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# UCC

**University College Cork, Ireland**  
Coláiste na hOllscoile Corcaigh

1 Title:

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

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5 Running title:

6 **A meta-analysis of UV and drought effects**

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## 22 **Abstract**

23 Interactions between climate change and UV penetration in the biosphere are resulting  
24 in exposure of plants to new combinations of UV radiation and drought. In theory, impacts  
25 of combinations of UV and drought may be additive, synergistic or antagonistic. Lack of  
26 understanding of impacts of combined treatments creates substantial uncertainties that  
27 hamper predictions of future ecological change. Here, we compiled information from 52  
28 publications and analysed relative impacts of UV and/or drought. Both UV and drought  
29 have substantial negative effects on biomass accumulation, plant height, photosynthesis,  
30 leaf area, and stomatal conductance and transpiration, while increasing stress associated  
31 symptoms such as malondialdehyde accumulation, and reactive-oxygen-species content.  
32 Contents of proline, flavonoids, antioxidants, and anthocyanins, associated with plant  
33 acclimation, are upregulated, both under enhanced UV and drought. In plants exposed to

34 both UV and drought, increases in plant defence responses are less-than-additive, and so  
35 are the damage and growth retardation. Less-than-additive effects were observed across  
36 field, glasshouse and growth-chamber studies, indicating similar physiological response  
37 mechanisms. Induction of a degree of cross-resistance seems the most likely  
38 interpretation of the observed less-than-additive responses. The data show that in future  
39 climates, the impacts of increases in drought exposure may be lessened by naturally high  
40 UV regimes.

41

42 **Keywords**

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

44

## 45 **Introduction**

46 Awareness that stratospheric ozone concentrations were decreasing as a result of human  
47 activities, triggered a substantial research effort in the 1980's, aimed at understanding  
48 the impacts of ambient (and enhanced) UV-B radiation doses on microorganisms, algae,  
49 plants, animals, and human health (Farman *et al.*, 1985; Stapleton, 1992). Some (but not  
50 all, e.g. Barnes *et al.*, 1996) early UV studies indicated severe, damaging impacts of UV-B  
51 (280-315 nm) radiation on plants (Tevini *et al.*, 1989; Tevini & Teramura, 1989). Many of  
52 these effects were found to depend not just on the UV dosage, but also the spectral  
53 balance, i.e. the distribution of UV-B wavelengths, as well as the background of UV-A and  
54 photosynthetically active radiation (Aphalo & Albert, 2012). Relatively little work was  
55 done on characterising impacts of UV-A radiation (315-400 nm), as these longer  
56 wavelengths are not affected by stratospheric ozone layer depletion (Middleton &  
57 Teramura, 1994; Verdaguer *et al.*, 2017). However, more recent studies have  
58 contradicted some of the findings of early UV-B studies, and emphasise that UV-radiation  
59 is predominantly an environmental regulator that modulates plant growth and  
60 developmental processes via a dedicated UV-B photoreceptor (Bornman *et al.*, 2019). UV-  
61 mediated damage is now considered a relatively rare event in plants that are grown  
62 under otherwise favourable conditions. Notwithstanding these advances in  
63 understanding, UV-B radiation is still an important player in plant stress biology as this  
64 type of radiation has been hypothesised to either diminish or aggravate the stress effects  
65 caused by exposure to other stressors. This particular point has been emphasised in the  
66 most recent UNEP-EEAP (United Nations Environment Programme – Environmental  
67 Effects Assessment Panel) report (Bornman *et al.*, 2019) which highlights potential  
68 interactive effects of UV radiation and climate change factors (i.e. heat, drought, and CO<sub>2</sub>).  
69 Interactions between climate change and stratospheric ozone depletion can occur at  
70 multiple levels. For example, stratospheric ozone depletion has been shown to alter the  
71 climate in the southern hemisphere (Bais *et al.*, 2019). Conversely, climate change can  
72 affect stratospheric ozone depletion by altering the temperature dynamics between the  
73 stratosphere and troposphere (Arblaster *et al.*, 2014). These interactions will ultimately  
74 impact on UV-B penetration in to the biosphere. Climate change is also contributing to  
75 changes in UV radiation in the biosphere through impacts on cloud patterns, aerosols and  
76 surface reflectivity and these impacts will affect both UV-B and UV-A wavelengths (e.g.  
77 Lubin & Frederick, 1991). For example, due to reduced cloudiness, areas such as the

78 Mediterranean are expected to be exposed to increasing intensities of UV, as well as  
79 aggravated periods of drought (Sanchez-Lorenzo *et al.*, 2017). Thus, it is predicted that  
80 plants will be exposed to new combinations of climate and UV radiation (Bornman *et al.*,  
81 2019), with largely unknown consequences for organisms and ecosystems.

82 Drought and UV-B both exert complex, multidimensional stress and stress acclimation  
83 responses that include molecular, biochemical, physiological, morphological and  
84 organismal aspects (Jansen *et al.*, 2019). In theory, exposure of a plant to both a climate  
85 change factor and UV-B can result in additive, synergistic, or antagonistic impacts  
86 (Sullivan & Teramura, 1990; Bandurska & Cieślak, 2013). In one of the earliest studies on  
87 the interactive effects of drought and UV-B, Sullivan and Teramura (1990) demonstrated  
88 that supplemental UV-B had no significant effect on soybean (*Glycine max*) grown under  
89 drought-stress conditions. As UV exerted a substantial negative effect on well-watered  
90 plants, it was hypothesised that UV-B effects were avoided by a suite of anatomical,  
91 biochemical and physiological acclimation responses induced by drought. Such  
92 observations are of considerable interest in the context of plant performance in future  
93 climates (Bornman *et al.*, 2019), and can also inform plant priming approaches. Other  
94 studies have also shown that UV-B can diminish the impact of abiotic stressors such as  
95 drought and heat by boosting plant resistance. For example, ambient UV-B radiation  
96 improved drought-resilience of silver birch (*Betula pendula*) saplings which were  
97 simultaneously exposed to UV and drought (Robson *et al.*, 2015). In such a scenario, it is  
98 thought that UV-B induces a degree of cross-protection by inducing a suite of acclimation  
99 responses. The mechanisms underlying such putative cross-resistance are not  
100 necessarily fully understood, but a study by Rodríguez-Calzada *et al.* (2019) showed a  
101 synergistic increase in some glycosylated phenolic compounds with antioxidant activity,  
102 when plants were exposed to UV and subsequently to drought. These observations have  
103 direct environmental relevance as seasonal droughts are commonly associated with, or  
104 trail, periods of sunny weather and thus exposure to high UV radiation (Robson *et al.*,  
105 2015; Jansen *et al.*, 2019).

106 Cross-resistance relates to the scenario whereby acclimation following exposure to one  
107 environmental factor does result in a degree of protection against another factor (Jansen  
108 *et al.* 2019). This may relate to a particular acclimation response yielding protection  
109 against multiple environmental factors. For example, both drought and UV-B can induce  
110 decreases in leaf area and stomatal gas exchange, and increases in leaf and cuticle

111 thickness. Also, both UV-B and drought can enhance concentrations of antioxidants,  
112 flavonoids and a range of other secondary metabolites such as proline and volatile  
113 terpenes (Alonso *et al.*, 2015). Therefore, it is conceivable that UV induced responses  
114 offer cross-protection against drought, and *vice versa*. An alternative scenario refers to  
115 “cross-talk”, a potential exchange of information between shared plant-signalling  
116 pathways. For example, UV induced changes in the concentration of the hormone abscisic  
117 acid can potentially trigger enhanced resistance to drought, extreme temperatures, and  
118 salinity (Pastori & Foyer, 2002).

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

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

138 Meta-analyses summarize data from multiple scientific studies allowing the identification  
139 of patterns or distinct relationships that would be unnoticed from individual studies. This  
140 meta-analysis study aimed to develop a more holistic insight into responses of plants  
141 exposed to combinations of drought and UV. Specifically, we asked the question whether  
142 there are interactive effects of UV and drought on overall growth, plant physiology, and  
143 protective mechanisms, and if so, whether these effects were antagonistic, additive or

144 even synergistic. For the purpose of this meta-analysis, drought refers to a temporal  
145 shortage of water that is available to the plant, and which will decrease plant growth. UV  
146 radiation includes both UV-B and UV-A wavelengths, in variable proportions. By  
147 integrating different studies in one meta-analysis new insights in dose-response  
148 relationships will be acquired, including how these relationships cause cross-resistance  
149 or cross-sensitivity. Thus, this study will contribute to better understanding of plant  
150 responses to complex environmental conditions, a key determinant of successful  
151 modelling forecasts of future climate change impacts.

152

153

## 154 **Materials and Methods**

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

174 For the purpose of this meta-analysis, controls in the case of supplementary UV exposure  
175 were either plants kept under energized UV tubes wrapped in polyester type film, plants  
176 under non-energized UV tubes, or plants not covered by UV tubes. Many published UV-B

177 exposure studies involve exposure to additional UV-A wavelengths emitted by UV-B  
178 emitting sources (Aphalo & Albert, 2012). Similarly, many commonly used UV-filters do  
179 not achieve a clean separation of UV-B and UV-A wavelengths (Aphalo & Albert, 2012).  
180 For the purpose of this study, such studies were included, and results are presented as  
181 generic effects of UV-B plus UV-A wavelengths.

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

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

208 In nearly all identified studies, plants were simultaneously exposed to UV and drought  
209 (i.e. “parallel” exposure). A total of six studies represent sequential exposure where

210 plants were typically first exposed to UV, and later to a combination of UV and drought.  
211 Just one study involves priming with drought, followed by parallel exposure to a  
212 combination of UV and drought. These studies are marked accordingly in Supplemental  
213 table 1.

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

#### 219 Plant acclimation responses

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

#### 239 Plant stress responses and/or markers

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

- 243 11. Reactive Oxygen Species (ROS) including data on concentrations of H<sub>2</sub>O<sub>2</sub> and other  
244 reactive species
- 245 12. Quantum yield of photosystem II photochemistry (QY) including parameters  
246 measured using chlorophyll *a* fluorometry, i.e. the maximum and effective  
247 quantum yield of photosystem II in dark and sun adapted leaves, respectively
- 248 13. Photosynthetic activity (Pn) including parameters measured using gas-exchange  
249 technology, i.e. the net photosynthetic rate
- 250 14. Stomatal conductance (Cond) including data on stomatal conductance, stomatal  
251 density, transpiration rate, and stomatal index
- 252 15. Leaf water content (LWC) including data on percentage water content, relative  
253 water content (RWC), and water potential of leaf or plant
- 254 16. Chlorophyll content (Chls) including data on contents of chlorophyll a, chlorophyll  
255 b, and total chlorophyll (a+b) in leaf extracts or intact leaves
- 256 17. Plant biomass (Mass) including data on plant biomass, weight, relative growth  
257 rate (RGR), fresh weight, dry weight.

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

264 Datasets were compiled using Excel 2016. This was followed by the analysis of the  
265 relationships between parameters, and of the significance of any difference, using the  
266 Comprehensive Meta-Analysis (CMA, Biostat Inc., Englewood, USA) software.  
267 Standardized Difference in Means (SDM) has been used for the calculation of the  
268 summary (net) effect across all investigated experiments. The SDM expresses the size of  
269 the intervention effect in each experiment relative to the data variability observed in that  
270 experiment. Necessary inputs for the meta-analysis are arithmetic mean, standard  
271 deviation and number of repetitions for both control and treated groups. In principle, two  
272 basic statistical models can be used for calculating the net effect, i.e. fixed and random  
273 effect models (Borenstein *et al.*, 2009). We selected the random effect model, since it  
274 accounts for the variability of the true effect among different studies, which is expected  
275 given the use of different plant species, experimental conditions, and set-ups, as well as

276 different measurement methods. The summary effect size and the statistical significance  
277 of all considered experiments is expressed by SDM and the probability ( $p$ ) value. The  
278 variability and spread of the effect is than expressed as 95% confidence (CI) and  
279 prediction (PI) intervals. While CI provides an absolute measure of statistical precision,  
280 the advantage of PI is that it provides an absolute measure of dispersion (i.e. variability)  
281 of the observed effect. For details and rationale behind the PI calculations, see Borenstein  
282 *et al.* (2017). For the details and mathematical formulas used to calculate SDMs, CIs and  
283  $p$  values, see Ač *et al.* (2015).

284

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

302

### 303 **Results**

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

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

323 A dataset of all studies was compiled, and this included basic information on the species  
324 as well as the experimental treatments (Supplemental table 1). Also listed were the  
325 impacts of UV, drought, and a combination of UV and drought on a range of parameters,  
326 relative to control values, as well as the extent of replication. Overall, UV had a significant  
327 negative impact on seven variables (Figure 1). Drought also had a significant negative  
328 impact on seven variables, although these were not fully identical to those affected by UV.  
329 Drought had a significant negative impact on LWC, unlike UV, while UV had a significant  
330 negative impact on chlorophyll content, unlike drought. UV had a positive effect on  
331 another six variables, while drought had a significant positive on the same six variables,  
332 as well as on the R/S ratio (Figure 1). A comparison of the effects of UV compared to  
333 drought, UV compared to a combination of UV and drought, and drought compared to a  
334 combination of UV and drought, showed that UV dominates only effects on antioxidants,  
335 anthocyanins, and root-shoot ratio (Table 1). Drought dominates effects on most of  
336 variables including proline, flavonoids, leaf area, quantum yield and photosynthetic CO<sub>2</sub>  
337 uptake, stomatal conductance, LWC, and plant biomass.

338 Interestingly, even though the proportion of statistically significant experiments for any  
339 given variable was in most cases less than half, only a few variables showed insignificant  
340 net effects of UV and/or drought treatments (Supplemental table 2). The highest  
341 proportion of statistically significant experiments for a UV effect was observed for

342 anthocyanins (91%) and ROS (70%). Drought impacted in most experiments significantly  
343 on stress markers (82%) and stomatal conductance (81%), while a combined drought  
344 and UV treatment showed the highest number of statistically significant experiments for  
345 anthocyanins (81%), stress markers (79%), plant biomass and the R/S ratio (75%).  
346 Considering the scale of the absolute *variability* among experiments and parameters as  
347 quantified by the 95% PI (Supplemental table 3), only the UV effect on ROS (positive) and  
348 the drought effects on photosynthesis (negative) and proline (positive) don't cross 0  
349 threshold and fall with 95% probability into one direction only (Figure 1).

350 With respect to individual variables, proline accumulation is a well characterised defence  
351 response. Yet, only half the experiments show a statistically significant UV effect  
352 (Supplemental table 2). However, the resulting net effect of UV is strong, since all but two  
353 experiments have the same (positive) effect on proline content. As for the drought effect  
354 on proline accumulation, the response is one of the few showing a 95% PI interval in the  
355 positive territory only ( $p_{\text{SUM}} = 7.3 \times 10^{-15}$ ), with just one experiment with a negative SDM,  
356 and almost 30% of experiments with no statistical significance. On the other hand, there  
357 is no statistically significant difference between the effect of drought and the combined  
358 effect of UV and drought.

359 Another commonly observed stress response is the decrease in stomatal conductance.  
360 The net UV effect on stomatal conductance is significantly negative ( $p_{\text{SUM}} = 1.28 \times 10^{-9}$ ),  
361 however, only 33% of experiments were statistically significant and five experiments  
362 even showed a positive effect (Supplemental table 2). The net effect of UV was statistically  
363 different from the effect of drought and also from the combined effect of UV and drought.  
364 Amongst drought experiments, the highest proportion (81%) of significant experiments  
365 was found for the effect on stomatal conductance. Regarding the combined drought plus  
366 UV effect, in only one case the SDM was negative (Supplemental table 3), thus showing a  
367 consistent (but variable) net response.

368 Biomass can be regarded as an integrating or "final response" quantity. A higher than  
369 average proportion of significant experiments was found for the effects of UV (46%),  
370 drought (67%), and combined UV plus drought effect (75%) on plant biomass  
371 (Supplemental table 2). All but one (with zero change) experiment showed a negative  
372 SDM of the UV effect, and all experiments showed a negative response to drought ( $p_{\text{SUM}} =$   
373 0.00) and the combined exposure ( $p_{\text{SUM}} = 0.00$ ) (Supplemental table 3). The overlap of PI  
374 over the 0 threshold was relatively small in the case of all treatments.

375 In contrast, the R/S ratio displayed only a limited response to UV exposure ( $p_{\text{SUM}} = 0.89$ )  
376 with only one experiment showing a significant response. However, the net impact of  
377 drought was significant ( $p_{\text{SUM}} = 8.7 \times 10^{-5}$ ) and across all experiments had a positive SDM  
378 with only two experiments which were not significant. Combined effects of UV and  
379 drought showed lower statistical significance ( $p_{\text{SUM}} = 0.043$ ) but the highest proportion  
380 of significant experiments (86% with one outlier case study showing a negative change)  
381 (Supplemental table 3). Yet, only seven experiments were available for analysis.

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

389

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

391 UV, and especially drought, enhance the proline content in plants. Under mild stress  
392 conditions (as defined by no, or limited accumulation of MDA and/or  $\text{H}_2\text{O}_2$ ), the increases  
393 in proline induced by UV and drought appear to match those induced by a combination  
394 of UV and drought. However, when the plant stress becomes more severe, responses to a  
395 combination of UV and drought are significantly less-than-additive (Figure 2A)  
396 (Supplemental table 4). This pattern can also be observed in the case of flavonoid content  
397 (Figure 2B), carotenoid content (Figure 2E) and antioxidant capacity (Figure 2C), albeit  
398 less pronounced. In the case of morphological parameters such as leaf mass per area, leaf  
399 area, and plant height (Figures 2F, 2G and 2H) and branching (data not shown), the  
400 observed effects under a combination of drought and UV are similarly less than expected,  
401 while effects on root-to-shoot ratio (Figure 2I) under combinations of UV and drought  
402 can be described as additive. The less-than-additive effect on plant height is particularly  
403 pronounced under more severe exposure conditions. It was anticipated that under more  
404 severe stress conditions the combined exposure to two factors would result in aggravated  
405 stress. This is, however, not obvious from the results.

406

#### 407 *Exposure to drought and/or UV causes stress*

408 Exposure to UV or drought increased stress markers such as MDA accumulation (Figure  
409 1, Figure 3A). Where plants were exposed to a combination of UV and drought, effects  
410 appear to be additive under mild stress conditions (Figure 3A). However, under more  
411 severe conditions, the stress caused by exposure to a combination of UV and drought is  
412 somewhat less than additive, compared to the sum of the impacts of UV and drought alone  
413 (Figure 3A) (Supplemental table 4). The tendency to have significantly smaller than  
414 expected impacts exerted by combinations of UV and drought, can also be seen in the  
415 measured photosynthetic CO<sub>2</sub> uptake (Figure 3E) as well as in the chlorophyll content  
416 (Figure 3G), especially under more severe conditions. Photosynthetic CO<sub>2</sub> uptake and  
417 chlorophyll content are negatively affected by both UV and drought, however, impacts of  
418 these two factors in combination are significantly less-than-additive (Supplemental table  
419 4). Additive effects can be observed in the case of quantum yield of photosystem II  
420 photochemistry (Figure 3D) and leaf water content (Figure 3C). Both positive effects and  
421 negative impacts of combinations of UV and drought on leaf water content are closely  
422 matched by the arithmetic sum of impacts of UV and drought alone (Figure 3C). Thus, in  
423 the case of leaf water content, predicted values (i.e. additive) closely match measured  
424 values. This may relate to the fact that leaf water content only responds to drought  
425 treatment (Figure 1). In the case of ROS (mostly hydrogen peroxide) the slope of the  
426 predicted versus the measured impact is not significantly different from the one-to-one  
427 line (Figure 3B). However, a considerable intercept is observed. Yet, this intercept is not  
428 significant (Supplemental table 4).

429 Stomatal conductance and transpiration rate, were strongly affected by drought but also,  
430 to a lesser extent, by UV. Measured decreases in stomatal conductance or transpiration  
431 in plants exposed to mixtures of UV and drought were significantly less-than-additive as  
432 compared to the calculated sum of responses to UV and drought alone (Figure 3F)  
433 (Supplemental table 4). Decreases in stomatal conductance and transpiration are  
434 typically measured on a per fixed leaf area basis. However, leaf area itself is also  
435 diminished in plants grown under drought conditions, and to a lesser extent under UV  
436 radiation and or a combination of UV and drought (Figures 1 and 2G) (Supplemental table  
437 4).

438 Drought was found to have a strong negative effect on biomass production. When plants  
439 were exposed to a combination of UV and drought, effects were significantly less-than-

440 additive under mild as well as under more severe stress-inducing conditions (Figure 3H)  
441 (Supplemental table 4).

442

### 443 **Discussion**

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

466

#### 467 *Published datasets are biased towards more extreme UV-effects*

468 Large discrepancies are present in the published literature with respect to the  
469 quantification and characterisation of drought and UV exposure. This precludes direct  
470 quantitative comparisons of impact as a function of UV or drought doses. Indeed, no clear  
471 relationship was observed between biological impacts and used UV-doses (Supplemental  
472 figure 4). Therefore, the biological impacts of UV and drought were used as a proxy for

473 the intensity these factors. Thus, where studies reported plant stress (MDA accumulation,  
474 and H<sub>2</sub>O<sub>2</sub> content), this was perceived as a high UV effect, while a lack of stress was seen  
475 as indicative of milder UV conditions.

476 The data show that UV and drought have overlapping effects on a range of plant variables.  
477 For example, both UV and drought negatively impact on biomass accumulation, height,  
478 photosynthesis, leaf area, stomatal conductance and transpiration, while increasing  
479 stress associated variables such as MDA and H<sub>2</sub>O<sub>2</sub> contents (Figure 1). UV-induced stress  
480 is commonly associated with unnaturally high UV doses and/or high ratios of UV to  
481 photosynthetically active radiation (Hideg *et al.*, 2013; Aphalo *et al.*, 2015). Low, natural  
482 UV-doses do not necessarily induce stress, but rather regulate plant responses.  
483 Therefore, it can be argued that the acquired dataset of published studies is biased  
484 towards more extreme UV-impacts, and is not fully representative of the often mild,  
485 acclimative UV-effects measured in the natural environment. Consistent with this point,  
486 the number of field studies is low, and this is a major impediment to understanding  
487 ecologically relevant interactive effects between UV exposure and drought. Furthermore,  
488 all but two of the field studies used supplemental (i.e. above ambient) UV radiation.  
489 Interestingly, there were significant differences in the effects of UV on net carbon fixation,  
490 flavonoid content and biomass when UV exclusion studies were compared with  
491 supplementation studies (Supplemental figures 5, 6 and 7), suggesting a dose-response  
492 effect. Of the two field studies using natural UV radiation (i.e. exclusion approach), one  
493 showed particularly modest impacts of UV on photosynthesis (Rapantová *et al.*, 2016),  
494 while the second reported a protective effect of UV-B on drought stressed silver birch  
495 (*Betula pendula*) (Robson *et al.*, 2015). Conversely, supplemental UV-B or UV-A did not  
496 alleviate the mild stress exerted by drought in pea (*Pisum sativum*) plants under outdoor  
497 conditions (Allen *et al.*, 1999). While recognising the limitations of a comparison between  
498 birch seedlings and pea plants, it is notable that the protective effect reported by Robson  
499 *et al.* (2015) relates to below ambient intensities of UV, while the lack of protection noted  
500 by Allen *et al.* (1999) concerns a 30% increase above ambient solar UV. It has been  
501 hypothesised that where plants are exposed to high doses of the two stressors, defences  
502 can be overwhelmed resulting in cross-sensitivity (Jansen *et al.*, 2019). Conversely, where  
503 a plant is simultaneously exposed to low levels of two potential environmental stressors,  
504 a degree of cross-protection may occur. Thus, an important question for future research  
505 concerns the importance of the UV dose as a determinant of interactive effects of UV and

506 drought. Unfortunately, virtually all published studies are limited to just one UV and/or  
507 drought-dose. The current analysis incorporates UV-B, UV-A, and UV-A and UV-B  
508 exposure studies. Both UV-B and UV-A can have deleterious effects on plants, and induce  
509 acclimation. However, there are strong mechanistic differences between these two UV  
510 wavelength bands in terms of photoreceptors and signalling pathways activated  
511 (Verdaguer *et al.*, 2017). Thus, spectral analysis of interactive effects of UV and drought  
512 is required as UV-B and UV-A wavelengths are differentially affected by phenomena such  
513 as stratospheric ozone layer recovery and cloud cover.

514

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

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

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

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

544 2) Some defence responses may follow a bell-shaped dose-response curve (Figure 4).  
545 In this scenario, low doses of UV boost antioxidant defences (eustress) while high  
546 doses do the opposite (distress) (Sztatelman *et al.*, 2015). This may potentially  
547 explain less-than-additive increases in proline and flavonoid accumulation.  
548 However, a bell-shaped dose-response curve is unlikely to explain less-than-  
549 additive accumulation of plant stress markers, biomass production, height, and  
550 chlorophyll content. Thus, this scenario seems also unlikely.

551 3) A third scenario is the induction of cross-resistance. In the case of exposure to two  
552 stressors, expression of a common response may be enhanced and/or defence  
553 responses are utilised more effectively. In this scenario, there will be less stress,  
554 less growth retardation and a lesser need to induce further defence responses  
555 (compared to separate effects of two stressors summed up). Underlying cross-  
556 resistance would be the observed substantial similarity in protective responses  
557 induced by drought and UV (Figure 1). It is likely that common responses are  
558 mediated by partially overlapping signalling cascades, involving shared  
559 transcription factors, ROS, antioxidants and plant hormones such as salicylic acid  
560 (Potters *et al.*, 2009; Bandurska & Cieślak, 2013; Kovács *et al.*, 2014) (Figure 4). In  
561 this cross-resistance scenario, drought exposure may trigger a degree of UV-  
562 protection, while UV exposure may also induce drought resistance. Indeed, work  
563 by He *et al.* (2011) showed that pre-acclimation to drought yields a degree of  
564 resistance to UV-B, just as pre-acclimation to UV-B yields resistance to drought.

565

566 On balance, induction of cross-protection is the most likely interpretation of the less-  
567 than-additive responses. UV is an important regulatory factor, perceived by the  
568 photoreceptors UVR8, CRY and PHOT which, in turn, activate signalling cascades and  
569 control expression of 100s of genes (Verdaguer *et al.*, 2017). The functional importance  
570 of UV-sensing, and especially UV-B sensing, has been questioned, given that UV-B  
571 radiation is unlikely to cause substantial distress in plants exposed to realistic UV-

572 conditions (Hideg *et al.*, 2013). Rather, it has been speculated that plants exploit UV-B as  
573 a proxy for drought, heat and photoinhibitory conditions (Hideg *et al.*, 2013; Jansen *et al.*,  
574 2019). Indeed, in natural environments, positive associations occur between UV-B,  
575 photosynthetically active radiation, temperature and drought exposure (Jansen *et al.*,  
576 2019). In such a scenario, UV exposure early in the growing season may result in priming  
577 of plants for exposure to subsequent drought. This has been demonstrated in a  
578 horticultural setting, where UV-B was exploited to pre-acclimate lettuce plants to  
579 withstand drought (Wargent *et al.*, 2011). Thus, UV radiation can potentially be exploited  
580 as part of a more sustainable system of cropping, less dependent on supplemental  
581 watering. In the natural environment, droughts linked to climate change will be  
582 accompanied by increased UV exposure where decreases in cloudiness occur. Thus, less-  
583 than-additive impacts may be an important factor that moderates climate change impacts  
584 (Bornman *et al.*, 2019). An early UV study showed that supplemental UV exposure of pine  
585 (*Pinus pinea* and *Pinus halepensis*) seedlings during the hot, dry Mediterranean summer  
586 resulted in substantial increases in aboveground biomass production relative to trees  
587 kept under ambient light conditions (Petropoulou *et al.*, 1995). Yet, it is important to  
588 recognise that the current meta-analysis does not reveal positive effects of UV on growth,  
589 but rather indicates that combined impacts of UV and drought in a future climate will be  
590 less than additive.

591

## 592 **Conclusions**

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

604

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610

611 **Conflict of interest**

612 The authors declare no competing financial interests.

613

614 **Author contributions**

615 M.A.K.J., A.A., K.K., and O.U. conceived and designed the study; M.A.K.J. and O.U.  
616 aggregated the input data; A.A. and K.K. conducted analyses and statistical comparisons;  
617 A.A. and O.U. produced the figures and tables; M.A.K.J., A.A., K.K., and O.U. interpreted  
618 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.  
619 revised the paper.

620

621 **Data availability statement**

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

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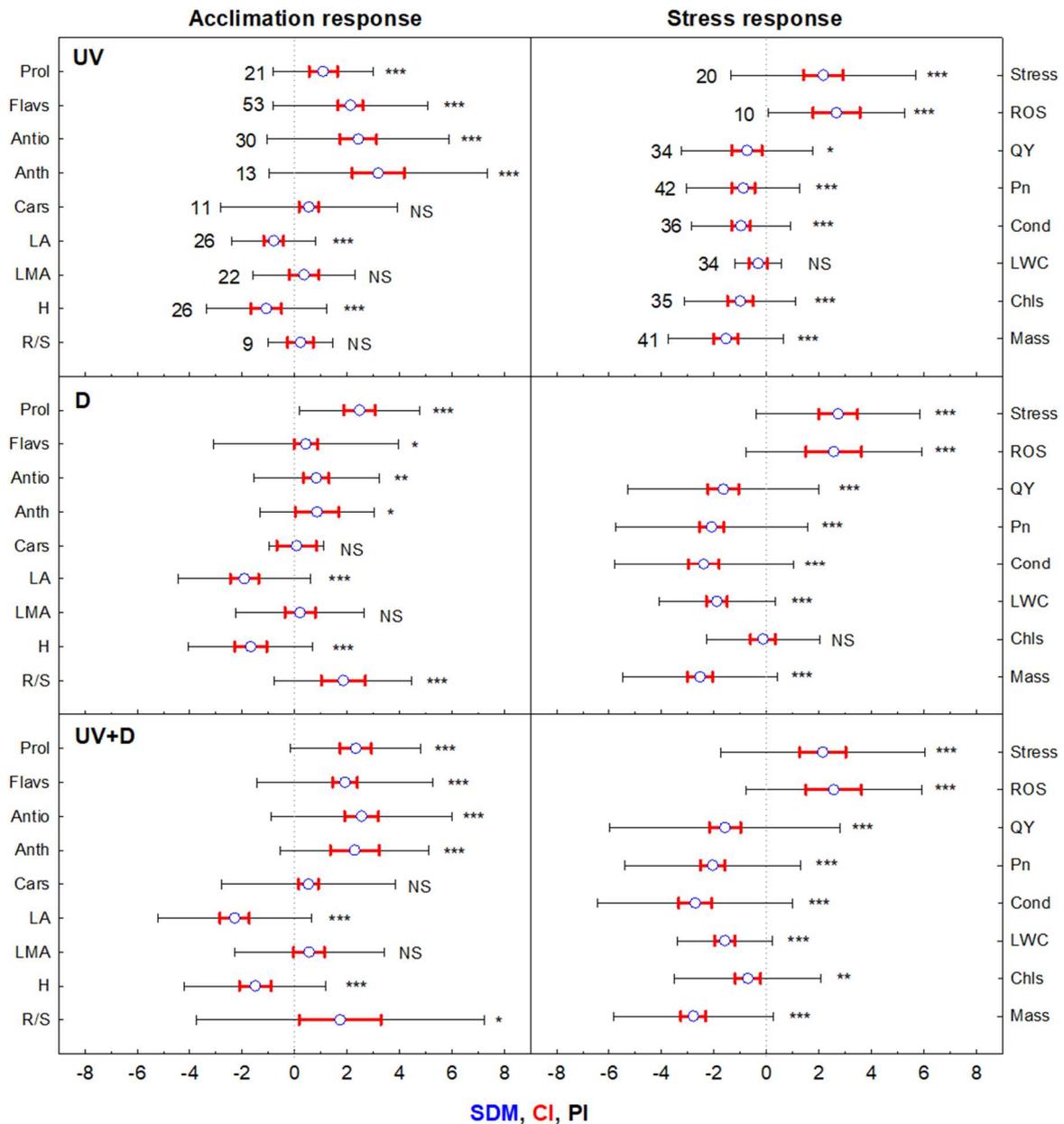
875 **Tables**

876

877 **Table 1.** Overview of statistically significant differences between plant responses to UV  
 878 (UV), drought (D) and UV plus drought (UV+D). Data are extracted from 52 peer-  
 879 reviewed papers. Variables are grouped in two categories: acclimation responses (Prol =  
 880 Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth =  
 881 Anthocyanin content, Cars = Carotenoid content, LA = Leaf area, LMA = Leaf mass per  
 882 area, H = Height, R/S = Root/shoot-ratio), and stress responses (Stress = Stress markers,  
 883 ROS = Reactive Oxygen Species, QY = Quantum yield of photosystem II photochemistry,  
 884 Pn = Photosynthetic CO<sub>2</sub> assimilation rate, Cond = Stomatal conductance, LWC = Leaf  
 885 water content, Chls = Chlorophyll content, Mass = Plant biomass). \* ( $p \leq 0.05$ ), \*\* ( $p \leq$   
 886  $0.01$ ), \*\*\* ( $p \leq 0.001$ ), NS = Not Significant ( $p > 0.05$ ).  
 887

	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

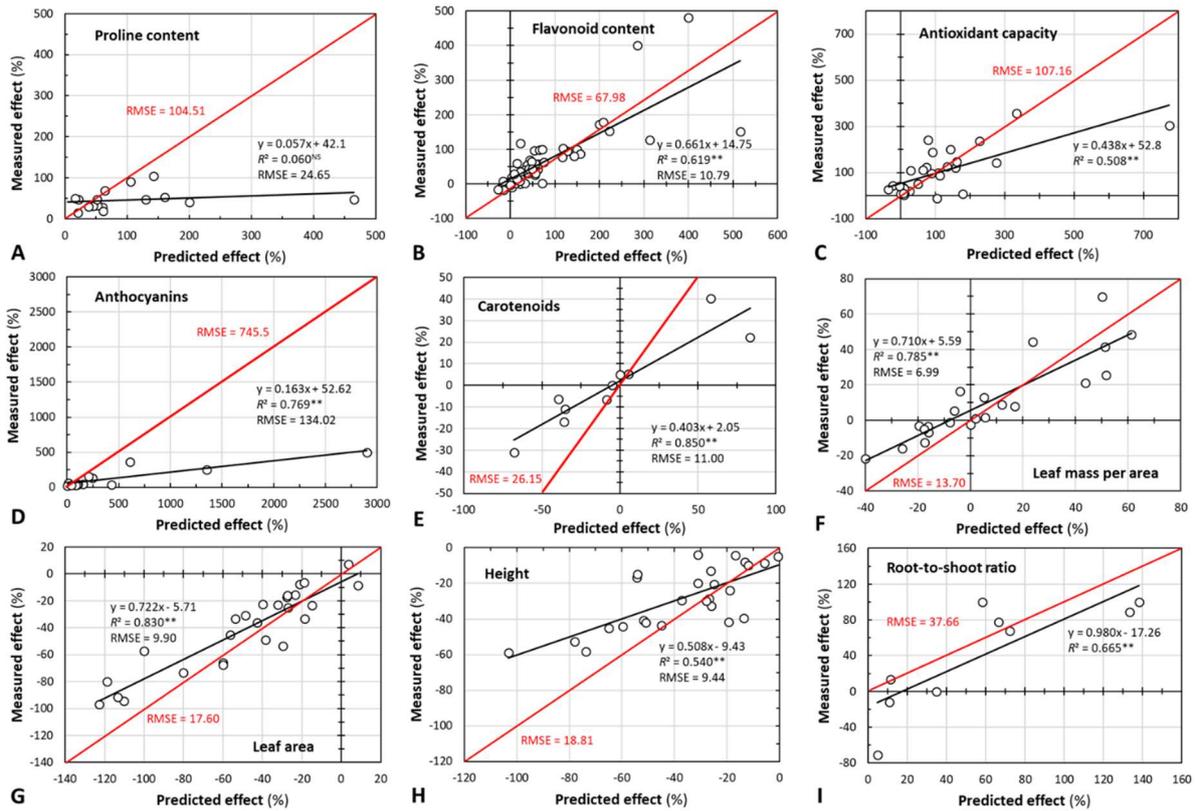
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890

891 **Figure 1** Overview of plant responses to UV (UV), drought (D) and UV plus drought  
 892 (UV+D). Data are extracted from 52 peer-reviewed papers. Variables are grouped in two  
 893 categories: acclimation responses (Prol = Proline content, Flavs = Flavonoid content,  
 894 Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA  
 895 = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root/shoot-ratio) and stress  
 896 responses (Stress = Stress markers, ROS = Reactive Oxygen Species, QY = Quantum yield  
 897 of photosystem II photochemistry, Pn = Photosynthetic CO<sub>2</sub> assimilation rate, Cond =  
 898 Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass =  
 899 Plant biomass). SDM = Standard Difference in Means, CI = 95% Confidence Interval, PI =  
 900 95% Prediction Interval, \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\* ( $p \leq 0.001$ ), NS = Not Significant ( $p$   
 901  $> 0.05$ ). The numbers indicate number of experiments included in the meta-analysis. See  
 902 Supplemental table 3 for exact values of SDM, CI, and PI.

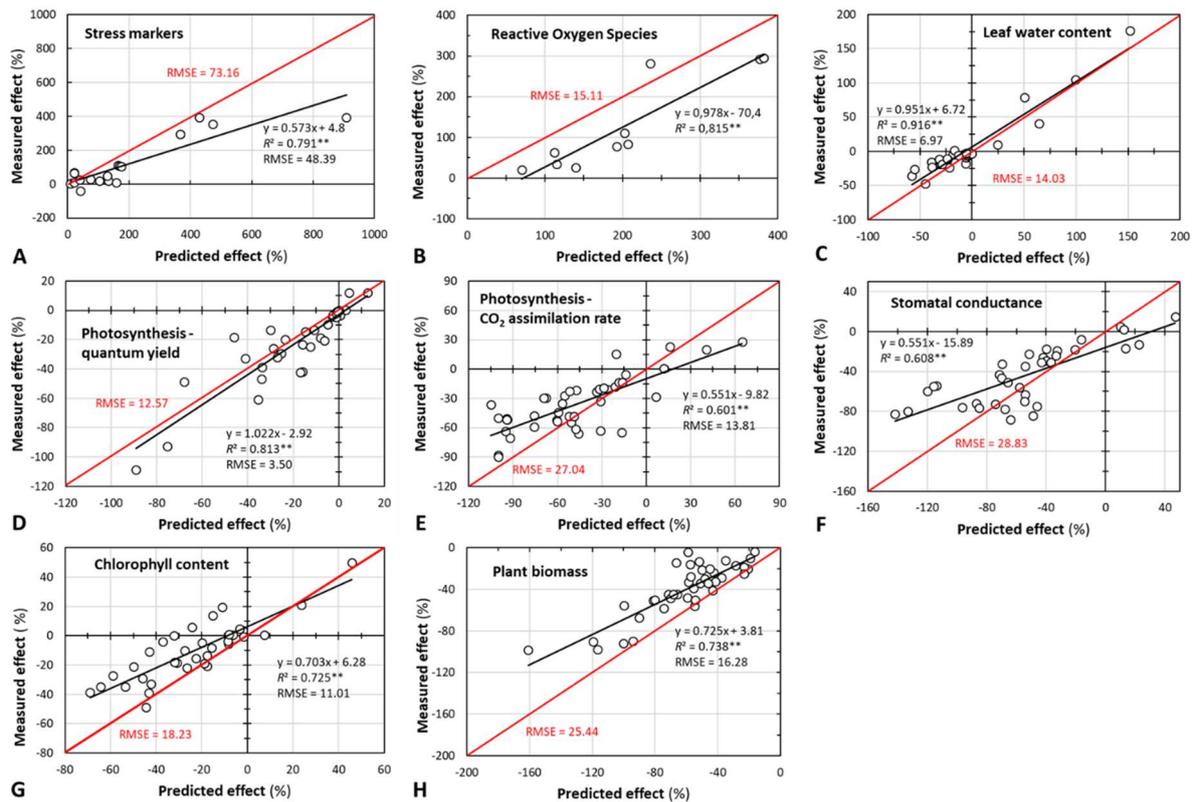
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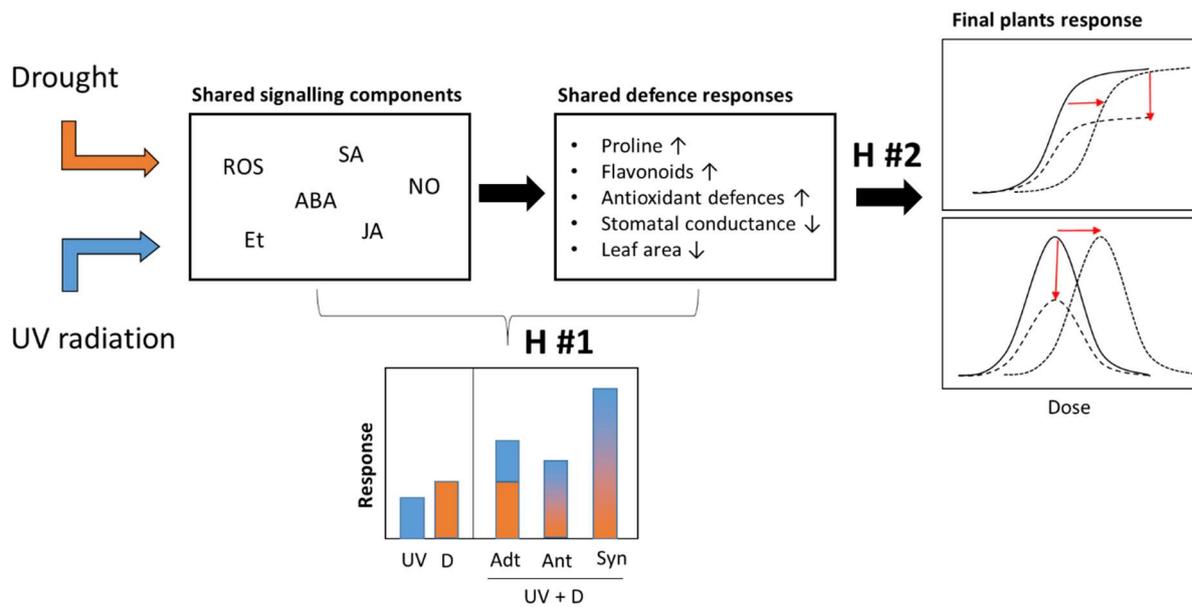
905 **Figure 2** Relationship between observed (Measured effect) and calculated (Predicted effect) effects of combined exposure to UV radiation and drought for variables describing  
 906 plant acclimation responses: proline content (A), flavonoid content (B), antioxidant  
 907 capacity (C), anthocyanin content (D), carotenoid content (E), leaf mass per area (F), leaf  
 908 area (G), height (H), and root-to-shoot ratio (I). The predicted effect was calculated as the  
 909 sum of individual UV and drought effects. The data were fitted using linear regression  
 910 (best linear fit). Coefficients of determination ( $R^2$ ) and significance levels (\*  $p \leq 0.05$ , \*\*  $p$   
 911  $\leq 0.01$ , NS  $p > 0.05$ ) are shown. Root Mean Square Error (RMSE) was calculated for both  
 912 the 1:1 line (red) and the best linear fit (black). See Supplemental table 2 for the  
 913 statistically significant differences between linear fits and 1:1 line.  
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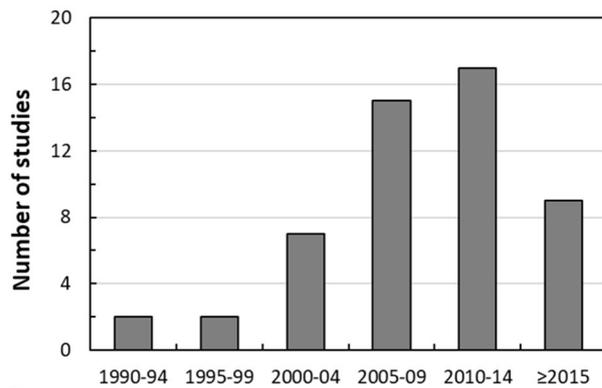
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917 **Figure 3** Relationship between observed (Measured effect) and calculated (Predicted effect) effects of combined exposure to UV radiation and drought for variables indicating  
 918 plant stress responses: stress markers (A), Reactive Oxygen Species (B), leaf water  
 919 content (C), photosynthetic activity – quantum yield of the photosystem II  
 920 photochemistry (D), photosynthetic activity – net CO<sub>2</sub> assimilation rate (E), stomatal  
 921 conductance (F), chlorophyll content (G), and plant biomass (H). The predicted effect was  
 922 calculated as the sum of individual UV and drought effects. The data were fitted using  
 923 linear regression (best linear fit). Coefficients of determination ( $R^2$ ) and significance  
 924 levels (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , NS  $p > 0.05$ ) are shown. Root Mean Square Error (RMSE)  
 925 was calculated for both the 1:1 line (red) and the best linear fit (black). See Supplemental  
 926 table 2 for the statistically significant differences between linear fits and 1:1 line.  
 927  
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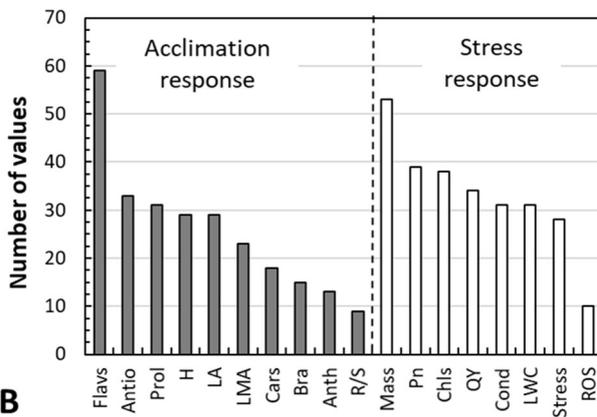


929

930 **Figure 4** Schematic overview of potential cross-talk and cross-protection in plants  
 931 exposed to UV radiation (blue) and drought (orange). Potential shared signalling  
 932 components are Reactive Oxygen Species (ROS), salicylic acid (SA), jasmonic acid (JA),  
 933 abscisic acid (ABA), nitric oxide (NO), and ethylene (Et), with responses additive (Adt),  
 934 antagonistic (Ant) or synergistic (Syn). It is hypothesised that shared signalling pathways  
 935 and defence mechanisms lead to interactive effects of ultraviolet radiation (UV) and  
 936 drought on individual variables (hypothesis #1) and consequently may result in shifts of  
 937 plant sensitivity to stress conditions (hypothesis #2) seen as a shift in the dose response,  
 938 and/or a decreased magnitude of the stress response.  
 939



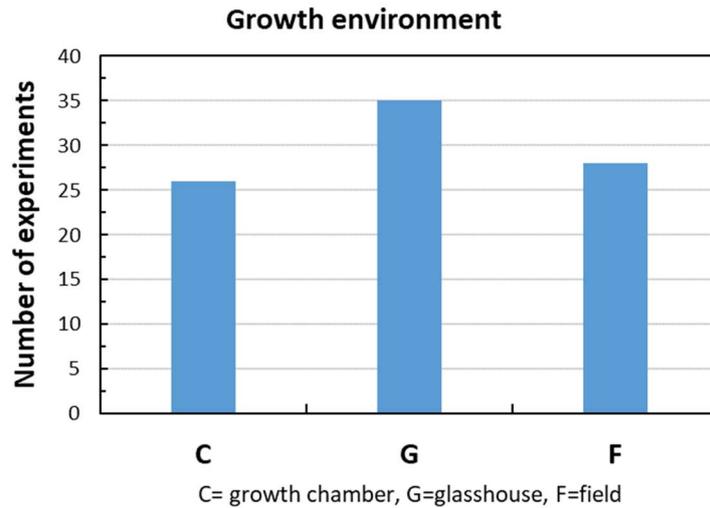
**A**



**B**

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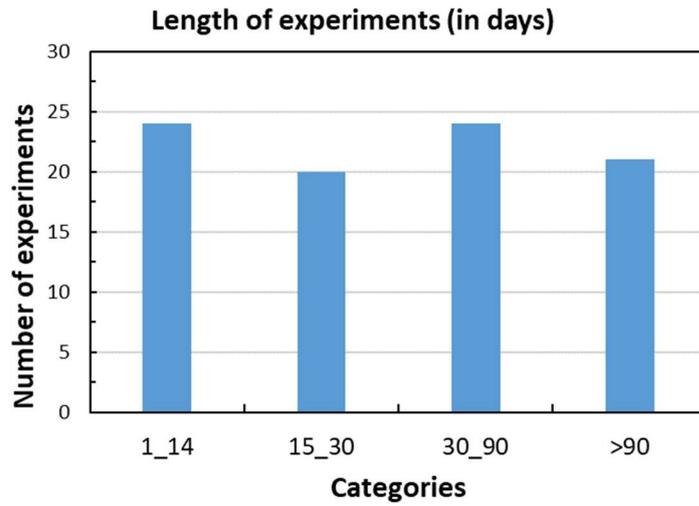
942 **Supplemental figure 1. (A)** A total of 52 papers were analysed, and these were  
 943 published in peer-reviewed journals in the period 1990 through to 2019. **(B)** Variables  
 944 investigated were grouped into two main categories characterising plant acclimation  
 945 responses (black columns), and plant stress responses (white columns). Investigated  
 946 variables are: Flavs = Flavonoid content, Antio = Antioxidant capacity, Prol = Proline  
 947 content, H = Height, LA = Leaf area, LMA = Leaf mass per area, Cars = Carotenoid content,  
 948 Bra = Branching, Anth = Anthocyanin content, R/S = Root-to-shoot ratio, Mass = Plant  
 949 biomass, Pn = Photosynthetic CO<sub>2</sub> uptake, Chls = Chlorophyll content, QY = Quantum yield  
 950 of photosystem II photochemistry, Cond = Stomatal conductance, LWC = Leaf water  
 951 content, Stress = Stress markers, ROS = Reactive Oxygen Species..  
 952



953

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

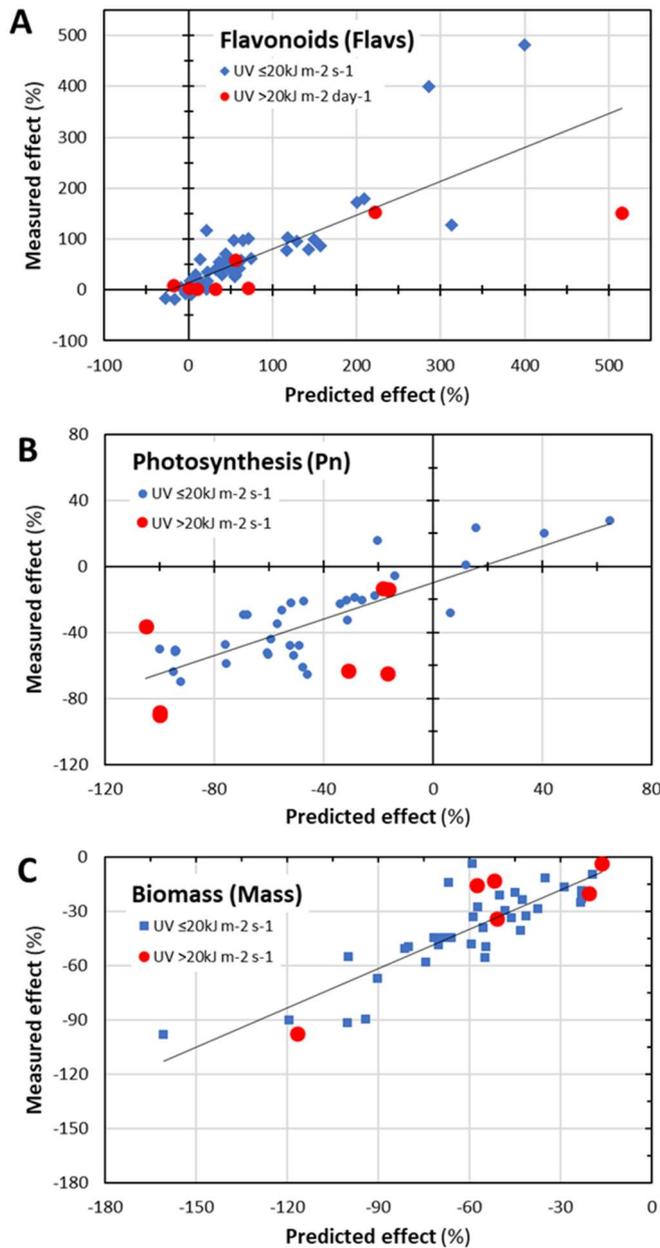
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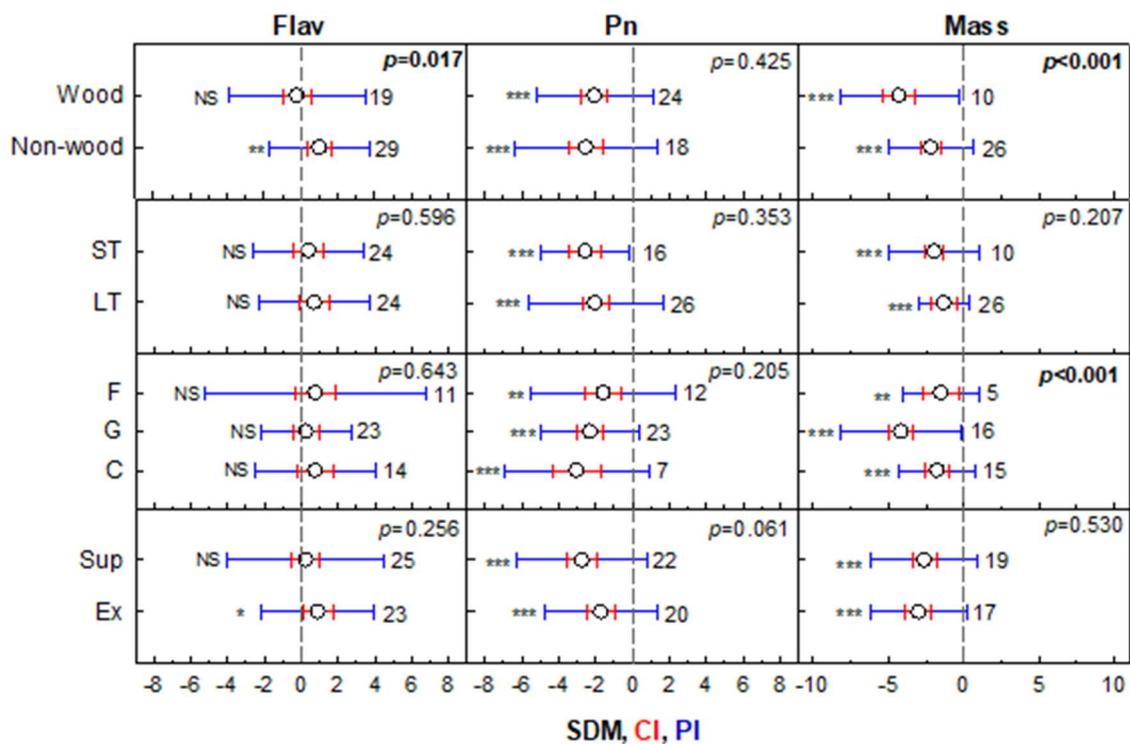
960 **Supplemental figure 3.** Duration of the analysed experiments. The duration of the  
961 experiments varied between 3 and 900 days. Moreover, there is one extraordinary long  
962 study by Arróniz-Crespo *et al.* (2011) in *Annals of Botany* 108: 557-565 on Bryophytes –  
963 13-15 years.

964



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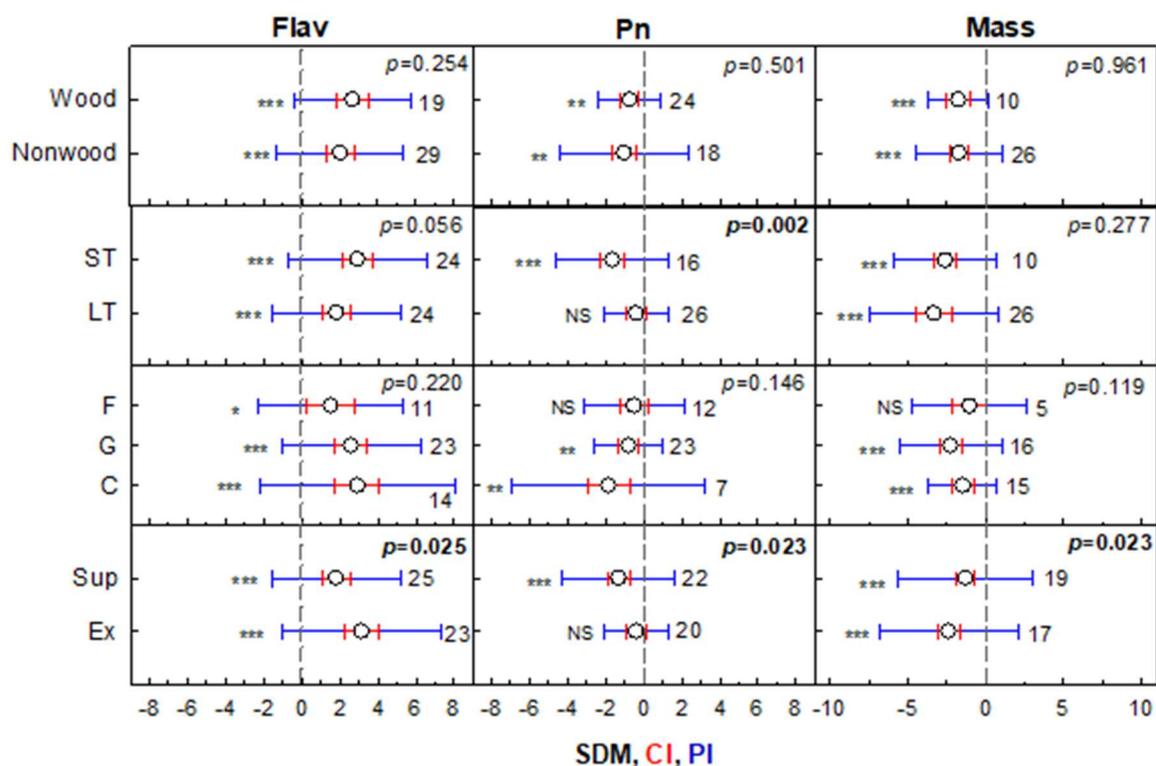
966 **Supplemental figure 4.** Relationship between observed (Measured effect) and  
 967 calculated (Predicted effect) effects of combined exposure to UV radiation and drought  
 968 for selected variables (Flavonoids – panel **A**, Photosynthetic CO<sub>2</sub> uptake – panel **B**, and  
 969 Biomass – panel **C**). The experiments where high UV doses (above 20 kJ m<sup>-2</sup> day<sup>-1</sup>) were  
 970 applied are shown in red. The data were fitted using linear regression (best linear fit).  
 971



972

973 **Supplemental figure 5.** Detailed analysis of drought effects on flavonoid content (Flav),  
 974 photosynthetic CO<sub>2</sub> uptake (Pn), and plant biomass (Mass). The data are categorized  
 975 according to anatomical structure (woody × non-woody plants), duration of the  
 976 experiment (short- × long-term), treatment conditions (field × greenhouse × growth  
 977 chamber), and UV application (supplementary × excluded). SDM = Standard Difference in  
 978 Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval. Stars (\*) refer to  
 979 significance of the experimental treatment \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\* ( $p \leq 0.001$ ), NS =  
 980 Not Significant ( $p > 0.05$ ).  $p$ -values in the top right-hand corner indicate the significance  
 981 of the differential response between compared categories. The numbers indicate the  
 982 number of experiments included in the meta-analysis.

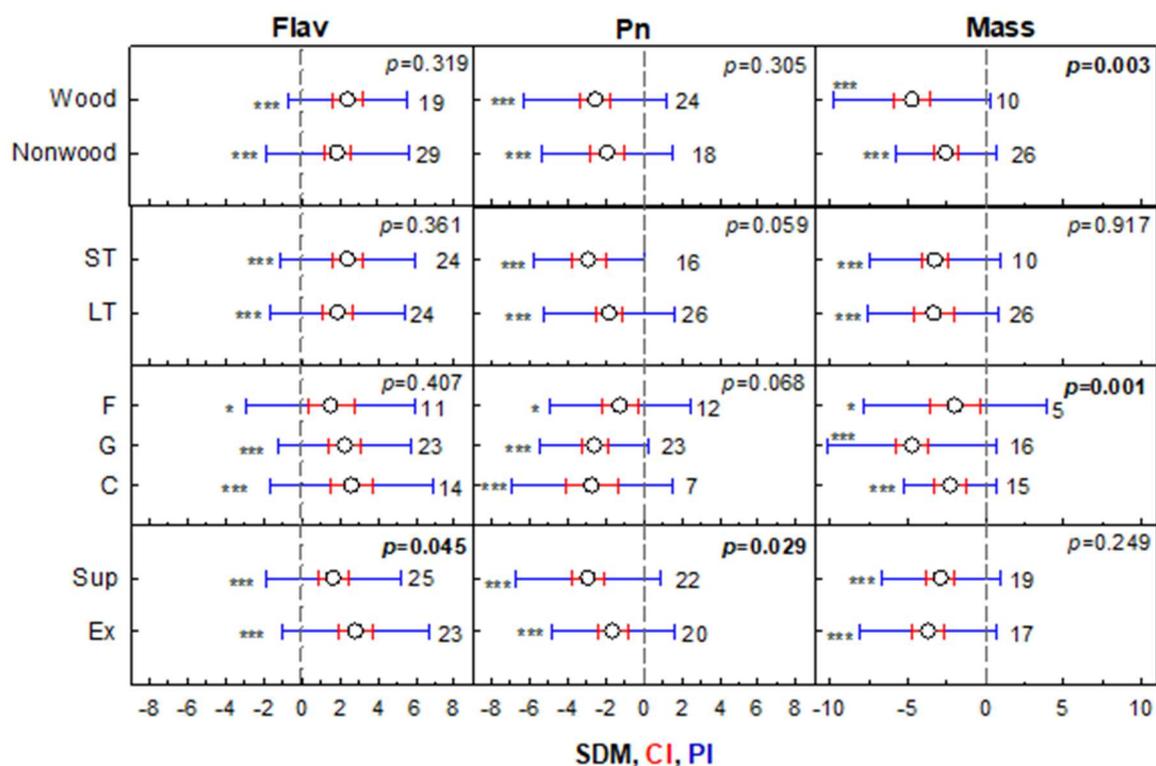
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984

985 **Supplemental figure 6.** Detailed analysis of UV effects on flavonoid content (Flav),  
 986 photosynthetic CO<sub>2</sub> uptake (Pn), and plant biomass (Mass). The data are categorized  
 987 according to anatomical structure (woody × non-woody plants), duration of the  
 988 experiment (short- × long-term), treatment conditions (field × greenhouse × growth  
 989 chamber), and UV application (supplementary × excluded). SDM = Standard Difference in  
 990 Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval. Stars (\*) refer to  
 991 significance of the experimental treatment \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\* ( $p \leq 0.001$ ), NS =  
 992 Not Significant ( $p > 0.05$ ).  $p$ -values in the top right-hand corner indicate the significance  
 993 of the differential response between compared categories. The numbers indicate number  
 994 of experiments included in the meta-analysis.

995



996

997 **Supplemental figure 7.** Detailed analysis of combined effects of UV and drought on  
 998 flavonoid content (Flav), photosynthetic CO<sub>2</sub> uptake (Pn), and plant biomass (Mass). The  
 999 data are categorized according to anatomical structure (woody × non-woody plants),  
 1000 duration of the experiment (short- × long-term), treatment conditions (field ×  
 1001 greenhouse × growth chamber), and UV application (supplementary × excluded). SDM =  
 1002 Standard Difference in Means, CI = 95% Confidence Interval, PI = 95% Prediction Interval.  
 1003 Stars (\*) refer to significance of the experimental treatment \* ( $p \leq 0.05$ ), \*\* ( $p \leq 0.01$ ), \*\*\*  
 1004 ( $p \leq 0.001$ ), NS = Not Significant ( $p > 0.05$ ).  $p$ -values in the top right-hand corner indicate  
 1005 the significance of the differential response between compared categories. The numbers  
 1006 indicate number of experiments included in the meta-analysis.

1007

1008 **Supplemental table 1**

1009 Overview of all analysed experiments including details on plant material, experimental  
 1010 set up and measured variables. (Uploaded as a separate supplementary file.)

1011

1012 **Supplemental table 2**

1013 The percentage of statistically significant ( $p < 0.05$ ) effects on specific variables, and  
 1014 across the experiments included in the database. Variables are grouped into two main  
 1015 categories characterising plant acclimation responses (dark grey; Prol = Proline content,  
 1016 Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth = Anthocyanin content, Cars  
 1017 = Carotenoid content, LA = Leaf area, LMA = Leaf mass per area, H = Height, R/S = Root-  
 1018 to-shoot ratio), and stress responses (while cells; Stress = Stress markers, ROS = Reactive  
 1019 Oxygen Species, QY = Quantum yield of photosystem II photochemistry, Pn =  
 1020 Photosynthetic CO<sub>2</sub> assimilation rate, Cond = Stomatal conductance, LWC = Leaf water  
 1021 content, Chls = Chlorophyll content, Mass = Plant biomass).

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

1022

1023 **Supplemental table 3**

1024 Summary of comprehensive meta-analysis outcomes: SDM = Standard Difference in  
 1025 Means, 95% CI = 95% confidence interval, 95% PI = 95% prediction interval. Effects of  
 1026 ultraviolet radiation (UV), drought (D) and their combination (UV+D) are shown.  
 1027 Variables are grouped into two main categories characterising plant acclimation  
 1028 responses (grey cells; Prol = Proline content, Flavs = Flavonoid content, Antio =  
 1029 Antioxidant capacity, Anth = Anthocyanin content, Cars = Carotenoid content, LA = Leaf  
 1030 area, LMA = Leaf mass per area, H = Height, R/S = Root-to-shoot ratio), and stress  
 1031 responses (white cells; Stress = Stress markers, ROS = Reactive Oxygen Species, QY =  
 1032 Quantum yield of photosystem II photochemistry, Pn = Photosynthetic CO<sub>2</sub> assimilation  
 1033 rate, Cond = Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content,  
 1034 Mass = Plant biomass). Bold rows (**Antio\*** and **Mass\***) indicate additional analyses  
 1035 whereby duplicate (or triplicate) entries were removed from the “antioxidant” and  
 1036 “biomass” datasets.  
 1037

	SDM	95% CI		95% PI	
<b>UV</b>					
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
<b>Antio*</b>	<b>2.02</b>	<b>1.27</b>	<b>2.77</b>	<b>1.24</b>	<b>5.28</b>
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
<b>Mass*</b>	<b>-1.56</b>	<b>-2.05</b>	<b>-1.08</b>	<b>-4.03</b>	<b>0.91</b>
<b>Drought</b>					
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
<b>Antio*</b>	<b>0.62</b>	<b>0.20</b>	<b>1.21</b>	<b>-1.90</b>	<b>3.13</b>
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
<b>Mass*</b>	<b>-2.69</b>	<b>-3.33</b>	<b>-2.04</b>	<b>-6.07</b>	<b>0.70</b>
<b>UV+D</b>					
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
<b>Antio*</b>	<b>2.05</b>	<b>1.36</b>	<b>2.75</b>	<b>-0.86</b>	<b>4.97</b>
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
<b>Mass*</b>	<b>-3.18</b>	<b>-3.93</b>	<b>-2.43</b>	<b>-7.08</b>	<b>0.73</b>

1039 **Supplemental table 4**

1040 Summary of slopes and intercepts of linear regression between observed and predicted  
 1041 values for individual variables, and their statistically significant differences from 1:1\_fit.  
 1042 Variables are grouped into two main categories characterising plant acclimation responses  
 1043 (Prol = Proline content, Flavs = Flavonoid content, Antio = Antioxidant capacity, Anth =  
 1044 Anthocyanin content, Cars = Carotenoid content, LMA = Leaf mass per area, LA = Leaf  
 1045 area, H = Plant height, R/S = Root-to-shoot ratio), and plant stress responses (Stress =  
 1046 Stress markers content, ROS = Reactive Oxygen Species, Pn = Photosynthetic CO<sub>2</sub>  
 1047 assimilation rate, QY = = Quantum yield of photosystem II photochemistry, Cond =  
 1048 Stomatal conductance, LWC = Leaf water content, Chls = Chlorophyll content, Mass =  
 1049 Plant biomass). DF = Degree of freedom, s.e. = standard error; statistically significant  
 1050 differences in slopes and intercepts between 1:1\_fit and best-linear\_fit are shown in bold  
 1051 (p).

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Parameter	DF	Slope	s.e.	T Score	p	Intercept	s.e.	T Score	p
Prol	19	0.057	0.0536	-18.039	<b>&lt;0.001</b>	42.1	7.53	5.543	<b>&lt;0.001</b>
Flavs	51	0.661	0.0812	-4.221	<b>&lt;0.001</b>	14.7	11.33	1.039	0.268
Antio	28	0.438	0.0870	-6.473	<b>&lt;0.001</b>	52.79	16.59	3.159	<b>0.005</b>
Anth	11	0.163	0.0268	-31.231	<b>&lt;0.001</b>	52.6	24.64	2.136	0.056
Cars	9	0.403	0.0566	-10.548	<b>&lt;0.001</b>	2.0	2.36	0.867	0.409
LMA	20	0.710	0.0833	-3.481	<b>0.002</b>	5.6	2.41	2.321	<b>0.031</b>
LA	24	0.722	0.0644	-4.631	<b>&lt;0.001</b>	-5.7	3.97	-1.013	0.320
H	24	0.508	0.1028	-3.995	<b>&lt;0.001</b>	-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	<b>0.005</b>	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	<b>&lt;0.001</b>	-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	<b>&lt;0.001</b>	-15.9	6.49	-2.288	<b>0.031</b>
LWC	32	0.951	0.0593	-0.458	0.651	6.7	2.85	2.631	<b>0.021</b>
Chls	33	0.703	0.0644	-5.107	<b>0.001</b>	6.2	4.23	1.424	0.078
Mass	39	0.725	0.0723	-3.663	<b>&lt;0.001</b>	3.8	4.92	1.038	0.306

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