly, our objective was to investigate the impact of ultraviolet-B radiation, a neglected environmental factor varying with ongoing global change, on stomatal morphology and function by means of a comprehensive meta-analysis. We found 45 peer-reviewed publications containing altogether 143 case studies for analysis.

The overall UV effect at the leaf level is to decrease stomatal conductance, stomatal aperture and stomatal size, although stomatal density was increased. The significant decline in conductance is marked in short-term experiments, with more modest decreases noted in long-term UV studies. We found that short-term experiments in growth chambers are not representative of long-term field UV effects on stomatal conductance. Further, we found a stronger UV effect in grasses than in herbs, while the reduction of stomatal conductance was insignificant in trees. It is hypothesised that these alterations in stomatal function have important potential consequences for plant life. In the short term, UV-mediated stomatal closure may reduce transpiration and alleviate drought stress. However, in the long term more complex changes in stomatal aperture, size and density may reduce carbon sink capacity, and enhance leaf and surface warming, potentially exacerbating the negative effects of drought and/or heatwaves on plant ecosystems and endangering long-term plant survival.

**Keywords**

Carbon sink, review, plant stress responses, stomatal aperture, stomatal size and density, stomatal conductance and transpiration, ultraviolet radiation, UV-B

**Statement**

UV-B radiation reduces stomatal conductance, aperture and size while increasing density. Short-term effects are stronger than long ones, affecting grasses more than trees. Reduced conductance may lessen drought stress, but raise leaf warming, worsening heatwave damage and reducing carbon uptake.

**Introduction**

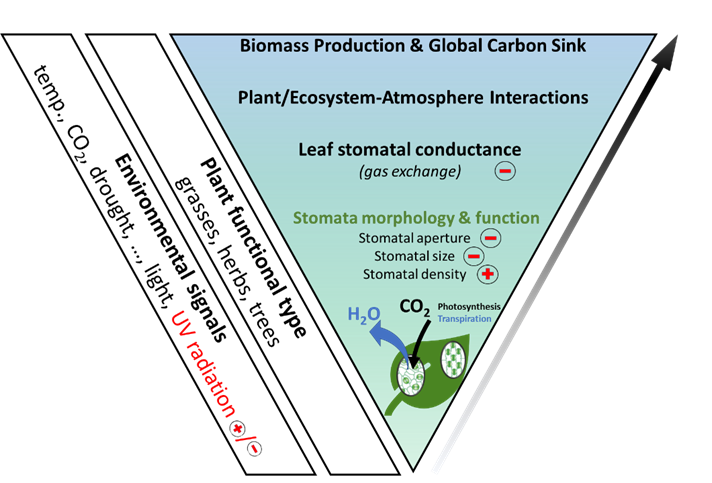
Global environmental change involves many inter-related processes (IPCC, 2021). The response of plants and/or ecosystems to individual global change variables is further complicated by the interactive effects of a range of environmental factors (Mittler, 2006). Among others, ultraviolet-B radiation (UV-B; 280–315 nm) has been shown to be an important and interacting factor, increasing the complexity, uncertainty and non-linearity of the biosphere’s response to global change (Jansen et al., 2022; Barnes et al., 2023). Thanks to the Montreal Protocol, the destruction of the UV-shielding stratospheric ozone layer is now largely halted (Barnes et al., 2021). However, UV irradiance levels are still a threat as they are expected to change in tandem with progressing climate change (Eleftheratos et al., 2022; Barnes et al., 2023). Increases in UV irradiance are linked to changes in cloud cover, aerosol concentrations and surface reflectivity, and may reach 3–8% relative to 2017–2020 over the tropics and mid-latitudes, respectively, by 2100 (Barnes et al., 2023). It is suggested that a decline in aerosol pollution will lead to enhanced warming through “brightening” of the atmosphere, i.e. less clouds and more direct sunshine (Bartoszek et al., 2020; Wild et al., 2021; Quaas et al., 2022). In parallel, decreases in air aerosol pollution may further lead to enhanced UV penetration into the biosphere (Wild et al., 2021), especially as observed trends in sun radiation already exceed worst-case scenarios in parts of Europe by 2100 (KNMI, 2023). Thus, plants and ecosystems are exposed to new and rapidly changing combinations of solar UV radiation and climate change factors, raising the question of how rising UV irradiances, or its natural variability, impact terrestrial plant life under climate change.

The largest uncertainty regarding biological feedbacks to climate warming is represented by processes related to terrestrial vegetation (O’Sullivan et al., 2022; Raoult et al., 2023) and its ability to provide a net carbon sink (Duffy et al., 2021). Apart from temperature effects on photosynthesis and respiration as the main drivers of carbon sink/source balance (Duffy et al., 2021), stomatal conductance is a critical regulator of CO2 and H2O exchange at the vegetation-atmosphere interface (Liang et al., 2023). Ongoing research efforts attempt to reduce the uncertainty associated with the vegetation-carbon feedback. However, most current models still deal exclusively with photosynthetic (or carbon assimilation) rate and temperature as the main input variables (Raoult et al, 2023).

There are many studies dealing with impacts of environmental drivers on leaf stomatal conductance, such as elevated CO2 concentration (Ainsworth and Rogers, 2007), vapour pressure deficit (Grossiord et al., 2020), temperature (Urban et al., 2017; Drake et al., 2018), drought (Marchin et al., 2022; Wu et al., 2020), nutrient availability (Zhu et al., 2020), soil moisture (Xu et al., 2023), and their various combinations and interactions. Generally, a relatively clear and consistent picture of stomatal response to these factors has emerged, whereby under stress conditions stomatal conductance tends to decrease, except under specific extreme conditions and/or in geographically limited areas (Purcell et al., 2018; Marchin et al., 2022). In turn, changes in leaf stomatal conductance may impact photosynthetic performance. Although the processes of photosynthetic CO2 assimilation and stomatal conductance are tightly linked (Wong et al., 1979; Jarvis and Davies, 1998; Lichtenthaler et al., 2007), many studies investigating the effects of environmental change on carbon assimilation fail to report co-occurring changes in stomatal conductance. This is also true for many earlier UV studies (e.g., Flint et al., 1985; Naidu et al., 1993; Šprtová et al., 1999), where attention was focused on the photo-inhibitory effects of UV-B radiation on photosystem II and other parts of the photosynthetic apparatus.

Theoretically, leaf stomatal conductance is dictated by the size, density and aperture of stomata (Dow et al., 2014) and inevitably affects plant/ecosystem interactions with the atmosphere (Figure 1). However, little is known about UV effects on stomatal morphology and function and the data in the literature are often contradictory. While some studies have shown, that UV mediates stomatal closure (Noqués et al., 1999) and can thus contribute to a higher leaf temperature (Williams et al., 2022), many other studies reported negligible or even stimulatory effects of UV radiation on the degree of stomatal opening (Jansen and van den Noort, 2000). The diverse range of responses raises the question of species-specific UV radiation effects, the role of the applied UV dose as well as the importance of the entire growth environment.

In this study, using a meta-analytical approach, we investigate and summarize the effects of UV radiation on stomatal conductance and related stomatal traits. In accordance with the above-mentioned uncertainties, the primary research question of our meta-analysis is to summarize the effects of UV radiation on (i) stomatal morpho-functional traits, and (ii) leaf stomatal conductance for gas exchange. In turn, this information is used to (iii) suggest potential consequences of UV-modulated stomatal conductance for global plant-atmosphere interactions and land carbon sink modelling efforts.

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**Figure 1.** Schematic overview of the interactive effects of environmental signals, and plant functional type on stomatal characteristics, such as size, density and aperture, with consequences for leaf conductance, and plant/ecosystem atmosphere interactions.

**Materials and methods**

*Literature search and exclusion criteria*

The terms “UV\*”, and “Stoma\*” were used to search the Google Scholar database for relevant publications. The asterisk \* provides for results that contain a variation of the keyword. The Boolean operator AND was used to combine these keywords during the search. Only peer-reviewed studies were considered for analysis. Excluded were papers that included UV-C as part of the UV treatment, papers focused on just UV-A exposure, papers detailing UV priming of the seed-stage only, and papers for which experimental details were not clear and/or papers where a ‘no-UV’ control was lacking.

Papers were scrutinised for a number of physiological and morphological traits which were compiled into five categories:

1. Stomatal conductance (*G*s), defined as the rate of CO2 entering through the stomata of leaves per unit of surface area, including stomatal conductance, stomatal limitation and stomatal resistance data, and measured using a gas-exchange technique. For quantification purposes, the inverted value was used for stomatal limitation and stomatal resistance data.
2. Leaf transpiration (*T*r), defined as the rate of water loss through the stomata of leaves.
3. Stomatal aperture (Aperture), defined as the pore size of stomata.
4. Stomatal size (Size), including data of stomatal length, stomatal area, and stomatal width.
5. Stomatal density (Density), including the number of stomata per leaf area, and abaxial/adaxial stomatal density (the stomata number per unit leaf area) and stomatal index (the ratio of the number of stomata to the total number of stomata and epidermal cells).

As data on leaf stomatal conductance and leaf transpiration were found to be strongly interlinked (Ehleringer et al., 1993), these two categories were merged to give a total of four representative categories:

* Conductance and transpiration (representing a leaf-level response)
* Stomatal aperture (representing a cellular, physiological response)
* Stomatal size (representing a cellular, morphological trait)
* Stomatal density (representing a cellular, morphological trait)

In parallel, background information was also tabulated including plant functional types (tree, herb or grass), together with the technical approach (growth chamber, glasshouse or field; UV-exclusion or supplementation approach), and UV-exposure details (background intensity of photosynthetically active radiation (PAR), UV irradiance and dose, and duration of the UV-exposure). The data obtained from the various studies were compiled in Excel together with information on the citation, common plant name, Latin name, cultivar name, and growth conditions (Supplemental Table S1).

A total of 45 published studies were incorporated into the analysis presented in this paper. Where studies reported on more than one plant species, cultivar, plant developmental stage (or treatment duration), or growth (light) conditions, each was treated as a separate “case study”, providing altogether 143 case studies for analysis.

In the analysed studies, UV treatment refers to exposure to either UV-B alone, or a combination of UV-B and UV-A radiation (for example natural sunlight studies, or studies using UV-B tubes that have some emission in the UV-A part of the spectrum). Pure UV-A exposure studies were excluded. In some studies, UV exposure was complemented by exposure to another stressor (e.g., drought, excess PAR intensity, etc.). In these cases, only control and UV treatments were considered for the current analysis.

In the subsequent data processing, control vs. treated groups included the following: UV supplementation studies (where the untreated plants represent the control), and UV exclusion studies (where the UV‐shielded plants were considered as the control). In order to quantify the magnitude of net UV effect, relative changes induced by UV radiation in % (presented in Figures 3B and 6B) were calculated as [(UV treated – UV control)/UV control]\*100.

**Meta-analysis**

Standardized difference in means (SDM) was used for the calculation of the summary (net) effect across all experiments. The SDM quantitatively determines the size of the intervention effect in each case study relative to the data variability observed in that case study. See Equation 1 in Ač et al. (2015) for details. In brief, for the calculation of SDM, the standard deviation or standard error (whichever was recorded) and the number of replicates (*n*) were recorded for both control and treated plants. Prior to meta-analysis, standard errors were converted to standard deviations. In principle, two basic statistical models can be used for calculating the net effect, that is, fixed and random effect models (Borenstein et al., 2009). The random effect model was selected since it accounts for the variability of the true (i.e. real world) effect among different case studies, which is expected given the use of different plant species, experimental conditions and set‐ups, as well as different measurement methods. The summary effect size and the statistical significance of all considered case studies are expressed by SDM and the probability (*p*) value. The variability and spread of the effect are then expressed as the 95% confidence interval (CI) and where appropriate, also prediction intervals (PIs). For the details and mathematical formulas used to calculate SDMs, CIs and p values, see Ač et al. (2015).

**Results & Discussion**

*Description of the dataset*

The literature search identified a total of 45 separate publications that comprised a total of 143 case studies. Case studies refer to a scenario whereby a publication presents data on two or more plant species, cultivars, or in some cases UV irradiances or doses. For the current analysis, case studies were treated as being statistically independent. The substantial number of case studies identified constitutes a robust dataset.

Most studies have been published since 1995 (Supplemental Figure S1), within a decade of the discovery of the hole in the Antarctic stratospheric ozone layer in 1985 (Farman et al., 1985). The delay in publications is likely to reflect the initial research focus on UV-mediated DNA damage, inactivation of photosynthesis and impairment of growth (e.g. Caldwell et al., 1989; Jansen et al., 1998). Earlier studies of gas-exchange in UV-exposed plants often reported CO2 assimilation rates, without considering stomatal conductance. As a result, it is not possible to distinguish between direct UV effects on photosynthesis and those mediated through stomatal performance. The persistent interest in UV-mediated changes in stomatal responses since 1995 shows that stomatal effects are considered to be relevant for both plant biology and agricultural applications (Wargent and Jordan, 2013).

A broad range of UV-exposure protocols has been developed (Aphalo et al., 2012), and this is reflected in a range of advanced experimental approaches used in published studies. It was found that approximately 53% of case studies were done under environmentally-relevant field conditions (76 in total), while only around a quarter were done under protected, indoor conditions in growth chambers (Figure 2A).



**Figure 2:** Number of case studies performed under different growth environments (**A**; growth chamber, greenhouse or field conditions), functional plant groups (**B**; grasses, herbs or trees), UV treatment (**C**; exclusion or supplementation experiments), and experiment duration (**D**; Short-term (≤30 days), Medium-term (>30 days and ≤90 days), and Long-term (>90 days)). In panel C: Supplemental UV doses applied were categorized as Sup\_Low (below 5 kJ m–2 day–1), Sup\_Mid (5 to 10 kJ m–2 day–1) or Sup\_High (above 10 kJ m–2 day–1); ambient UV doses are referred to as aUV; and N/D shows the number of case studies where the biologically effective UV dose in kJ m–2 day–1 was not reported.

Analysis of the species used in the published studies resulted in a grouping of case studies into three broad functional categories; grasses, herbs and trees (including shrubs) (Figure 2B). Among investigated studies, we found only four C4 species, all of which show a decline in stomatal conductance following UV treatment. Grasses are relatively under-represented, with just 13 case studies on monocotyledonous species (*Colocasia esculenta, Calamagrostis sp., Eragrostis tef, Hordeum vulgare, Agrostis capillaris, Holcus mollis, Panicum miliaceum, Triticum aestivum, Sorgum bicolor*). This presents a knowledge gap given the importance of this group of plant species for human nutrition. The sub-category trees, including shrubs, is well presented in the database with 62 case studies in total. Nevertheless, this sub-category contains just one study on a coniferous tree (*Pseudotsuga menziesii*), while broad-leaved trees are highly represented. It is not entirely clear why so few papers report on the effects of UV on conifers. One possible reason is that there is a lack of UV impacts, a suggestion that is backed up by a classical study by Day et al. (1992) who demonstrated minimal penetration of UV through the epidermis of a variety of gymnosperm needles (including *Larix occidentalis*, *Abies lasiocarpus*, and *Pinus* species), compared to the epidermis from woody and herbaceous dicots, as well as grasses.

Most of the case studies were UV supplementation experiments (110 in total), while just 33 case studies were UV exclusion experiments (less than 25%)(Figure 2C). Exclusion studies use UV filters to block out the UV wavelengths present in natural sunlight, and are therefore normally outdoor, field studies. In the current data set, circa 41% of the field studies uses supplemental lighting, and are focussed on the effects of above ambient UV irradiances, while the other 59% are exclusion studies focussed on impacts of below ambient UV irradiances.

As has been noted before (Aphalo et al., 2012), the comparison of irradiance levels and/or doses between studies can be notoriously difficult due to the use of different light sources (artificial or natural), filters, spectroradiometers and action spectra. While being aware of the limitations of published UV irradiance levels and/or doses, where possible the UV dose was re-calculated in kJ m-2 day-1 (Figure 2C, and Supplemental Figure S2). Subsequently, experiments were, somewhat arbitrarily, grouped into four broad categories;

1. Below ambient UV dose experiments (aUV) – this category refers to “exclusion type” experiments whereby control plants are exposed to filtered natural sunlight.

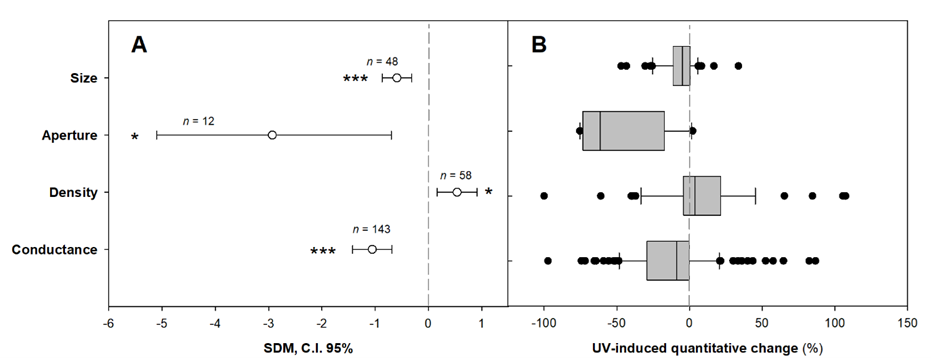
For “supplementary type” experiments, three categories were created:

1. Low UV dose experiments (Sup\_Low; below 5 kJ m-2 day-1)
2. Medium UV dose experiments (Sup\_Mid; between 5 and 10 kJ m-2 day-1)
3. High UV dose experiments (Sup\_High; above 10 kJ m-2 day-1 and with a maximum of 190 kJ m-2 day-1)

In the dataset, below ambient (aUV) and high UV doses (Sup\_High) are particularly prevalent, with smaller numbers of case studies using low or medium levels of supplemental UV. Overall, there is a reasonable spread of case studies across the four UV dose categories.

Historically, many UV-impact studies were short-term, and failed to adequately capture plant acclimatory responses, such as the relatively slow adjustment of morphological parameters (Flint et al., 1985; Robson et al., 2015). However, the current meta-analysis shows a broad range of UV exposure durations, ranging from a few hours (1.5 hours) up to 1,460 days (four-year experiment) (Figure 2D). For the current analysis, data on the experimental duration were placed into three categories based on the length of the experiment: short-term effect (≤30 days), medium-term effect (>30 days and ≤90 days), and long-term effects (>90 days). Although short-term experiments are the most represented experiments, there is a good spread of short, medium-term and long-term studies, and therefore the dataset includes environmentally relevant studies that facilitate acclimatory plant responses (Figure 2D).

*Analysis of the dataset: stomatal morpho-functional traits*



**Figure 3**: Overview of UV effects on stomatal size (Size), stomatal aperture (Aperture), stomatal density (Density), and leaf stomatal conductance and transpiration (Conductance). Data are extracted from 45 peer‐reviewed papers. (A) Meta-analysis significance of UV-induced effects: SDM = standard difference in means; C.I. 95% = 95% confidence interval. Asterisks indicate the level of statistical significance: \* *p* ≤ 0.05, \*\*\* *p* ≤ 0.001. The numbers indicate the number of case studies included in the meta‐analysis. (B) Quantitative changes induced by UV radiation: vertical bars = medians, boxes = 1st and 3rd quartiles, whiskers = 5th and 95th percentiles, points = outliers identified.

The random effect model was used to determine the variability of the true UV effect among different studies (Figure 3A). In this model, the Z-value (which indicates the closeness of a particular value to the group mean) alongside the *p*-value were used to determine the significance of net effects of UV radiation on stomatal characteristics and leaf conductance. UV treatment resulted in significant net negative effects on stomatal size and aperture (the median relative decline is 4.8 and 61.4%, respectively). Conversely, it was found that the stomatal density increased in UV-exposed plants (the median relative increase is 3.7%). At the leaf level, UV exposure is associated with a net decrease in stomatal conductance and transpiration (the median relative decline is 8.7%; Figure 3B). All changes were statistically significant based on the meta-analysis.



**Figure 4:** Detailed analysisof UV effects on stomatal size including 143 case studies. Data are further categorized according to plant functional groups (Gr – grass, H – herb– T – tree), length of the experiment (short – ≤30 days, medium – between 30 days and 90 days, long – >90 days), growth environment (C – growth chamber, G – greenhouse, F – field conditions), UV treatment (Sup – UV supplementation, Ex – UV exclusion), and UV intensity applied (Sup\_Low – below 5 kJ m-2 day-1, Sup\_Mid – between 5 and 10 kJ m-2 day-1, Sup\_High – above 10 kJ m-2 day-1; aUV –ambient UV (category relevant only for the “exclusion type” of the experiment)). SDM = standard difference in means; C.I. 95% = 95% confidence interval. Asterisks indicate the statistical significance of UV effects in a given group: n.s. *p* > 0.05, \* *p* ≤ 0.05, \*\* *p* ≤ 0.01, \*\*\* *p* ≤ 0.001. The numbers indicate the number of experiments included in the meta‐analysis for a given group. In addition, *p* values indicate statistically significant differences within the categories tested. Missing bars indicate that data are not available for a given category.

To investigate in more detail the negative UV effect on stomatal size (*n*=48, *p*<0.001), the relationships between the UV response and experimental treatments and/or plant characteristics were analysed (Figure 4). The data show that the negative effect of UV on stomatal size is largely associated with medium doses of supplemental UV, albeit no data were available on the effects of high supplemental UV doses. No clear effects are observed in the case of low supplemental UV doses, or below ambient UV doses. Indeed, when analysing results as a function of experimental design, UV-effects on stomatal size are strongly linked with supplementation experiments, i.e. exposure to above ambient UV doses. Thus, supplementation experiments yield different results than exclusion experiments, consistent with earlier observations (i.e. Rousseaux et al., 2004). Further, the analysis showed that the effect of supplemental UV doses was clearly notable in environmentally relevant UV field studies. It has been argued that UV effects are most notable in growth chamber studies due to the combination of high UV versus low background PAR (Teramura, 1983). Therefore, it could be speculated that the stomatal size would be even smaller in growth chamber studies, but this remains to be shown.

Further analysis showed that UV effects on stomatal size are only significant in medium-duration experiments (Figure 4). Given that morphological change requires time, it can be speculated that there will be no UV-mediated changes in stomatal size in short-term experiments. This is indeed what the data show. However, surprisingly, the study also failed to identify the effects of UV exposure on stomatal size in long-term studies (*p*=0.71, *n*=18). As trees were found not to amend stomatal size in response to UV exposure, it might be speculated that the lack of long-term UV response is due to the dominance of trees in long-term UV experiments. However, this is not supported by the data, trees are also used as experimental species in short and medium where changes in stomatal size were noted (Figure 2D). Rather, it is speculated that when plants reach a state of full acclimation, in long-term experiments, the trigger that drives a reduction in stomatal size, is removed.

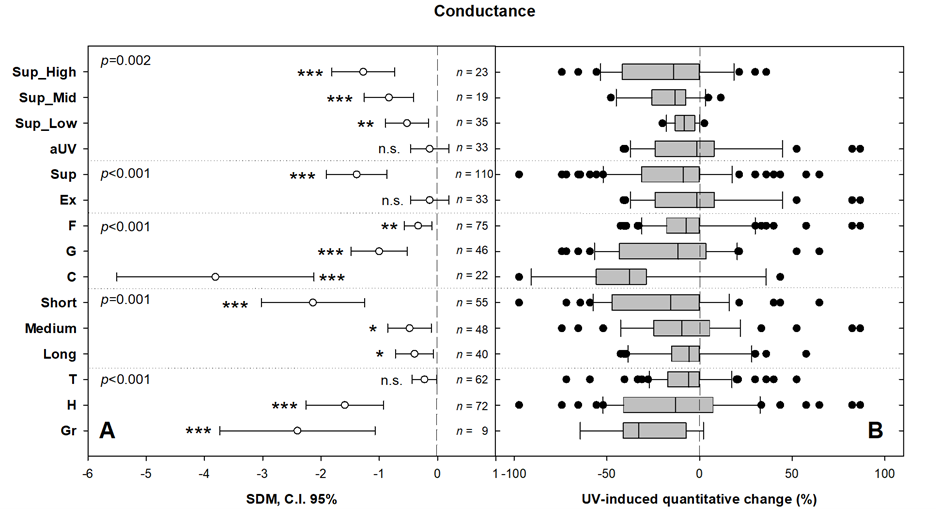
Recent studies have shown that the UVR8 (UV-B resistance 8) photoreceptor can mediate stomatal closure (Tossi et al., 2014; Ge et al., 2020) and an increase in stomatal index (Wargent et al., 2009). It might be speculated that the UV-mediated decrease in stomatal size is similarly associated with UVR8 activity, perhaps in conjunction with UVR8-mediated decreases in leaf area (Robson et al., 2015). Unfortunately, the current dataset does not facilitate quantitative testing of this hypothesis as only a small number of studies present both leaf area and stomatal size. For that small number of studies, negative effects on stomatal size are associated with negative effects on leaf area (Supplemental Figure S3). However, decreases in stomatal size are not necessarily of the same magnitude as the decreases in leaf area. For example, Tripathi et al. (2019) show that a 44% decrease in stomatal size is matched by a decrease of the leaf area of less than 8%. In other cases, the two responses are of a similar magnitude. Thus, at present, the association between stomatal size and leaf area in UV-exposed plants can neither be confirmed nor rejected. However, it should be noted that changes in stomatal size can be triggered by a range of environmental factors, e.g. decreases in stomatal size are associated with limited water availability in potato plants (Sun et al., 2014). Thus, it appears that control of stomatal size is closely linked with drought tolerance and this is, in turn, consistent with postulated UV-mediated drought residence (Jansen et al., 2022).



**Figure 5:** Detailed analysisof UV effects on stomatal density including 143 experiments. Data are further categorized according plant functional groups (Gr – grass, H – herb, T – tree), length of the experiment (short – ≤30 days, medium – between 30 days and 90 days, long – >90 days), growth environment (C – growth chamber, G – greenhouse, F – field conditions), UV treatment (Sup – UV supplementation, Ex – UV exclusion), and UV intensity applied (Sup\_Low – below 5 kJ m–2 day–1, Sup\_Mid – between 5 and 10 kJ m–2 day–1, Sup\_High – above 10 kJ m–2 day–1; aUV – ambient UV (category relevant only for the “exclusion type” of the experiment)). SDM = standard difference in means; C.I. 95% = 95% confidence interval. Asterisks indicate the statistical significance of UV effect in a given group: n.s. *p* > 0.05, \* *p* ≤ 0.05, \*\* *p* ≤ 0.01, \*\*\* *p* ≤ 0.001. The numbers indicate the number of experiments included in the meta‐analysis for a given group. In addition, *p* values indicate statistically significant differences within the categories tested.

The observed positive UV effect on stomatal density was associated with low and medium doses of supplemental UV (Figure 5). No clear UV effects are observed in the case of below-ambient UV doses. Interestingly, neither was there an effect of high supplemental UV doses on stomatal density. This implies a bell-shaped UV-dose response curve, with the strongest response at intermediate doses, as has previously been reported in a small number of studies (Brodführer, 1955). The UV effects on stomatal density are associated with supplementation experiments and can be observed in both growth chamber and field studies. Further analysis showed that UV effects on stomatal density are not significantly associated with the duration of experiments. This is surprising, given that morphological changes require time to develop. It could have been argued that UV-mediated changes in stomatal density were not expected in short-term experiments. A possible explanation may relate to the UV-mediated impediment of leaf elongation, in the later stages of leaf development, which would result in a change of leaf area, but not a change in stomatal numbers (Robson et al., 2015). To test the hypothesis that increased stomatal density (number of stomata per unit leaf area) under UV radiation is simply due to a reduction in leaf area, the percentage change in both traits was analysed. Data show no clear statistical correlation between leaf size and stomatal density (Supplemental Figure S4). For example, in one study the stomatal density nearly doubled while the leaf area decreased by less than 10%. Thus, there is apparently no simple one-to-one relationship between leaf area and stomatal density. Rather, a paper by Wargent et al. (2009) reports specific UV-mediated increases in the stomatal index, i.e. the number of stomatal cells versus total epidermal cells. UV effects are mediated through the photoreceptor UVR8, which is postulated to regulate several aspects of cell development. Thus, it appears that UV exposure results in an increasing number of cells entering the developmental differentiation pathway leading to the formation of stomata. The observation that high UV doses have no such effect can then be attributed to UV-mediated stress overriding regulatory UV effects.

Remarkably, the UV effect on stomatal density is most pronounced in the case of trees (Figure 5), despite the stomatal size not being affected by this functional group. Thus, the overall effects of UV on stomatal size appear to be unconnected to effects on stomatal density.



**Figure 6:** Detailed analysisof UV effects on leaf stomatal conductance including 143 experiments. Data are further categorized according to plant functional groups (Gr – grass, H – herb, T – tree), length of the experiment (short - ≤30 days, medium – between 30 days and 90 days, long - >90 days), growth environment (C – growth chamber, G – greenhouse, F – field conditions), UV treatment (Sup – UV supplementation, Ex – UV exclusion), and UV intensity applied (Sup\_Low – below 5 kJ m–2 day–1, Sup\_Mid – between 5 and 10 kJ m–2 day–1, Sup\_High – above 10 kJ m–2 day–1; aUV – ambient UV (category relevant only for the “exclusion type” of the experiment)). (**A**) Meta-analysis significance of UV-induced effects: SDM = standard difference in means; C.I. 95% = 95% confidence interval. Asterisks indicate the statistical significance of UV effect in a given group: n.s. *p* > 0.05, \* *p* ≤ 0.05, \*\* *p* ≤ 0.01, \*\*\* *p* ≤ 0.001. The numbers indicate the number of experiments included in the meta‐analysis for a given group. In addition, *p* values indicate statistically significant differences within the categories tested. (**B**) Quantitative changes induced by UV radiation: vertical bars = medians, boxes = 1st and 3rd quartiles, whiskers = 5th and 95th percentiles, points = outliers identified.

*Analysis of the dataset: UV effects on leaf stomatal conductance*

Despite a positive UV effect on stomatal density, the overall effect of the three measured parameters (aperture, density, size) is a clear negative UV effect on conductance and transpiration at the leaf level (Figure 6A). Previous studies have shown that stomatal density and size are inversely proportional, i.e. plants with higher stomatal density usually have smaller stomata, possibly as a result of a shared molecular control pathway (Doheny-Adams et al., 2012). This finding is consistent with the data presented in this paper on plant UV responses (Figure 4 vs 5), but raises questions concerning a possible functional role of this response. Laboratory-grown *Arabidopsis* genotypes with higher stomatal density, but smaller stomata, show increased leaf stomatal transpiration and decreased growth rates and biomass production (Doheny-Adams et al., 2012). Such a decrease in growth is possibly associated with a deteriorated plant water status, under conditions where the rate of CO2 diffusion through stomata, and its intercellular concentration, are not limiting factors. Interestingly, the literature data reveal that leaf transpiration especially correlated with stomatal density under the experimental conditions used (Doheny-Adams et al., 2012). In contrast, in this study it was found that net UV-mediated changes in leaf stomatal conductance match the net effects of UV on stomatal size in all plant functional groups investigated (Figure 3). Conversely, UV-induced changes in stomatal density (Figure 3), although significant for some plant groups, had only a minor effect on the final value of stomatal conductance. However, it should be recognised that the three measured parameters are likely to exhibit quite distinct UV response dynamics. Fast (minutes) changes in stomatal aperture, are complemented by slow changes in stomatal density and size (days to weeks). Thus, it might be speculated that short-term changes in leaf conductance and transpiration are governed by changes in stomatal aperture, while more realistic long-term UV responses are also affected by morphological changes such as stomatal size and density.

Negative UV effects on leaf stomatal conductance and transpiration are associated with low, medium and high doses of supplemental UV, with stronger decreases in conductance observed under higher UV doses (Figure 6B). Median relative decreases amounted to 8.2, 13.1, and 13.9% for low, medium and high doses, respectively. No significant UV effects (median relative decrease of 1.3%) are observed in the case of exposure to below-ambient UV doses. Consistently, no clear UV effects were noted in UV exclusion studies, and effects were restricted to field supplementation experiments. A remarkable observation concerns the different dose responses for the increase in stomatal density (increase induced by low to medium UV doses) (Figure 5) versus the decrease in leaf conductance (strongest effect at highest UV dose) (Figure 6). In plant UV studies, bell-shaped dose-response curves have rarely been reported (but see Brodführer et al., 1955; Qaderi et al., 2008; van de Staaij et al., 1997) and are thought to relate to a physiological scenario whereby the outcome depends on the balance of two processes, for example UVR8 signalling and plant stress, or UVR8-mediated signalling with additional regulatory interactions with downstream elements including HY5, HYHCOP1, RUP1 and RUP2 (Heijde and Ulm, 2012; Liao et al., 2020). Irrespective of the underlying mechanism, the data strongly imply that distinct UV response pathways operate for different plant responses, emphasising that UV-mediated changes in leaf conductance, and ultimately water-use efficiency, are the outcome of complex, interactive plant UV responses.

UV-mediated decreases in leaf conductance are particularly notable in short-term studies (the median relative decrease is 15.6%), with smaller effects observed in medium and long-term studies (median of 9.6 and 5.7%, respectively). Indeed, experiments with isolated epidermal strips have demonstrated that UV-mediated stomatal opening or closure can occur on a timescale of hours (Jansen and van den Noort, 2000). In comparison, UV-mediated increases in stomatal density and decreases in stomatal size are markedly slower, as is to be anticipated for any morphological response. As a consequence, our analysis shows that medium- and long-term experiments do not display the dramatic decreases in stomatal conductance and transpiration that can be observed in short-term experiments. Thus, the use of short-term UV exposure experiments may lead to a substantial overestimation of UV-mediated decreases in leaf conductance, and presumable water-use efficiency. Indeed, there are ample long-term outdoor studies that fail to report any decrease in transpiration and/or increase in water-use efficiency (Gaberščik et al., 2002; Qaderi and Reid, 2005), although others do (de Paula Bernado et al., 2022). Similarly, some reports have noted an increase in leaf temperature associated with stomatal closure in UV-exposed plants (Williams et al., 2022). Thus, a picture emerges of highly dynamic and diverse plant UV responses. It is envisaged that rapid, daily changes in UV irradiance (e.g. see Neugart et al., 2021) are likely to cause rapid changes in stomatal aperture, while medium and long-term UV irradiances will cause more complex, morphological changes, which will ultimately determine overall leaf conductance, and plant water-use efficiency.

Grasses and herbs show the strongest decline in leaf conductance and transpiration (the median relative decline is 32.8 and 13.0%, respectively), and trees the smallest (median relative decline of 5.8%) (Figure 6). It could be speculated that the lack of UV effect on leaf transpiration in trees is caused by a preponderance of field experiments using below-ambient UV doses. However, this is not correct, as experiments using trees include substantial numbers of growth-chamber, glasshouse as well as supplementation field studies (Figure 2D). Therefore, it is considered that the distinct UV responses of tree species are associated with intrinsic, species-specific, characteristics of this functional group. It is generally accepted that tree leaves have the highest stomatal density followed by shrubs and herbs, while the opposite trend holds for stomatal size (Liu et al., 2019; Li et al., 2021). Since smaller stomata usually respond faster to environmental stimuli than larger stomata (Urban et al., 2007; Drake et al., 2013; Lawson and Blatt, 2014), the combination of high stomatal density and small stomata allows trees to effectively respond to adverse, especially dry, conditions. However, this argument does not appear to apply to UV-exposure conditions as leaf transpiration is not affected. A possible explanation for this lack of UV effect may relate to other species-specific leaf characteristics, such as variability in UV penetration into leaves, differential accumulation of UV-absorbing pigments and distinct leaf anatomy, particularly epidermal thickness. Indeed, several measuring approaches have confirmed deeper penetration of UV-B radiation into grasses and broad-leaved herbs compared to broad-leaved shrubs and needle-leaved trees (Day et al., 1992; Barnes et al., 2015). Similarly, the accumulation of UV-B absorption pigments (flavonoids and phenylpropanoid derivatives) tends to increase from herbaceous plants and monocotyledonous grass species to evergreen trees (Day, 1993; Veselá et al., 2022), increasing shielding of cellular targets from UV exposure. It is worth noting that most of these anatomical and functional features of trees are associated with leaf/plant longevity (Day, 1993) and support the observation of a relatively limited effect of UV radiation on the acclimation of stomata in trees.

*Consequences for plant-atmosphere interactions*

We have shown that UV-B causes a decrease in leaf conductance and so we can expect the rate of photosynthesis to decrease in much the same way (Wong et al., 1979; Miner et al., 2017). Furthermore, alterations in stomatal conductance have been reported to play a pivotal role in regulating plant transpiration and water status, water-use efficiency, CO2 uptake and growth at canopy and/or ecosystem levels (Peñuelas et al., 2008; Guerrieri et al., 2019; Strange et al. 2023). Consequently, the question should be asked whether models of the impact of climate change need to consider UV-mediated changes in stomatal behaviour. Will UV-mediated changes in stomatal behaviour affect drought resistance, water-use efficiency and/or CO2 utilisation, and will this impact on vegetation-carbon-climate models that aim to predict carbon sinking into the future?

The magnitude of observed UV-mediated (both short and long-term) reductions in stomatal conductance (Figure 6B) may have significant implications for the responses of plant ecosystems to continued climate warming at the regional to global level. Accordingly, accurate modelling of future developments of carbon and water cycles requires a consideration of UV-effects, particularly in regions where an increase in UV radiation will accompany climate change (Bernhard et al., 2023). However, most of the experiments on the impact of UV radiation on plants is at the scale of single plants. At canopy level, it would be necessary to consider the attenuation of direct-beam radiation within the canopy, and the fraction of the leaves that are sun-lit (see Kováč et al., 2023).

What does this analysis mean in terms of the global rates of photosynthesis and by extension to the carbon cycle? As well as the variations in the UV-shielding stratospheric ozone, UV irradiances in the biosphere depend on a range of further factors such as the extent of cloud cover, surface reflectivity and/or aerosols from pollutants, fires and volcanoes (Wild, 2021). A neglected process may be the influence of global warming on cloud formation (Eleftheratos et al., 2022; Liu et al., 2023). Satellite data show that cloud cover over the land surface is tending to decrease as the air warms (Liu et al., 2023), and we may expect UV in future decades to increase as a result.

Furthermore, the closure of stomata results in a decrease in transpiration and an increase in leaf (Williams et al., 2022) as well as whole vegetation surface temperature (Field et al., 1995). This could potentially amplify plant respiratory processes over assimilatory processes leading to a decoupling between stomatal conductance and photosynthesis and the reduction of net carbon uptake (Marchin et al., 2023). In addition, enhanced leaf temperature could intensify the adverse impacts of droughts and heatwaves on plant ecosystems (Reichstein et al., 2013) and/or even pose a threat to the survival of plant species (Brodribb et al., 2020).

**Conclusions**

Processes related to climate-carbon dynamics continue to present one of the largest uncertainties (spreads) in projections of climate models (Booth et al., 2012). Temporarily and functionally diverse, but largely one-directional, plant responses to UV radiation identified in this study introduce another potentially large – yet previously unqualified and unquantified – source of uncertainty. The results of the analysis create a level of uncertainty about the extent to which vegetation will provide a net sink of carbon through the combined responses of photosynthesis and respiration (Duffy et al., 2021). Likewise, any change (irrespective of its origin) in stomatal response is crucial for accurate modelling of carbon and water cycling under future climatic conditions (Liang et al., 2023). Here we show that leaf stomatal conductance is significantly (on average by about 6 % in trees and by more than 10 % in grasses and herbs) reduced in UV-exposed plants in all investigated categories and experiments, except under ambient conditions and in UV exclusion experiments. Apart from a very strong short-term UV response, a significant decline in conductance is sustained in long-term experiments. Consequently, climate models including vegetation feedback, are likely to overestimate the future strength of carbon sink capacity in regions where an increase in UV radiation will accompany climate change (Bernhard et al., 2023), especially in combination with extreme weather and/or climate events (Barnes et al., 2023). It appears that most current, global models underestimate the true reduction of carbon sink capacity during extreme events (Schewe et al., 2019). Apart from reduced sink capacity, stomatal closure leads to reduced transpiration and enhanced leaf (Williams et al., 2022) and surface (Field et al., 1995) warming, potentially further exacerbating negative effects of drought/heatwaves on plant ecosystems (Reichstein et al., 2013).

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**Conflict of interest**

The authors declare no competing financial interests.

**Author contributions**

A.A., O.U., and M.A.K.J. conceived and designed the study; A.A., O.U., and M.A.K.J. aggregated the input data; A.A. and O.U. conducted analyses and statistical comparisons; A.A. and O.U. produced the figures and tables; A.A., J.G., M.A.K.J., and O.U. interpreted the results; A.A. and M.A.K.J. designed and wrote the paper; A.A., J.G., M.A.K.J., and O.U. revised the paper.

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**Supplemental Table S1**

See the Excel file

*Reference list to Supplemental Table S1*

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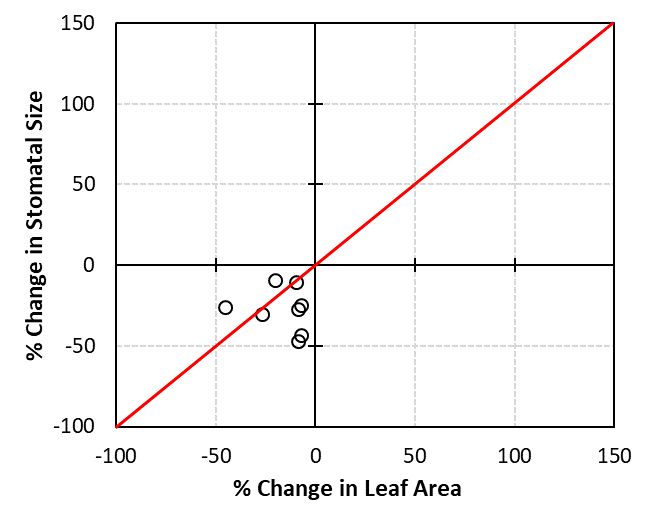
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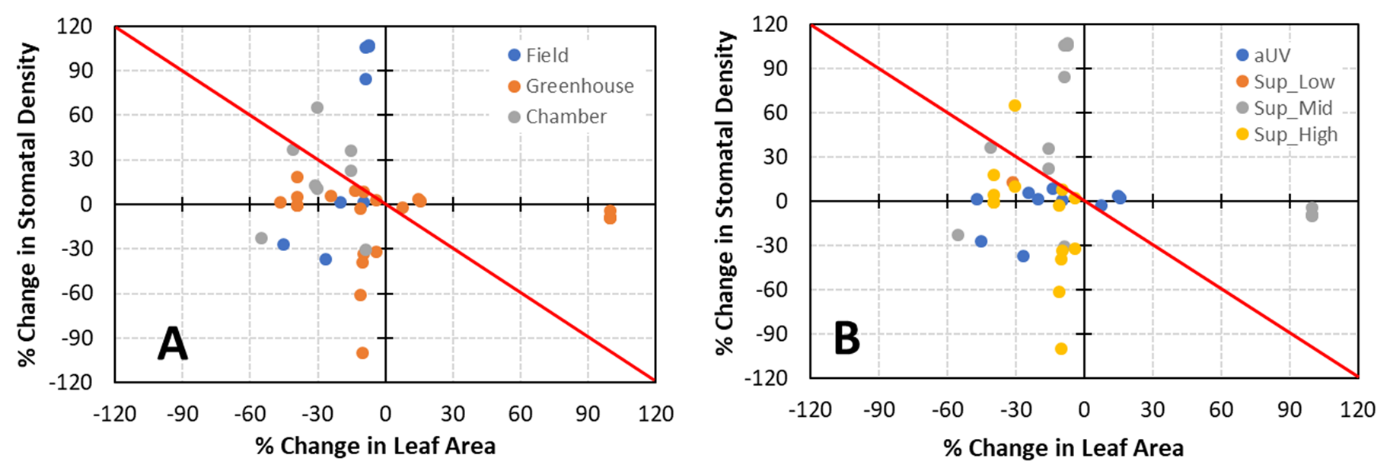
**Supplemental figures**

**Supplemental Figure S1:** Number of publications as a function of publication date.

**Supplemental Figure S2:** Ultraviolet radiation conditions of case studies. UV exclusion (Ex; white column) and UV supplementation experiments (Sup; grey columns) are shown. aUV refers to ambient UV intensity which is relevant only for the “exclusion type” of the experiments. The levels of UV dose applied in the “supplementation type” of experiments were grouped as Sup\_Low (below 5 kJ m-2 day-1), Sup\_Mid (between 5 and 10 kJ m-2 day-1), and Sup\_High (above 10 kJ m-2 day-1). NotDef – refers to studies where UV dose in kJ m-2 day-1 was not defined.



**Supplemental Figure S3:** Relationship between UV-induced changes in leaf area and stomatal size. The red line indicates a 1:1 correlation.



**Supplemental Figure S4:** Relationship between UV-induced changes in stomatal density and leaf area. Available data were categorized according to growth environment (panel A) and the level of UV dose applied (panel B). See the main text or Supplemental Figure S2 for details.