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Title:

A meta-analysis of the interactive effects of UV and drought on plants

Running title:

A meta-analysis of UV and drought effects

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Abstract

Interactions between climate change and UV penetration in the biosphere are resulting in exposure of plants to new combinations of UV radiation and drought. In theory, impacts of combinations of UV and drought may be additive, synergistic or antagonistic. Lack of understanding of impacts of combined treatments creates substantial uncertainties that hamper predictions of future ecological change. Here, we compiled information from 52 publications and analysed relative impacts of UV and/or drought. Both UV and drought have substantial negative effects on biomass accumulation, plant height, photosynthesis, leaf area, and stomatal conductance and transpiration, while increasing stress associated symptoms such as malondialdehyde accumulation, and reactive-oxygen-species content. Contents of proline, flavonoids, antioxidants, and anthocyanins, associated with plant acclimation, are upregulated, both under enhanced UV and drought. In plants exposed to both UV and drought, increases in plant defence responses are less-than-additive, and so are the damage and growth retardation. Less-than-additive effects were observed across field, glasshouse and growth-chamber studies, indicating similar physiological response mechanisms. Induction of a degree of cross-resistance seems the most likely interpretation of the observed less-than-additive responses. The data show that in future climates, the impacts of increases in drought exposure may be lessened by naturally high UV regimes.

Keywords

Drought, UV, stress, cross-resistance, additive effect, synergistic effect

Introduction

Awareness that stratospheric ozone concentrations were decreasing as a result of human activities, triggered a substantial research effort in the 1980's, aimed at understanding the impacts of ambient (and enhanced) UV-B radiation doses on microorganisms, algae, plants, animals, and human health (Farman *et al.*, 1985; Stapleton, 1992). Some (but not all, e.g. Barnes *et al.,* 1996) early UV studies indicated severe, damaging impacts of UV-B (280-315 nm) radiation on plants (Tevini *et al.*, 1989; Tevini & Teramura, 1989). Many of these effects were found to depend not just on the UV dosage, but also the spectral balance, i.e. the distribution of UV-B wavelengths, as well as the background of UV-A and photosynthetically active radiation (Aphalo & Albert, 2012). Relatively little work was done on characterising impacts of UV-A radiation (315-400 nm), as these longer wavelengths are not affected by stratospheric ozone layer depletion (Middleton & Teramura, 1994; Verdaguer *et al.*, 2017). However, more recent studies have contradicted some of the findings of early UV-B studies, and emphasise that UV-radiation is predominantly an environmental regulator that modulates plant growth and developmental processes via a dedicated UV-B photoreceptor (Bornman *et al.*, 2019). UV-mediated damage is now considered a relatively rare event in plants that are grown under otherwise favourable conditions. Notwithstanding these advances in understanding, UV-B radiation is still an important player in plant stress biology as this type of radiation has been hypothesised to either diminish or aggravate the stress effects caused by exposure to other stressors. This particular point has been emphasised in the most recent UNEP-EEAP (United Nations Environment Programme – Environmental Effects Assessment Panel) report (Bornman *et al.*, 2019) which highlights potential interactive effects of UV radiation and climate change factors (i.e. heat, drought, and CO_2). Interactions between climate change and stratospheric ozone depletion can occur at multiple levels. For example, stratospheric ozone depletion has been shown to alter the climate in the southern hemisphere (Bais *et al.*, 2019). Conversely, climate change can affect stratospheric ozone depletion by altering the temperature dynamics between the stratosphere and troposphere (Arblaster *et al.*, 2014). These interactions will ultimately impact on UV-B penetration in to the biosphere. Climate change is also contributing to changes in UV radiation in the biosphere through impacts on cloud patterns, aerosols and surface reflectivity and these impacts will affect both UV-B and UV-A wavelengths (e.g. Lubin & Frederick, 1991). For example, due to reduced cloudiness, areas such as the

Mediterranean are expected to be exposed to increasing intensities of UV, as well as aggravated periods of drought (Sanchez-Lorenzo *et al.*, 2017). Thus, it is predicted that plants will be exposed to new combinations of climate and UV radiation (Bornman *et al.*, 2019), with largely unknown consequences for organisms and ecosystems.

Drought and UV-B both exert complex, multidimensional stress and stress acclimation responses that include molecular, biochemical, physiological, morphological and organismal aspects (Jansen *et al.*, 2019). In theory, exposure of a plant to both a climate change factor and UV-B can result in additive, synergistic, or antagonistic impacts (Sullivan & Teramura, 1990; Bandurska & Cieślak, 2013). In one of the earliest studies on the interactive effects of drought and UV-B, Sullivan and Teramura (1990) demonstrated that supplemental UV-B had no significant effect on soybean (*Glycine max*) grown under drought-stress conditions. As UV exerted a substantial negative effect on well-watered plants, it was hypothesised that UV-B effects were avoided by a suite of anatomical, biochemical and physiological acclimation responses induced by drought. Such observations are of considerable interest in the context of plant performance in future climates (Bornman *et al.*, 2019), and can also inform plant priming approaches. Other studies have also shown that UV-B can diminish the impact of abiotic stressors such as drought and heat by boosting plant resistance. For example, ambient UV-B radiation improved drought-resilience of silver birch (*Betula pendula*) saplings which were simultaneously exposed to UV and drought (Robson *et al.*, 2015). In such a scenario, it is thought that UV-B induces a degree of cross-protection by inducing a suite of acclimation responses. The mechanisms underlying such putative cross-resistance are not necessarily fully understood, but a study by Rodríguez-Calzada *et al.* (2019) showed a synergistic increase in some glycosylated phenolic compounds with antioxidant activity, when plants were exposed to UV and subsequently to drought. These observations have direct environmental relevance as seasonal droughts are commonly associated with, or trail, periods of sunny weather and thus exposure to high UV radiation (Robson *et al.*, 2015; Jansen *et al.*, 2019).

Cross-resistance relates to the scenario whereby acclimation following exposure to one environmental factor does result in a degree of protection against another factor (Jansen *et al*. 2019). This may relate to a particular acclimation response yielding protection against multiple environmental factors. For example, both drought and UV-B can induce decreases in leaf area and stomatal gas exchange, and increases in leaf and cuticle thickness. Also, both UV-B and drought can enhance concentrations of antioxidants, flavonoids and a range of other secondary metabolites such as proline and volatile terpenes (Alonso *et al.*, 2015). Therefore, it is conceivable that UV induced responses offer cross-protection against drought, and *vice versa*. An alternative scenario refers to "cross-talk", a potential exchange of information between shared plant-signalling pathways. For example, UV induced changes in the concentration of the hormone abscisic acid can potentially trigger enhanced resistance to drought, extreme temperatures, and salinity (Pastori & Foyer, 2002).

In contrast to observed cross-resistance, some studies have shown that UV-B radiation increases the susceptibility of plants. For example, Bandurska *et al.* (2012) showed that spring barley (*Hordeum vulgare*) leaves exposed to a combination of UV and drought contained synergistically enhanced concentrations of stress-associated malondialdehyde (MDA), compared to the low MDA concentrations measured in leaves exposed to just UV or drought. These data suggest that plant defences can be overwhelmed by the combined exposure of UV and drought.

A key factor responsible for the seemingly contradictory interactive effects of UV and drought is the applied dose of the two environmental factors. Stress-dose-response curves are, by-and-large, unknown, and this applies especially to UV. Typically, a dose-response curve comprises a eustress phase where acclimation dominates, and a distress phase during which cellular damage is prevalent (Jansen *et al.*, 2019). Thus, it can be speculated that when doses of the two combined environmental factors (i.e. UV and drought) are low, acclimation responses will dominate. Conversely, where higher doses of two environmental factors are used, protective capacity may be overwhelmed and deleterious effects prevail. Yet, this speculation underestimates the complexity of the responses of plants exposed to two simultaneously applied environmental change factors. This aspect was well captured by Mittler *et al.* (2006) who postulated that any interaction between two stressors creates effectively a new stressor.

Meta-analyses summarize data from multiple scientific studies allowing the identification of patterns or distinct relationships that would be unnoticed from individual studies. This meta-analysis study aimed to develop a more holistic insight into responses of plants exposed to combinations of drought and UV. Specifically, we asked the question whether there are interactive effects of UV and drought on overall growth, plant physiology, and protective mechanisms, and if so, whether these effects were antagonistic, additive or even synergistic. For the purpose of this meta-analysis, drought refers to a temporal shortage of water that is available to the plant, and which will decrease plant growth. UV radiation includes both UV-B and UV-A wavelengths, in variable proportions. By integrating different studies in one meta-analysis new insights in dose-response relationships will be acquired, including how these relationships cause cross-resistance or cross-sensitivity. Thus, this study will contribute to better understanding of plant responses to complex environmental conditions, a key determinant of successful modelling forecasts of future climate change impacts.

Materials and Methods

The search of the peer-reviewed literature centred on studies that explored the effects of UV, drought, and the combination of UV and drought on growth, physiological and/or biochemical parameters. The relevant literature was systematically searched using the on-line scientific database Scopus. An additional search for peer-reviewed literature was performed using Google Scholar. All searches were completed in February 2019. The principle search terms used to identify relevant publications were "drought AND UV*". Additionally, the citation-lists of identified publications were inspected for further relevant papers. Identified papers were screened for the quality of the information. In particular, it was assessed whether separate as well as combined impacts of drought and UV were documented. Excluded were studies using UV-C lamps, studies using UV-B lamps where radiation with a wavelength shorter than 280 nm was not effectively filtered out, studies where controls comprised plant material taken prior to the actual UV and drought treatments, and studies where responses were not measured on leaves or stems but, for example, on berries. Also excluded were studies in which confounding factors were likely to affect data, for example a comparison of UV effects in wetter and drier locations. Finally, where very few papers reported a particular plant response, this response was excluded as it could not be subjected to meta-analysis criteria of minimal number of cases. This applies, amongst others, to measurements of plant hormones, reproduction, water use efficiency, and leaf number.

For the purpose of this meta-analysis, controls in the case of supplementary UV exposure were either plants kept under energized UV tubes wrapped in polyester type film, plants under non-energized UV tubes, or plants not covered by UV tubes. Many published UV-B exposure studies involve exposure to additional UV-A wavelengths emitted by UV-B emitting sources (Aphalo & Albert, 2012). Similarly, many commonly used UV-filters do not achieve a clean separation of UV-B and UV-A wavelengths (Aphalo & Albert, 2012). For the purpose of this study, such studies were included, and results are presented as generic effects of UV-B plus UV-A wavelengths.

Large discrepancies were identified in the quantification and characterisation of UV doses and spectra. Furthermore, only a fraction of the published papers on interactive effects of UV and drought reported biologically weighted UV doses. Similarly, different methods were used to impose and quantify drought. This precludes direct quantitative comparisons of impact as a function of UV or drought dose. Therefore, the biological impact on plant parameters was used as a proxy for the intensity of drought and UV radiation. Most studies imposed drought by withholding water. However, for the purpose of this meta-analysis, we included studies (six in total) in which polyethyleneglycol (PEG) was used as a drought-proxy (see Supplemental table 1). In most studies, the untreated plants represent the control. However, in some outdoor experiments plants experienced natural drought conditions. In these cases, watered plants were taken as the control, while untreated plants represent the drought treatment. Similarly, in UV supplementation studies, the untreated plants represent the control. Conversely, in outdoor exclusion studies, the UV-shielded plants were treated as the control, while plants experiencing ambient UV were considered as UV-treatments.

It was identified that some publications reported on more than one plant species, cultivar, or plant developmental stage. In such cases, the results obtained with each species, cultivar or developmental stage were treated as a separate "experiment". Thus, separate experiments presented in the meta-analysis are not necessarily fully independent. No single publication presented more than four "experiments". Similarly, no single experiment presented more than two entries for any individual parameter, except for the parameter "flavonoid contents", where some experiments presented three entries. To ascertain whether this may impact on the outcomes of the meta-analysis, additional analyses were performed whereby duplicate (or triplicate) entries were removed from the "antioxidant" and "biomass" datasets (Supplemental table 3). This had no effect on the outcomes of the analysis.

In nearly all identified studies, plants were simultaneously exposed to UV and drought (i.e. "parallel" exposure). A total of six studies represent sequential exposure where plants were typically first exposed to UV, and later to a combination of UV and drought. Just one study involves priming with drought, followed by parallel exposure to a combination of UV and drought. These studies are marked accordingly in Supplemental table 1.

Papers included in this meta-analysis present impacts of UV and/or drought on a broad range of parameters. To facilitate meta-analysis, these variables were grouped into two major categories; (1) Plant acclimation responses, and (2) Plant stress responses. Within each category, related parameters were grouped as variables. The following two categories and 17 variables were constituted:

Plant acclimation responses

1. Proline content (Prol) including data on concentrations of proline, and free proline
2. Flavonoid contents (Flavs) including data on concentrations of total flavonoids determined spectrophotometrically in methanolic extracts, phenolic acids determined using the Folin-Ciocalteau method, total quercetin, total myricetin, and overall UV-absorbing pigments determined spectrophotometrically or using the Dualex leaf clip sensor
3. Antioxidant capacity (Antio) including data on SOD enzyme content or activity, peroxidase enzyme content or activity, glutathione reductase enzyme or activity, ascorbate-dehydroascorbate ratio, trolox-equivalent antioxidant capacity (TEAC), Ferric Reducing Antioxidant Potential(FRAP)
4. Anthocyanin content (Anth) including data on concentrations of anthocyanin
5. Carotenoid content (Cars) including data on concentrations of total carotenoids
6. Leaf area (LA) including data on individual leaf area and total leaf area
7. Leaf mass to area ratio (LMA) including data on specific leaf area (SLA = 1/LMA), and leaf thickness
8. Height (H) including data on stem length, plant height, and inflorescence height in Arabidopsis
9. Root/shoot-ratio (R/S) including data on root-to-shoot ratio and the inverse of shoot-to-root ratio

Plant stress responses and/or markers

10. Stress markers (Stress) including data on MDA (sometimes reported as TBARS, thiobarbituric acid-reactive substances) concentration, and other measures of lipid peroxidation

11. Reactive Oxygen Species (ROS) including data on concentrations of H_2O_2 and other reactive species
12. Quantum yield of photosystem II photochemistry (QY) including parameters measured using chlorophyll *a* fluorometry, i.e. the maximum and effective quantum yield of photosystem II in dark and sun adapted leaves, respectively
13. Photosynthetic activity (Pn) including parameters measured using gas-exchange technology, i.e. the net photosynthetic rate
14. Stomatal conductance (Cond) including data on stomatal conductance, stomatal density, transpiration rate, and stomatal index
15. Leaf water content (LWC) including data on percentage water content, relative water content (RWC), and water potential of leaf or plant
16. Chlorophyll content (Chls) including data on contents of chlorophyll a, chlorophyll b, and total chlorophyll (a+b) in leaf extracts or intact leaves
17. Plant biomass (Mass) including data on plant biomass, weight, relative growth rate (RGR), fresh weight, dry weight.

These 17 variables revolve around the grouping of loosely related, but not identical, plant parameters. For example, the variable “antioxidant capacity” (Antio) included measurements of content and activity of SOD, peroxidases, and glutathione reductase as well as on the ascorbate-dehydroascorbate ratio, TEAC, and FRAP. The advantage of grouping parameters into broader variables is an increase in replication, and this outweighs the disadvantage of grouping non-identical, parameters.

Datasets were compiled using Excel 2016. This was followed by the analysis of the relationships between parameters, and of the significance of any difference, using the Comprehensive Meta-Analysis (CMA, Biostat Inc., Englewood, USA) software. Standardized Difference in Means (SDM) has been used for the calculation of the summary (net) effect across all investigated experiments. The SDM expresses the size of the intervention effect in each experiment relative to the data variability observed in that experiment. Necessary inputs for the meta-analysis are arithmetic mean, standard deviation and number of repetitions for both control and treated groups. In principle, two basic statistical models can be used for calculating the net effect, i.e. fixed and random effect models (Borenstein *et al.*, 2009). We selected the random effect model, since it accounts for the variability of the true effect among different 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 experiments is expressed by SDM and the probability (*p*) value. The variability and spread of the effect is than expressed as 95% confidence (CI) and prediction (PI) intervals. While CI provides an absolute measure of statistical precision, the advantage of PI is that it provides an absolute measure of dispersion (i.e. variability) of the observed effect. For details and rationale behind the PI calculations, see Borenstein *et al.* (2017). For the details and mathematical formulas used to calculate SDMs, CIs and *p* values, see Ač *et al.* (2015).

Concepts of antagonism, synergy, and additivity are commonly used in a poorly defined manner. For the purpose of this study, nomenclature as detailed by Piggott *et al.* (2015) was used. In short, the impacts of UV and drought were expressed as percentage change relative to the untreated control. The sum of these relative changes was compared to the measured impact of a combined UV and drought treatment. Thus, predicted values were calculated as the sum of the impacts of both environmental factors acting separately. Where the measured effect matches the calculated sum, effects are referred to as additive. Where the measured effect is greater than the sum of individual effects, the effects are considered synergistic. Where the measured effect is smaller than the sum of individual effects, the effect is considered less-than-additive or antagonistic. To evaluate the interactive effect of UV radiation and drought, linear regression was used to relate measured (i.e. observed) values (in the y-axis) vs. calculated (i.e. predicted) values (in the x-axis) for individual variables (Piñeiro *et al.*, 2008). Consequently, statistically significant differences between slope (a_1) and intercept (b_1) parameters for the best linear fit and the 1:1 line (i.e., $a_0 = 1$ and $b_0 = 0$) were evaluated using the t-test. In addition, the Root Mean Square Error (RMSE) was calculated for both the 1:1 line and the best linear fit.

Results

A comprehensive literature search resulted in a collection of 52 papers (89 experiments) published in peer-reviewed scientific journals. Although there was no restriction on publication year, the bulk of the analysed papers was published in the last 13 years (Supplemental figure 1A). Most of these studies were performed using supplemental UV radiation, in either glasshouse or growth chamber (Supplemental figure 2). About 50%

of the studies were short term with a duration of up to one month (Supplemental figure 3). Studies longer than 3 months represented about 20% of the data set. These long-term studies were mainly represented by work on tree species (broadleaved and coniferous), and shrubs (*Vaccinium* spp.), although there were also long-term studies on Arabidopsis and wheat, both with a duration of 120 days. A study by Duan *et al.* (2011) using spruce (*Picea asperata*) was exceptional as this was the only study that lasted more than one year. Studies were limited to terrestrial plants, but included crops and wild species, herbaceous and woody species, perennials and annuals (full details in supplemental table 1). UV doses ranged from 0.11 to 49 kJ m^{-2} day^{-1}. However, given the variation in both experimental approaches, lamps and UV quantification, these numbers need to be interpreted with extreme caution. Indeed, analysis of the data showed no link whatsoever between UV-dose and impact on the plant (Supplementary figure 4). Similarly, drought was quantified as water pressure in MPa, percentage water content of the soil, or simply deviation from the water regime.

A dataset of all studies was compiled, and this included basic information on the species as well as the experimental treatments (Supplemental table 1). Also listed were the impacts of UV, drought, and a combination of UV and drought on a range of parameters, relative to control values, as well as the extent of replication. Overall, UV had a significant negative impact on seven variables (Figure 1). Drought also had a significant negative impact on seven variables, although these were not fully identical to those affected by UV. Drought had a significant negative impact on LWC, unlike UV, while UV had a significant negative impact on chlorophyll content, unlike drought. UV had a positive effect on another six variables, while drought had a significant positive on the same six variables, as well as on the R/S ratio (Figure 1). A comparison of the effects of UV compared to drought, UV compared to a combination of UV and drought, and drought compared to a combination of UV and drought, showed that UV dominates only effects on antioxidants, anthocyanins, and root-shoot ratio (Table 1). Drought dominates effects on most of variables including proline, flavonoids, leaf area, quantum yield and photosynthetic CO_2 uptake, stomatal conductance, LWC, and plant biomass.

Interestingly, even though the proportion of statistically significant experiments for any given variable was in most cases less than half, only a few variables showed insignificant net effects of UV and/or drought treatments (Supplemental table 2). The highest proportion of statistically significant experiments for a UV effect was observed for anthocyanins (91%) and ROS (70%). Drought impacted in most experiments significantly on stress markers (82%) and stomatal conductance (81%), while a combined drought and UV treatment showed the highest number of statistically significant experiments for anthocyanins (81%), stress markers (79%), plant biomass and the R/S ratio (75%). Considering the scale of the absolute *variability* among experiments and parameters as quantified by the 95% PI (Supplemental table 3), only the UV effect on ROS (positive) and the drought effects on photosynthesis (negative) and proline (positive) don't cross 0 threshold and fall with 95% probability into one direction only (Figure 1).

With respect to individual variables, proline accumulation is a well characterised defence response. Yet, only half the experiments show a statistically significant UV effect (Supplemental table 2). However, the resulting net effect of UV is strong, since all but two experiments have the same (positive) effect on proline content. As for the drought effect on proline accumulation, the response is one of the few showing a 95% PI interval in the positive territory only ($p_{\mathrm{SUM}} = 7.3\times10^{-15}$), with just one experiment with a negative SDM, and almost 30% of experiments with no statistical significance. On the other hand, there is no statistically significant difference between the effect of drought and the combined effect of UV and drought.

Another commonly observed stress response is the decrease in stomatal conductance. The net UV effect on stomatal conductance is significantly negative ($p_{\mathrm{SUM}} = 1.28\times10^{-9}$), however, only 33% of experiments were statistically significant and five experiments even showed a positive effect (Supplemental table 2). The net effect of UV was statistically different from the effect of drought and also from the combined effect of UV and drought. Amongst drought experiments, the highest proportion (81%) of significant experiments was found for the effect on stomatal conductance. Regarding the combined drought plus UV effect, in only one case the SDM was negative (Supplemental table 3), thus showing a consistent (but variable) net response.

Biomass can be regarded as an integrating or "final response" quantity. A higher than average proportion of significant experiments was found for the effects of UV (46%), drought (67%), and combined UV plus drought effect (75%) on plant biomass (Supplemental table 2). All but one (with zero change) experiment showed a negative SDM of the UV effect, and all experiments showed a negative response to drought ($p_{\mathrm{SUM}} = 0.00$) and the combined exposure ($p_{\mathrm{SUM}} = 0.00$) (Supplemental table 3). The overlap of PI over the 0 threshold was relatively small in the case of all treatments.

In contrast, the R/S ratio displayed only a limited response to UV exposure ($p_{\mathrm{SUM}} = 0.89$) with only one experiment showing a significant response. However, the net impact of drought was significant ($p_{\mathrm{SUM}} = 8.7\times10^{-5}$) and across all experiments had a positive SDM with only two experiments which were not significant. Combined effects of UV and drought showed lower statistical significance ($p_{\mathrm{SUM}} = 0.043$) but the highest proportion of significant experiments (86% with one outlier case study showing a negative change) (Supplemental table 3). Yet, only seven experiments were available for analysis.

For all measured plant variables, the summary impacts of UV and drought went in the same direction (i.e. positive or negative impact), and therefore a simplified version of the scheme proposed by Piggott *et al.* (2015) was used to define additive, synergistic and antagonistic interactions. To assess whether the combined exposure to UV and drought caused additive, synergistic or antagonistic effects, the sum of the impacts of UV and drought was calculated and compared to the measured impact of a combined UV and drought treatment.

Exposure to drought and/or UV, and induction of plant acclimation responses

UV, and especially drought, enhance the proline content in plants. Under mild stress conditions (as defined by no, or limited accumulation of MDA and/or H_2O_2), the increases in proline induced by UV and drought appear to match those induced by a combination of UV and drought. However, when the plant stress becomes more severe, responses to a combination of UV and drought are significantly less-than-additive (Figure 2A) (Supplemental table 4). This pattern can also be observed in the case of flavonoid content (Figure 2B), carotenoid content (Figure 2E) and antioxidant capacity (Figure 2C), albeit less pronounced. In the case of morphological parameters such as leaf mass per area, leaf area, and plant height (Figures 2F, 2G and 2H) and branching (data not shown), the observed effects under a combination of drought and UV are similarly less than expected, while effects on root-to-shoot ratio (Figure 2I) under combinations of UV and drought can be described as additive. The less-than-additive effect on plant height is particularly pronounced under more severe exposure conditions. It was anticipated that under more severe stress conditions the combined exposure to two factors would result in aggravated stress. This is, however, not obvious from the results.

Exposure to drought and/or UV causes stress

Exposure to UV or drought increased stress markers such as MDA accumulation (Figure 1, Figure 3A). Where plants were exposed to a combination of UV and drought, effects appear to be additive under mild stress conditions (Figure 3A). However, under more severe conditions, the stress caused by exposure to a combination of UV and drought is somewhat less than additive, compared to the sum of the impacts of UV and drought alone (Figure 3A) (Supplemental table 4). The tendency to have significantly smaller than expected impacts exerted by combinations of UV and drought, can also be seen in the measured photosynthetic CO_2 uptake (Figure 3E) as well as in the chlorophyll content (Figure 3G), especially under more severe conditions. Photosynthetic CO_2 uptake and chlorophyll content are negatively affected by both UV and drought, however, impacts of these two factors in combination are significantly less-than-additive (Supplemental table 4). Additive effects can be observed in the case of quantum yield of photosystem II photochemistry (Figure 3D) and leaf water content (Figure 3C). Both positive effects and negative impacts of combinations of UV and drought on leaf water content are closely matched by the arithmetic sum of impacts of UV and drought alone (Figure 3C). Thus, in the case of leaf water content, predicted values (i.e. additive) closely match measured values. This may relate to the fact that leaf water content only responds to drought treatment (Figure 1). In the case of ROS (mostly hydrogen peroxide) the slope of the predicted versus the measured impact is not significantly different from the one-to-one line (Figure 3B). However, a considerable intercept is observed. Yet, this intercept is not significant (Supplemental table 4).

Stomatal conductance and transpiration rate, were strongly affected by drought but also, to a lesser extent, by UV. Measured decreases in stomatal conductance or transpiration in plants exposed to mixtures of UV and drought were significantly less-than-additive as compared to the calculated sum of responses to UV and drought alone (Figure 3F) (Supplemental table 4). Decreases in stomatal conductance and transpiration are typically measured on a per fixed leaf area basis. However, leaf area itself is also diminished in plants grown under drought conditions, and to a lesser extent under UV radiation and or a combination of UV and drought (Figures 1 and 2G) (Supplemental table 4).

Drought was found to have a strong negative effect on biomass production. When plants were exposed to a combination of UV and drought, effects were significantly less-than-additive under mild as well as under more severe stress-inducing conditions (Figure 3H) (Supplemental table 4).

Discussion

Analysis of published experiments revealed a mixture of short- and long-term studies, involving a variety of plant species. This variety includes gymnosperms and angiosperms, and herbaceous species, shrubs, and trees. Rapantová *et al.* (2016) demonstrated species-specific effects with UV amplifying negative effects of drought on bitter dock (*Rumex obtusifolius*) photosynthesis but ameliorating the same effect in common bent (*Agrostis capillaris*). This study revealed that negative impacts of drought and combinations of drought and UV (but not UV alone) on plant biomass were significantly greater for woody, compared to non-woody plants (Supplemental figures 5, 6 and 7). Experimental conditions might also be expected to affect these impacts. However, rather surprisingly, interactive effects of UV, drought and a combination of UV and drought on flavonoid accumulation, and net carbon assimilation were similar across growth-chamber, greenhouse and field studies (Supplemental figure 7). Yet, experimental growth conditions did effect the impacts of drought and a combination of UV and drought (but not UV alone) on plant biomass accumulation, emphasising the importance of the experimental approach. The survey of the literature revealed relatively low numbers of field studies (28 experiments out of 89) (Supplemental figure 2). Natural dynamics of drought and UV exposure are difficult to replicate under laboratory conditions (e.g. see Allen *et al.*, 1999; Aphalo, 2003; Aphalo *et al.*, 2015), with rapid fluctuations in momentary UV dose depending on cloud cover and time of day (Barnes *et al.*, 2016). Thus, field experiments are a critical component of an evidence-based assessment of UV-drought interactions, and more are needed to assess the importance of interactions between UV and drought in future climates.

Published datasets are biased towards more extreme UV-effects

Large discrepancies are present in the published literature with respect to the quantification and characterisation of drought and UV exposure. This precludes direct quantitative comparisons of impact as a function of UV or drought doses. Indeed, no clear relationship was observed between biological impacts and used UV-doses (Supplemental figure 4). Therefore, the biological impacts of UV and drought were used as a proxy for the intensity these factors. Thus, where studies reported plant stress (MDA accumulation, and H_2O_2 content), this was perceived as a high UV effect, while a lack of stress was seen as indicative of milder UV conditions.

The data show that UV and drought have overlapping effects on a range of plant variables. For example, both UV and drought negatively impact on biomass accumulation, height, photosynthesis, leaf area, stomatal conductance and transpiration, while increasing stress associated variables such as MDA and H_2O_2 contents (Figure 1). UV-induced stress is commonly associated with unnaturally high UV doses and/or high ratios of UV to photosynthetically active radiation (Hideg *et al.*, 2013; Aphalo *et al.*, 2015). Low, natural UV-doses do not necessarily induce stress, but rather regulate plant responses. Therefore, it can be argued that the acquired dataset of published studies is biased towards more extreme UV-impacts, and is not fully representative of the often mild, acclimative UV-effects measured in the natural environment. Consistent with this point, the number of field studies is low, and this is a major impediment to understanding ecologically relevant interactive effects between UV exposure and drought. Furthermore, all but two of the field studies used supplemental (i.e. above ambient) UV radiation. Interestingly, there were significant differences in the effects of UV on net carbon fixation, flavonoid content and biomass when UV exclusion studies were compared with supplementation studies (Supplemental figures 5, 6 and 7), suggesting a dose-response effect. Of the two field studies using natural UV radiation (i.e. exclusion approach), one showed particularly modest impacts of UV on photosynthesis (Rapantová *et al.*, 2016), while the second reported a protective effect of UV-B on drought stressed silver birch (*Betula pendula*) (Robson *et al.*, 2015). Conversely, supplemental UV-B or UV-A did not alleviate the mild stress exerted by drought in pea (*Pisum sativum*) plants under outdoor conditions (Allen *et al.,* 1999). While recognising the limitations of a comparison between birch seedlings and pea plants, it is notable that the protective effect reported by Robson *et al.* (2015) relates to below ambient intensities of UV, while the lack of protection noted by Allen *et al.* (1999) concerns a 30% increase above ambient solar UV. It has been hypothesised that where plants are exposed to high doses of the two stressors, defences can be overwhelmed resulting in cross-sensitivity (Jansen *et al.*, 2019). Conversely, where a plant is simultaneously exposed to low levels of two potential environmental stressors, a degree of cross-protection may occur. Thus, an important question for future research concerns the importance of the UV dose as a determinant of interactive effects of UV and drought. Unfortunately, virtually all published studies are limited to just one UV and/or drought-dose. The current analysis incorporates UV-B, UV-A, and UV-A and UV-B exposure studies. Both UV-B and UV-A can have deleterious effects on plants, and induce acclimation. However, there are strong mechanistic differences between these two UV wavelength bands in terms of photoreceptors and signalling pathways activated (Verdaguer *et al.*, 2017). Thus, spectral analysis of interactive effects of UV and drought is required as UV-B and UV-A wavelengths are differentially affected by phenomena such as stratospheric ozone layer recovery and cloud cover.

Less-than-additive increases in plant defence responses and plant stress, occur when plants are exposed to a combined treatment with UV and drought

Overall, a combination of two environmental factors caused a significantly less-than-additive decrease in plant stress, photosynthesis, and chlorophyll content. Yet, the impacts of the two combined factors on ROS concentrations and leaf water content were additive. This implies that the primary consequences of exposure to a stressor (i.e. increased ROS production and a decrease in water content) do not necessarily fully translate in secondary stress symptoms such as membrane damage and inactivation of the photosynthetic apparatus. Consistently, impacts of UV and drought on plant biomass are also less-than-additive. It is possible to explain these data based on the role of ROS as signalling compounds involved in the plants' response to stress. Such signalling may cause the synergistic upregulation of plant defence responses, as shown by several authors (Rajabbeigi *et al.*, 2013; Rodríguez-Calzada *et al.*, 2019; Mátai *et al.*, 2019), further decoupling stress and defence responses. However, this is not the case for defence responses that were analysed in this study. In fact, less-than-additive increases were found for flavonoid, proline, antioxidant, and anthocyanin content, and less-than-additive decreases in plant height and leaf area. Thus, a picture arises whereby increases in plant defence responses are less-than-additive, and so is the damage caused. The current study does not reveal the mechanism underlying the moderation of both stress and acclimation responses, but a schematic overview of potential contributing factors was assembled (Figure 4). Three distinct scenarios' can be envisaged to explain the observed less-than-additive responses:

1) Where a response adheres to a classical saturation curve, the addition of a second environmental factor may theoretically cause response saturation, i.e. a

diminishing increment, resulting in an less-than-additive response (Figure 4). However, in multiple experiments the response following exposure to two environmental factors is smaller than that in response to just one factor (e.g. Bandurska *et al.,* 2012; Basahi *et al.,* 2014). Therefore, saturation response kinetics are an unlikely explanation for less-than-additive responses.

2) Some defence responses may follow a bell-shaped dose-response curve (Figure 4). In this scenario, low doses of UV boost antioxidant defences (eustress) while high doses do the opposite (distress) (Sztatelman *et al.*, 2015). This may potentially explain less-than-additive increases in proline and flavonoid accumulation. However, a bell-shaped dose-response curve is unlikely to explain less-than-additive accumulation of plant stress markers, biomass production, height, and chlorophyll content. Thus, this scenario seems also unlikely.
3) A third scenario is the induction of cross-resistance. In the case of exposure to two stressors, expression of a common response may be enhanced and/or defence responses are utilised more effectively. In this scenario, there will be less stress, less growth retardation and a lesser need to induce further defence responses (compared to separate effects of two stressors summed up). Underlying cross-resistance would be the observed substantial similarity in protective responses induced by drought and UV (Figure 1). It is likely that common responses are mediated by partially overlapping signalling cascades, involving shared transcription factors, ROS, antioxidants and plant hormones such as salicylic acid (Potters *et al.*, 2009; Bandurska & Cieślak, 2013; Kovács *et al.*, 2014) (Figure 4). In this cross-resistance scenario, drought exposure may trigger a degree of UV-protection, while UV exposure may also induce drought resistance. Indeed, work by He *et al.* (2011) showed that pre-acclimation to drought yields a degree of resistance to UV-B, just as pre-acclimation to UV-B yields resistance to drought.

On balance, induction of cross-protection is the most likely interpretation of the less-than-additive responses. UV is an important regulatory factor, perceived by the photoreceptors UVR8, CRY and PHOT which, in turn, activate signalling cascades and control expression of 100s of genes (Verdaguer *et al.*, 2017). The functional importance of UV-sensing, and especially UV-B sensing, has been questioned, given that UV-B radiation is unlikely to cause substantial distress in plants exposed to realistic UV-conditions (Hideg *et al.*, 2013). Rather, it has been speculated that plants exploit UV-B as a proxy for drought, heat and photoinhibitory conditions (Hideg *et al.*, 2013; Jansen *et al.*, 2019). Indeed, in natural environments, positive associations occur between UV-B, photosynthetically active radiation, temperature and drought exposure (Jansen *et al.*, 2019). In such a scenario, UV exposure early in the growing season may result in priming of plants for exposure to subsequent drought. This has been demonstrated in a horticultural setting, where UV-B was exploited to pre-acclimate lettuce plants to withstand drought (Wargent *et al.*, 2011). Thus, UV radiation can potentially be exploited as part of a more sustainable system of cropping, less dependent on supplemental watering. In the natural environment, droughts linked to climate change will be accompanied by increased UV exposure where decreases in cloudiness occur. Thus, less-than-additive impacts may be an important factor that moderates climate change impacts (Bornman *et al.*, 2019). An early UV study showed that supplemental UV exposure of pine (*Pinus pinea* and *Pinus halepensis*) seedlings during the hot, dry Mediterranean summer resulted in substantial increases in aboveground biomass production relative to trees kept under ambient light conditions (Petropoulou *et al.*, 1995). Yet, it is important to recognise that the current meta-analysis does not reveal positive effects of UV on growth, but rather indicates that combined impacts of UV and drought in a future climate will be less than additive.

Conclusions

This study shows that both UV and drought have substantial negative effects on a range of plant traits including biomass accumulation, photosynthesis, and stomatal conductance and transpiration, while increasing stress associated symptoms such as MDA accumulation, and ROS content. Contents of proline, flavonoids, antioxidants, and anthocyanins, associated with plant acclimation, are upregulated, both under enhanced UV and drought. Similarly, protective responses such as a decrease in leaf area and plant height increase under UV and drought. A combined treatment with UV and drought leads to less-than-additive plant stress and acclimation responses. This is likely due to the induction of a cascade of cross-resistance processes, involving the enhanced expression and/or utilisation of shared defence responses. The data show that in future climates, the impacts of increases in drought exposure may be lessened by naturally, high UV regimes.

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Conflict of interest

The authors declare no competing financial interests.

Author contributions

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

Data availability statement

The data that support the findings of this study are available in the supplementary material of this article.

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Tables

Table 1. Overview of statistically significant differences between plant responses to UV (UV), drought (D) and UV plus drought (UV+D). Data are extracted from 52 peer-reviewed papers. Variables are grouped in two categories: acclimation responses (Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root/shoot-ratio), and stress responses (Stress = Stress markers, ROS = Reactive Oxygen Species, QY = Quantum yield of photosystem II photochemistry, Pn = Photosynthetic CO_2 assimilation rate, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass = Plant biomass). * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$), NS = Not Significant ($p > 0.05$).

	UV vs D	**UV vs (UV+D)**	**D vs (D+UV)**
Prol	**	***	NS
Flavs	NS	***	NS
Antio	***	NS	***
Anth	***	NS	**
Cars	NS	NS	NS
LA	***	***	NS
LMA	NS	NS	NS
Height	NS	NS	NS
R/S	**	NS	*
Stress	NS	NS	NS
ROS	NS	NS	NS
QY	***	**	NS
Pn	***	***	NS
Cond	***	***	NS
LWC	***	***	NS
Chls	*	NS	NS
Mass	***	***	NS

Figures

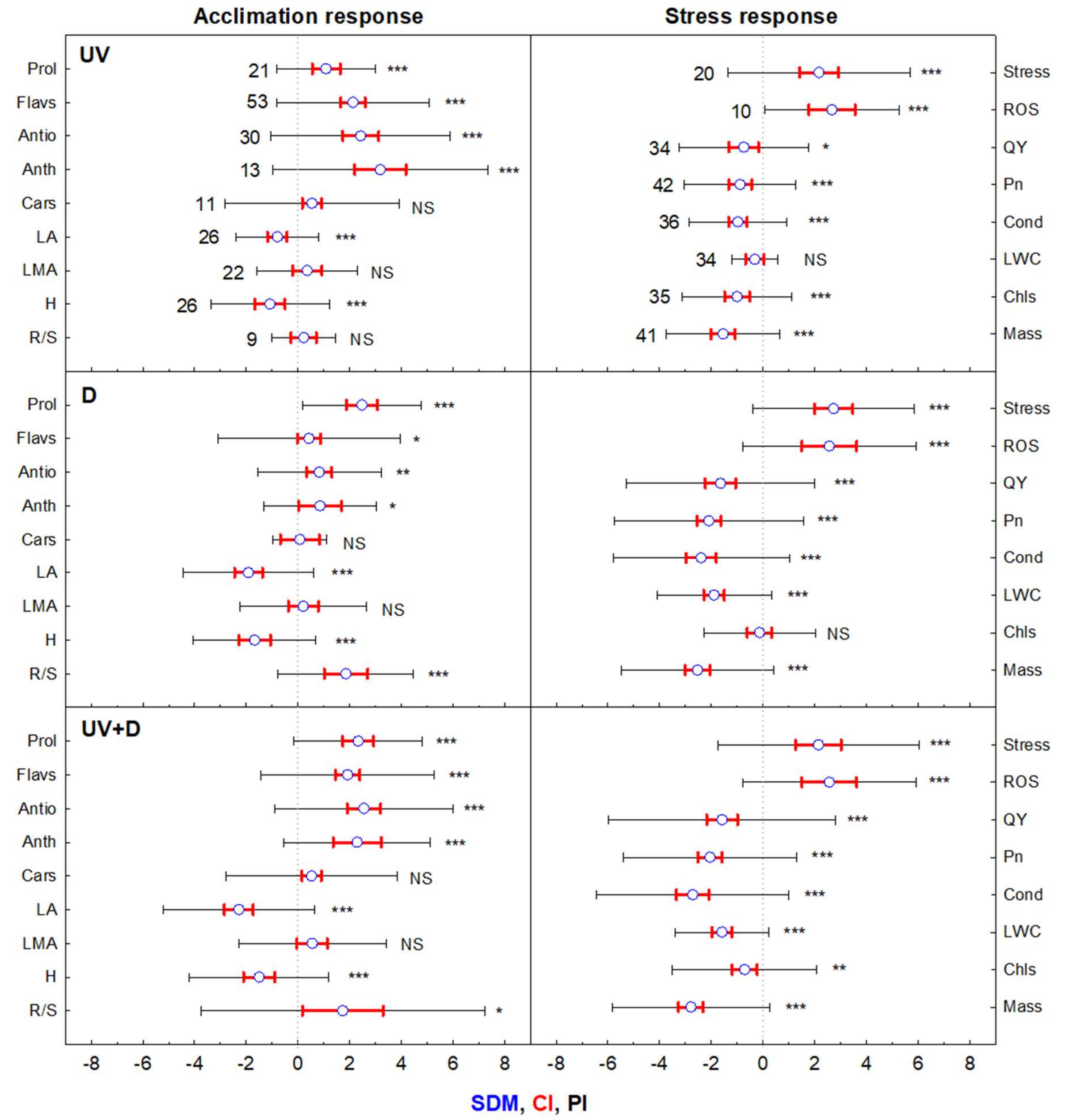


Figure 1 Overview of plant responses to UV (UV), drought (D) and UV plus drought (UV+D). Data are extracted from 52 peer-reviewed papers. Variables are grouped in two categories: acclimation responses (Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root/shoot-ratio) and stress responses (Stress = Stress markers, ROS = Reactive Oxygen Species, QY = Quantum yield of photosystem II photochemistry, Pn = Photosynthetic CO_2 assimilation rate, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass = Plant biomass). SDM = Standard Difference in Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval, * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$), NS = Not Significant ($p > 0.05$). The numbers indicate number of experiments included in the meta-analysis. See Supplemental table 3 for exact values of SDM, CI, and PI.

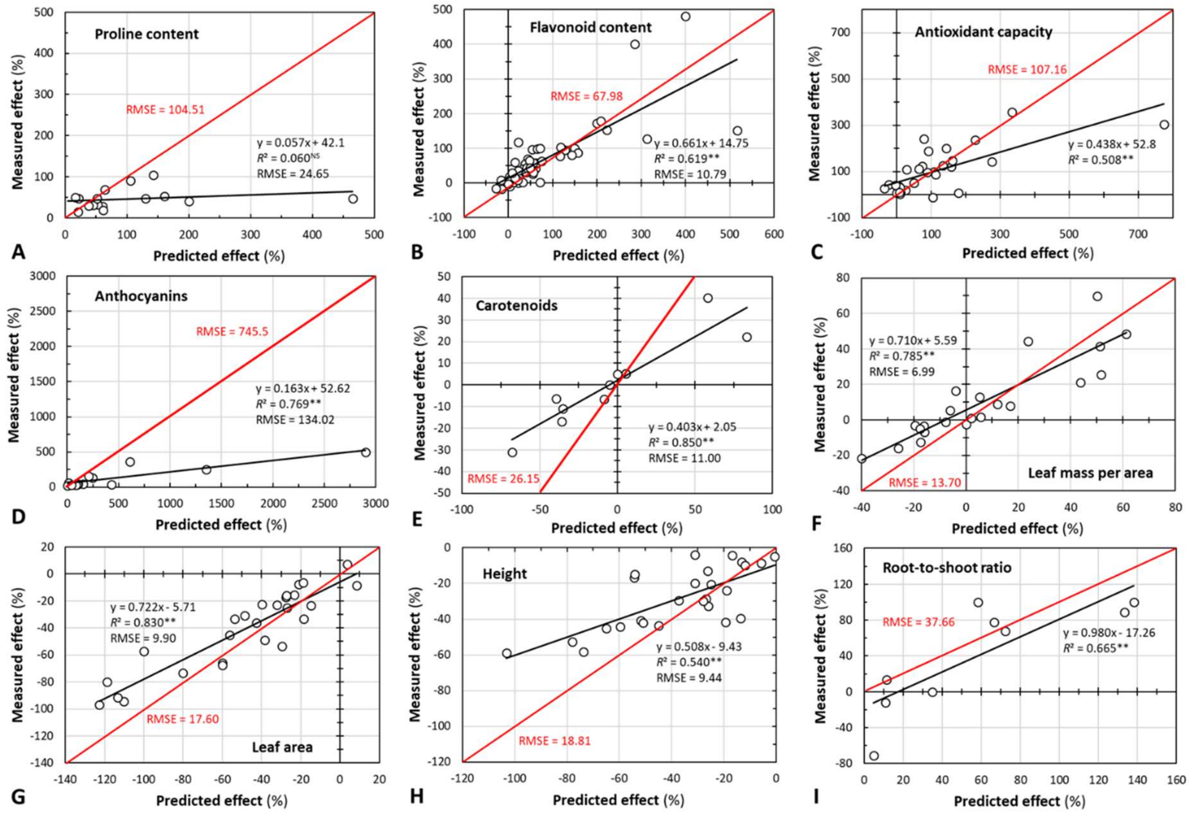


Figure 2 Relationship between observed (Measured effect) and calculated (Predicted effect) effects of combined exposure to UV radiation and drought for variables describing plant acclimation responses: proline content (A), flavonoid content (B), antioxidant capacity (C), anthocyanin content (D), carotenoid content (E), leaf mass per area (F), leaf area (G), height (H), and root-to-shoot ratio (I). The predicted effect was calculated as the sum of individual UV and drought effects. The data were fitted using linear regression (best linear fit). Coefficients of determination (R^2) and significance levels (* $p \leq 0.05$, ** $p \leq 0.01$, NS $p > 0.05$) are shown. Root Mean Square Error (RMSE) was calculated for both the 1:1 line (red) and the best linear fit (black). See Supplemental table 2 for the statistically significant differences between linear fits and 1:1 line.

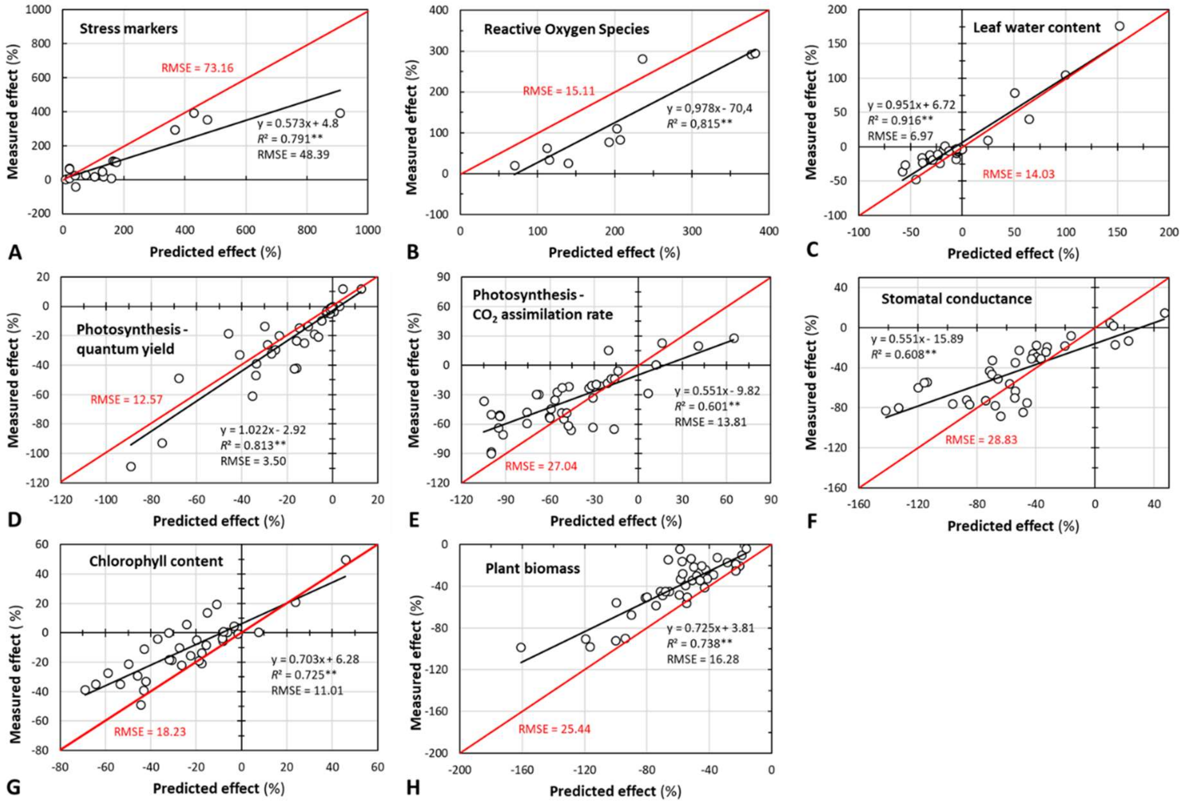


Figure 3 Relationship between observed (Measured effect) and calculated (Predicted effect) effects of combined exposure to UV radiation and drought for variables indicating plant stress responses: stress markers (A), Reactive Oxygen Species (B), leaf water content (C), photosynthetic activity – quantum yield of the photosystem II photochemistry (D), photosynthetic activity – net CO_2 assimilation rate (E), stomatal conductance (F), chlorophyll content (G), and plant biomass (H). The predicted effect was calculated as the sum of individual UV and drought effects. The data were fitted using linear regression (best linear fit). Coefficients of determination (R^2) and significance levels (* $p \leq 0.05$, ** $p \leq 0.01$, NS $p > 0.05$) are shown. Root Mean Square Error (RMSE) was calculated for both the 1:1 line (red) and the best linear fit (black). See Supplemental table 2 for the statistically significant differences between linear fits and 1:1 line.

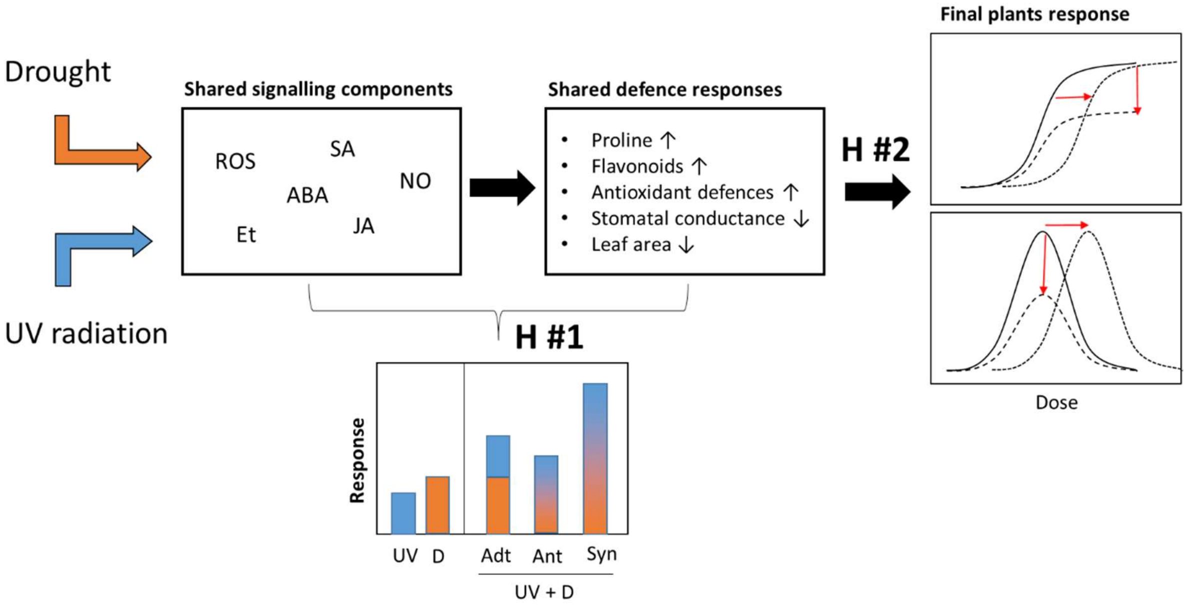
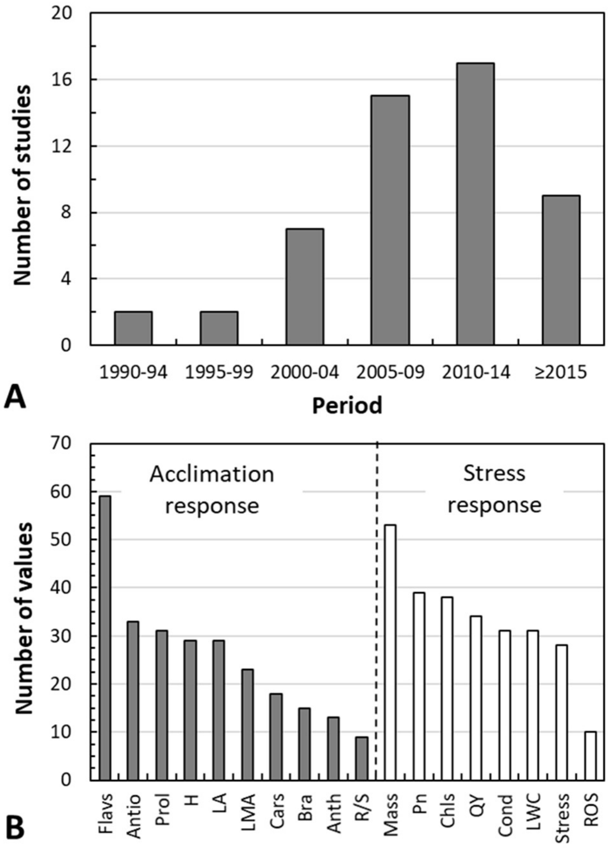
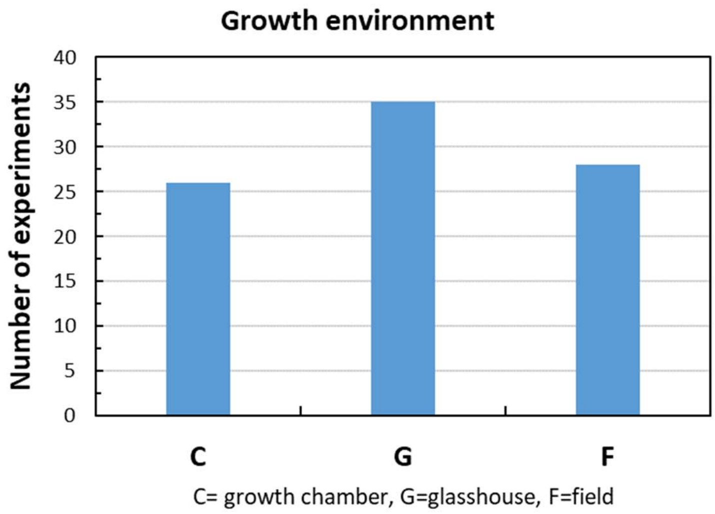


Figure 4 Schematic overview of potential cross-talk and cross-protection in plants exposed to UV radiation (blue) and drought (orange). Potential shared signalling components are Reactive Oxygen Species (ROS), salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA), nitric oxide (NO), and ethylene (Et), with responses additive (Adt), antagonistic (Ant) or synergistic (Syn). It is hypothesised that shared signalling pathways and defence mechanisms lead to interactive effects of ultraviolet radiation (UV) and drought on individual variables (hypothesis #1) and consequently may result in shifts of plant sensitivity to stress conditions (hypothesis #2) seen as a shift in the dose response, and/or a decreased magnitude of the stress response.

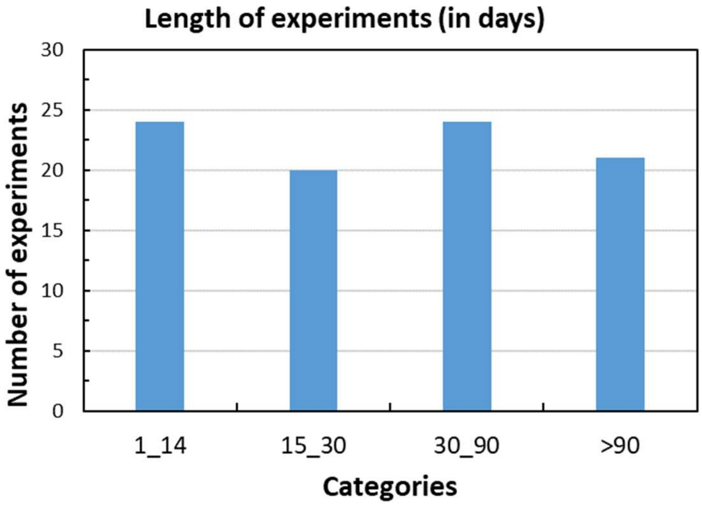
Supplemental figures



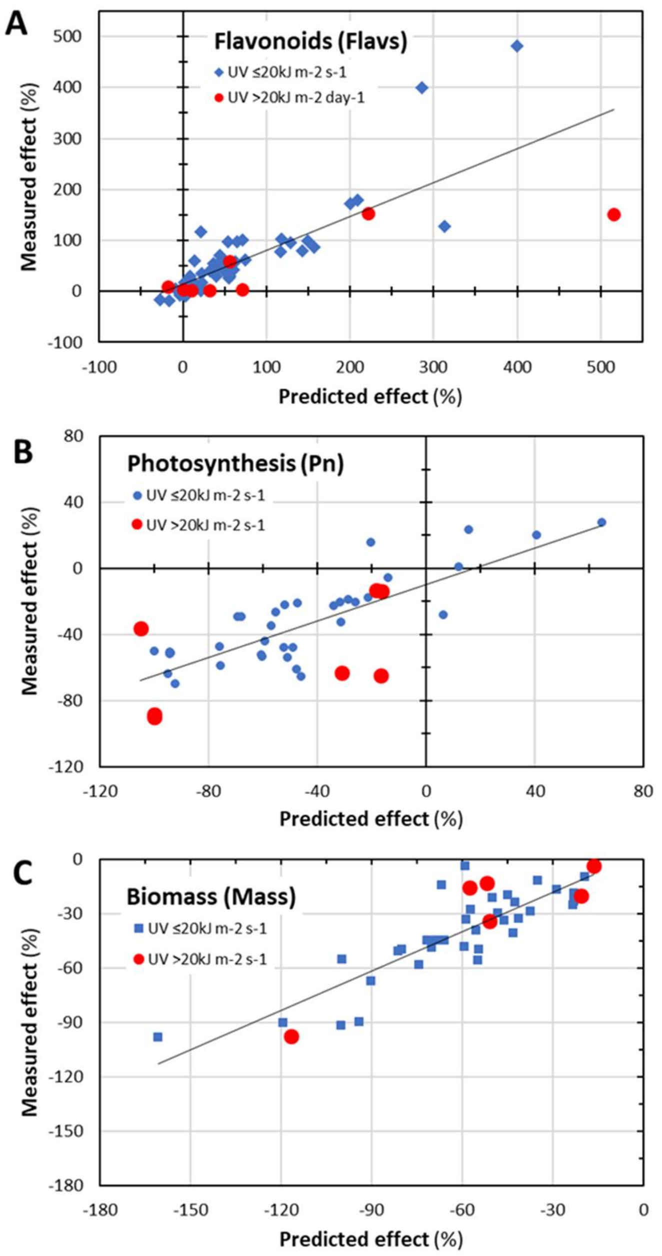
Supplemental figure 1. (A) A total of 52 papers were analysed, and these were published in peer-reviewed journals in the period 1990 through to 2019. **(B)** Variables investigated were grouped into two main categories characterising plant acclimation responses (black columns), and plant stress responses (white columns). Investigated variables are: Flavs = Flavonoid content, Antio = Antioxidant capacity, Prol = Proline content, H = Height, LA = Leaf area, LMA = Leaf mass per area, Cars = Carotenoid content, Bra = Branching, Anth = Anthocyanin content, R/S = Root-to-shoot ratio, Mass = Plant biomass, Pn = Photosynthetic CO_2 uptake, Chls = Chlorophyll content, QY = Quantum yield of photosystem II photochemistry, Cond = Stomatal conductance, LWC = Leaf water content, Stress = Stress markers, ROS = Reactive Oxygen Species..



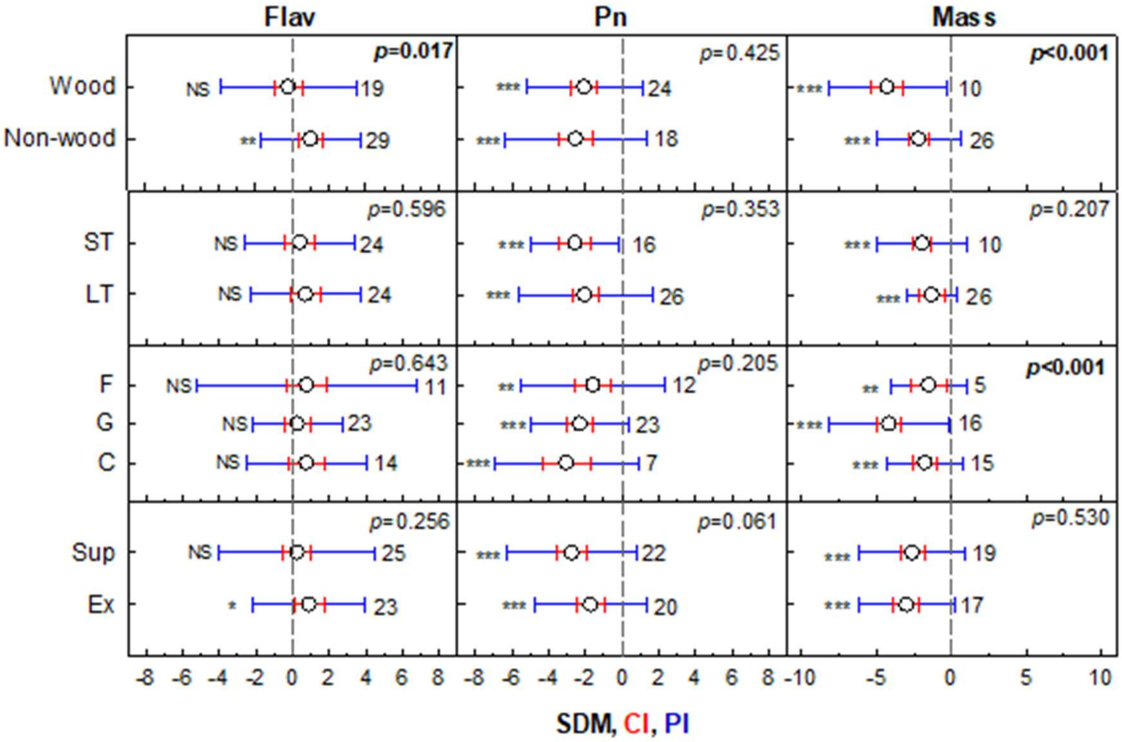
Supplemental figure 2. A total of 89 experiments were analysed, of which just 32% were performed under field conditions (28 experiments). Some 68% of experiments were performed under more artificial conditions, including growth chambers and/or glasshouses (26 and 35 studies, respectively).



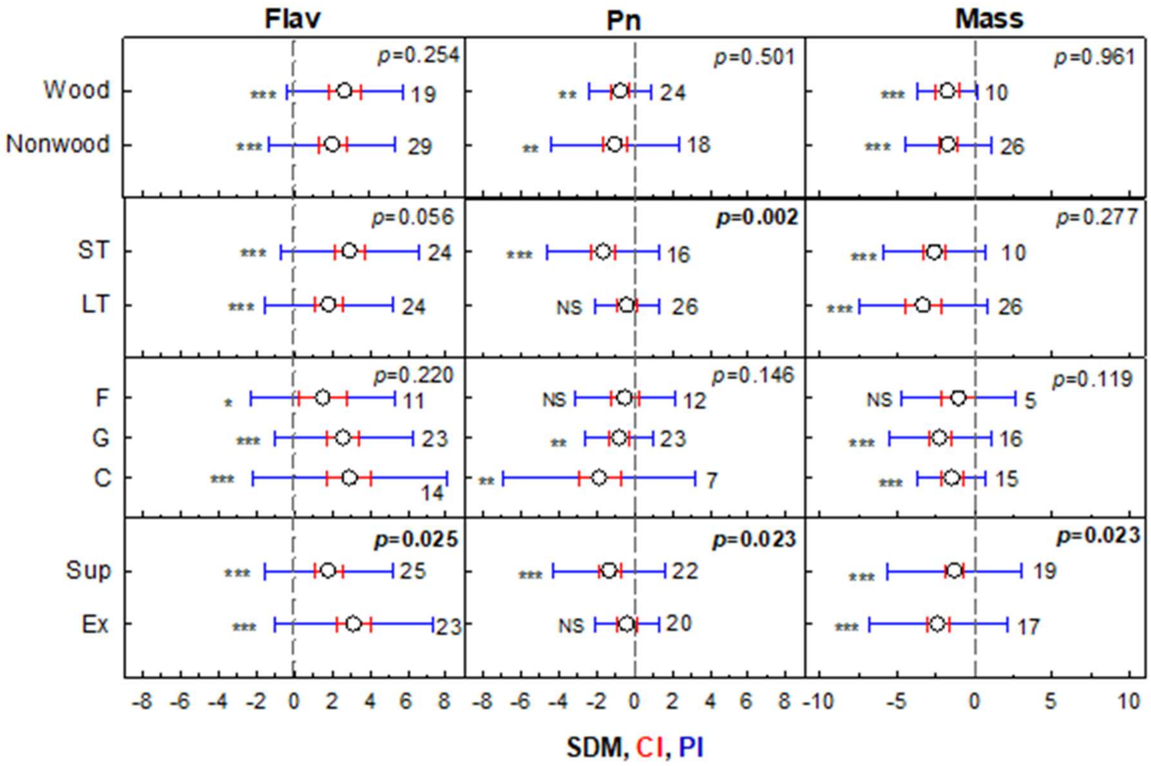
Supplemental figure 3. Duration of the analysed experiments. The duration of the experiments varied between 3 and 900 days. Moreover, there is one extraordinary long study by Arróniz-Crespo *et al.* (2011) in Annals of Botany 108: 557-565 on Bryophytes – 13-15 years.



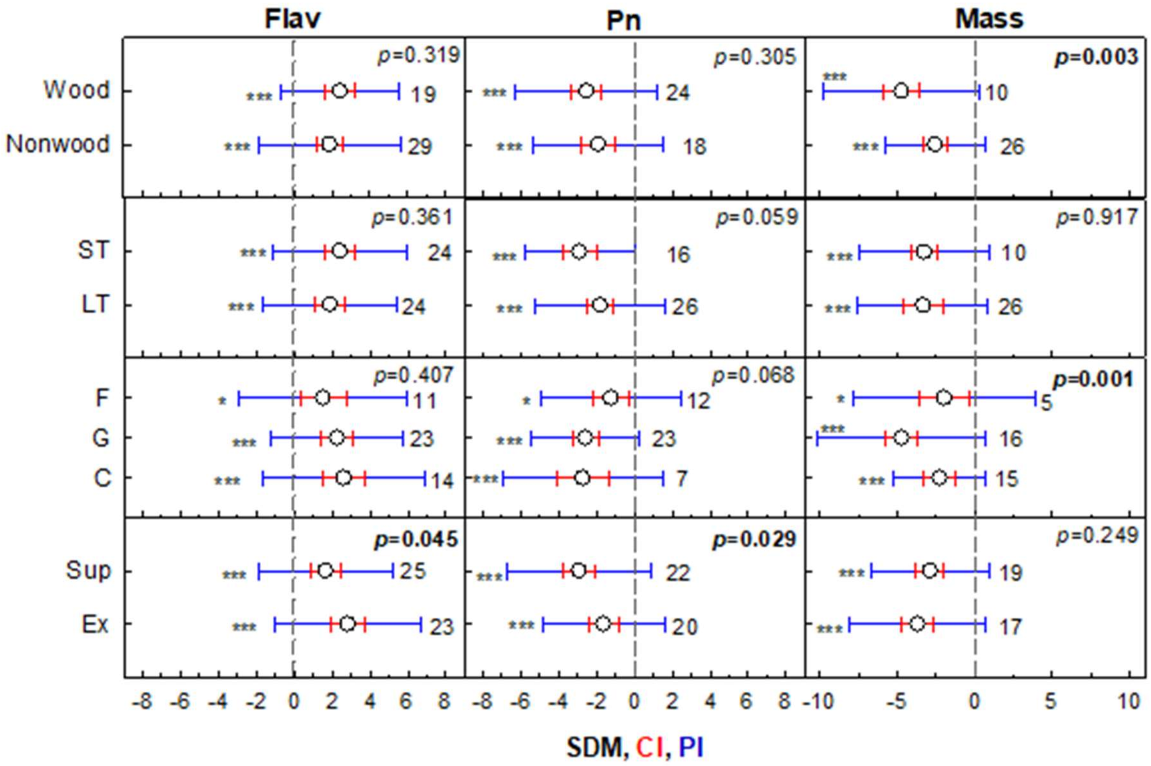
Supplemental figure 4. Relationship between observed (Measured effect) and calculated (Predicted effect) effects of combined exposure to UV radiation and drought for selected variables (Flavonoids – panel **A**, Photosynthetic CO_2 uptake – panel **B**, and Biomass – panel **C**). The experiments where high UV doses (above 20 kJ m^{-2} day^{-1}) were applied are shown in red. The data were fitted using linear regression (best linear fit).



Supplemental figure 5. Detailed analysis of drought effects on flavonoid content (Flav), photosynthetic CO_2 uptake (Pn), and plant biomass (Mass). The data are categorized according to anatomical structure (woody × non-woody plants), duration of the experiment (short- × long-term), treatment conditions (field × greenhouse × growth chamber), and UV application (supplementary × excluded). SDM = Standard Difference in Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval. Stars (*) refer to significance of the experimental treatment * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$), NS = Not Significant ($p > 0.05$). *p*-values in the top right-hand corner indicate the significance of the differential response between compared categories. The numbers indicate the number of experiments included in the meta-analysis.



Supplemental figure 6. Detailed analysis of UV effects on flavonoid content (Flav), photosynthetic CO_2 uptake (Pn), and plant biomass (Mass). The data are categorized according to anatomical structure (woody × non-woody plants), duration of the experiment (short- × long-term), treatment conditions (field × greenhouse × growth chamber), and UV application (supplementary × excluded). SDM = Standard Difference in Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval. Stars (*) refer to significance of the experimental treatment * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$), NS = Not Significant ($p > 0.05$). *p*-values in the top right-hand corner indicate the significance of the differential response between compared categories. The numbers indicate number of experiments included in the meta-analysis.



Supplemental figure 7. Detailed analysis of combined effects of UV and drought on flavonoid content (Flav), photosynthetic CO_2 uptake (Pn), and plant biomass (Mass). The data are categorized according to anatomical structure (woody × non-woody plants), duration of the experiment (short- × long-term), treatment conditions (field × greenhouse × growth chamber), and UV application (supplementary × excluded). SDM = Standard Difference in Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval. Stars (*) refer to significance of the experimental treatment * ($p \leq 0.05$), ** ($p \leq 0.01$), *** ($p \leq 0.001$), NS = Not Significant ($p > 0.05$). *p*-values in the top right-hand corner indicate the significance of the differential response between compared categories. The numbers indicate number of experiments included in the meta-analysis.

Supplemental table 1

Overview of all analysed experiments including details on plant material, experimental set up and measured variables. (Uploaded as a separate supplementary file.)

Supplemental table 2

The percentage of statistically significant (p < 0.05) effects on specific variables, and across the experiments included in the database. Variables are grouped into two main categories characterising plant acclimation responses (dark grey; Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root-to-shoot ratio), and stress responses (while cells; Stress = Stress markers, ROS = Reactive Oxygen Species, QY = Quantum yield of photosystem II photochemistry, Pn = Photosynthetic CO_2 assimilation rate, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass = Plant biomass).

	UV	**Drought**	**UV + drought**
Prol	47.6	71.4	71.4
Flavs	60.9	43.8	70.3
Antio	38.2	75.0	25.0
Anth	90.9	18.2	81.8
Cars	20.0	10.0	10.0
LA	32.0	59.1	72.0
LMA	23.8	23.8	42.9
H	38.5	38.5	50.0
R/S	25.0	71.4	75.0
Stress	57.1	82.1	78.6
ROS	70.0	70.0	70.0
QY	38.2	64.7	50.0
Pn	48.4	70.3	65.6
Cond	33.3	81.0	69.0
LWC	10.3	62.1	65.5
Chls	43.3	30.0	43.3
H	38.5	38.5	50.0
Mass	45.8	66.7	75.0

Supplemental table 3

Summary of comprehensive meta-analysis outcomes: SDM = Standard Difference in Means, 95% CI = 95% confidence interval, 95% PI = 95% prediction interval. Effects of ultraviolet radiation (UV), drought (D) and their combination (UV+D) are shown. Variables are grouped into two main categories characterising plant acclimation responses (grey cells; Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root-to-shoot ratio), and stress responses (while cells; Stress = Stress markers, ROS = Reactive Oxygen Species, QY = Quantum yield of photosystem II photochemistry, Pn = Photosynthetic CO_2 assimilation rate, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass = Plant biomass). Bold rows (**Antio*** and **Mass***) indicate additional analyses whereby duplicate (or triplicate) entries were removed from the “antioxidant” and “biomass” datasets.

	SDM	**95% CI**		**95% PI**	
UV					
Prol	1.09	0.55	1.63	-0.81	2.99
Flavs	2.13	1.66	2.60	-0.82	5.09
Antio	2.43	1.73	3.13	-1.04	5.90
Antio*	**2.02**	**1.27**	**2.77**	**1.24**	**5.28**
Anth	3.19	2.20	4.18	-0.98	7.36
Cars	0.55	0.17	0.92	-2.69	3.93
LA	-0.79	-1.17	-0.41	-2.40	0.82
LMA	0.36	-0.21	0.93	-1.59	2.31
H	-1.08	-1.66	-0.50	-3.38	1.21
R/S	0.23	-0.26	0.71	-1.00	1.45
Stress	2.18	1.43	2.93	-1.34	5.69
ROS	2.68	1.78	3.57	0.09	5.26
QY	-0.74	-1.31	-0.16	-3.25	1.78
Pn	-0.88	-1.32	-0.44	-3.04	1.28
Cond	-0.96	-1.32	-0.60	-2.86	0.94
LWC	-0.31	-0.68	0.05	-1.21	0.58
Chls	-1.00	-1.48	-0.51	-3.11	1,12
Mass	-1.54	-2.01	-1.07	-3.74	0.66
Mass*	**-1.56**	**-2.05**	**-1.08**	**-4.03**	**0.91**
Drought					
Prol	2.48	1.88	3.07	0.19	4.76
Flavs	0.43	-0.02	0.87	-3.11	3.96
Antio	0.83	0.33	1.32	-1.57	3.22
Antio*	**0.62**	**0.20**	**1.21**	**-1.90**	**3.13**
Anth	0.86	0.03	1.69	-1.32	3.03
Cars	0.08	-0.69	0.84	-0.97	1.12

LA	-1.92	-2.46	-1.38	-4.43	0.59
LMA	0.21	-0.37	0.79	-2.24	2.66
H	-1.68	-2.29	-1.07	-4.05	0.70
R/S	1.86	1.02	2.70	-0.76	4.47
Stress	2.74	2.00	3.48	-0.38	5.86
ROS	2.57	1.51	3.63	-0.78	5.92
QY	-1.64	-2.23	-1.05	-5.27	1.99
Pn	-2.09	-2.55	-1.63	-5.76	1.58
Cond	-2.39	-2.97	-1.81	-5.81	1.03
LWC	-1.89	-2.29	-1.49	-4.10	0.33
Chls	-0.13	-0.60	0.34	-2.29	2.04
Mass	-2.53	-3.01	-2.05	-5.49	0.43
Mass*	**-2.69**	**-3.33**	**-2.04**	**-6.07**	**0.70**
UV+D					
Prol	2.34	1.74	2.93	-0.15	4.82
Flavs	1.92	1.45	2.40	-1.44	5.28
Antio	2.56	1.91	3.20	-0.90	6.01
Antio*	**2.05**	**1.36**	**2.75**	**-0.86**	**4.97**
Anth	2.29	1.36	3.22	-0.55	5.13
Cars	0.53	0.16	.90	-2.52	3.86
LA	-2.29	-2.84	-1.73	-5.20	0.63
LMA	0.55	-0.04	1.14	-2.30	3.41
H	-1.50	-2.11	-0.90	-4.21	1.20
R/S	1.74	0.18	3.30	-3.77	7.24
Stress	2.15	1.28	3.08	-1.74	6.04
ROS	2.57	1.51	3.63	-0.78	5.92
QY	-1.58	-2.17	-0.98	-5.96	2.81
Pn	-2.05	-2.52	-1.58	-5.42	1.32
Cond	-2.71	-3.35	-2.09	-6.42	1.00
LWC	-1.58	-1.97	-1.19	-3.40	0.24
Chls	-0.71	-1.19	-0.22	-3.51	2.10
Mass	-2.79	-3.26	-2.31	-5.83	0.26
Mass*	**-3.18**	**-3.93**	**-2.43**	**-7.08**	**0.73**

Supplemental table 4

Summary of slopes and intercepts of linear regression between observed and predicted values for individual variables, and their statistically significant differences from 1:1_fit. Variables are grouped into two main categories characterising plant acclimation responses (Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LMA = Leaf mass per area, LA = Leaf area, H = Plant height, R/S = Root-to-shoot ratio), and plant stress responses (Stress = Stress markers content, ROS = Reactive Oxygen Species, Pn = Photosynthetic CO$_2$ assimilation rate, QY = = Quantum yield of photosystem II photochemistry, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass = Plant biomass). DF = Degree of freedom, s.e. = standard error; statistically significant differences in slopes and intercepts between 1:1_fit and best-linear_fit are shown in bold (p).

Parameter	*DF*	Slope	s.e.	*T Score*	*p*	Intercept	s.e.	*T Score*	*p*
Prol	19	0.057	0.0536	-18.039	**<0.001**	42.1	7.53	5.543	**<0.001**
Flavs	51	0.661	0.0812	-4.221	**<0.001**	14.7	11.33	1.039	0.268
Antio	28	0.438	0.0870	-6.473	**<0.001**	52.79	16.59	3.159	**0.005**
Anth	11	0.163	0.0268	-31.231	**<0.001**	52.6	24.64	2.136	0.056
Cars	9	0.403	0.0566	-10.548	**<0.001**	2.0	2.36	0.867	0.409
LMA	20	0.710	0.0833	-3.481	**0.002**	5.6	2.41	2.321	**0.031**
LA	24	0.722	0.0644	-4.631	**<0.001**	-5.7	3.97	-1.013	0.320
H	24	0.508	0.1028	-3.995	**<0.001**	-9.4	4.71	-1.766	0.093
R/S	7	0.980	0.2764	-0.111	0.932	-17.3	22.13	-0.632	0.553
Stress	18	0.573	0.0974	-3.217	**0.005**	6.8	8.35	-1.536	0.159
ROS	8	0.978	0.1650	-0.133	0.897	-70.4	37.31	-1.888	0.096
Pn	40	0.551	0.1066	-4.004	**<0.001**	-9.8	6.87	-1.742	0.095
QY	32	1.022	0.0312	-0.098	0.891	-2.92	2.92	-0.288	0.781
Cond	34	0.519	0.1002	-4.908	**<0.001**	-15.9	6.49	-2.288	**0.031**
LWC	32	0.951	0.0593	-0.458	0.651	6.7	2.85	2.631	**0.021**
Chls	33	0.703	0.0644	-5.107	**0.001**	6.2	4.23	1.424	0.078
Mass	39	0.725	0.0723	-3.663	**<0.001**	3.8	4.92	1.038	0.306