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1 **Water limitation affects weed competitive ability for light. A demonstration using a model-**
2 **based approach combined with an automated watering platform**

3

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14

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16

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18 Climate change, competition, trait, specific leaf area, height to biomass ratio, root to total
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20 *myosuroides*, *Amaranthus hybridus*

21

22 **Total word count:** 8143

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24

25 **1. Summary**

26 Because of climate change, investigating how morphological traits involved in competition for
27 light (main resource for which crops and weeds compete in conventional cropping systems and
28 temperate and tropical climate) respond to water limitation is crucial to better understand crop-
29 weed dynamics in the field. Our objective was to develop an innovative approach to quantify
30 the response of weed species to water limitation, and test it with three species. This approach
31 combined (1) key morphological traits involved in competition for light (taken from a
32 mechanistic crop-weed model) as criteria to analyze response to water limitation and (2) a
33 pot/greenhouse platform allowing automated precision-watering and daily quantification of soil
34 water availability in each pot. Response to water limitation differed among species/stages. For
35 all species/stages, increased plant height per unit of aboveground biomass and production of
36 smaller/thicker leaves were the most noteworthy responses. Plants with a strong increase of
37 plant height per unit of aboveground biomass in response to water limitation were able to
38 maintain high specific leaf area, even at low soil water availability. Increase in biomass
39 allocation to roots (vs. aboveground parts) and to leaves (vs. stems and reproductive organs)
40 were also observed, but not for all species/stages. Overall, these effects of water limitation on
41 morphological traits, suggest strong interactions between competition for light and water.

42

43 **2. Introduction**

44 Weeds can greatly reduce yield and harvest quality, mainly by competing with crops for
45 resources (Oerke, 2006). That is the reason (together with a high efficiency) why herbicides
46 generally play a key role in ensuring crop production efficiency in conventional cropping
47 systems. However, reducing the excessive use of herbicides has become necessary in view of
48 harmfulness for the environment and public health (Hasanuzzaman et al., 2020). In this context,
49 promoting weed ecological regulation by shifting resource availability and use from weed to
50 crop may provide a more sustainable weed management (Petit et al., 2018). One promising
51 option could be to use competitive crop plants, especially for light which is the main resource
52 for which crops and weeds compete in conventional cropping systems and in temperate and
53 tropical climates (Wilson and Tilman, 1993; Perry et al., 2003). However, the frequency of
54 water stress events may increase with climate change, especially in Southern Europe
55 (<http://discomap.eea.europa.eu/climate>). So, one challenge is to identify crops that are
56 competitive for light, even under water stress conditions.

57 Species competitive ability is directly related to their capacity to adapt to resource availability
58 (Navas and Violle, 2009). Thus, investigating the response of crop and weed species to water
59 limitation is crucial. Especially, we need to better understand how plant traits involved in
60 competition for light respond to water stress. Some studies characterized the response of weed
61 species to water stress. However, most of them focused on the germination phase (e.g. Gardarin
62 et al., 2010; Ruhl et al., 2016; Yuan and Wen, 2018) or on global plant growth (e.g. Chahal et
63 al., 2018; de Oliveira et al., 2018). Moreover, they were conducted on a low number of weed
64 species, which contrasts with the high number of weed species that may be found in arable
65 fields (Fried et al., 2008). To our knowledge, no study has yet quantified the diversity of the
66 response of weed species to water availability with a focus on the key morphological traits
67 involved in competition for light. The reasons for this are two-fold. Carrying out experiments
68 with a range of water treatments requires individual daily pot watering which is very time-
69 consuming when performed manually, especially on a large number of pots. Moreover, until
70 recently, the key morphological traits involved in crop-weed competition for light were not
71 identified. However, two main recent advances should make it possible to lift these limitations.
72 On the one hand, the development of innovative high-throughput platforms with automatic and
73 precise individual pot watering in greenhouse allows to overcome these technical limitations
74 (e.g. Granier et al., 2006; Jeudy et al., 2016; Bricchet et al., 2017). Up to now, such platforms
75 have almost entirely been used for crop species or for species used as models in genetic/genomic
76 studies. Even when the objective was to analyze crop competitive ability with weeds, only crop

77 plants were studied (Nguyen et al., 2018; Anandan et al., 2020). On the other hand, a recent
78 study using a mechanistic simulation model allowed to identify key morphological traits
79 involved in competition for light between arable crops and annual weeds (Colbach et al., 2019).
80 Considering competition for light only (i.e. competition for water was neglected), Colbach et
81 al. (2019) identified the key traits explaining weed harmfulness, crop ability to limit weed-
82 caused yield loss and/or crop potential yield. They were specific leaf area (SLA corresponding
83 to the leaf area per unit of leaf biomass), height to biomass ratio (HBR corresponding to plant
84 height per unit of aboveground biomass) and leaf to aboveground biomass ratio (LBR
85 corresponding to leaf biomass per unit of aboveground biomass).

86 Based on these recent advances, our objective was to quantify the response of weed species to
87 water stress in order to determine which morphological traits are influenced by water stress and
88 whether the response to water stress depends on plant species and stage. Our aim was also
89 technical: to test an innovative approach for weed characterization combining (1)
90 morphological traits derived from a simulation study as criteria to analyze weed response to
91 water limitation and (2) an experimental platform allowing automatic and precise plant
92 watering. The final aim was to determine whether the results from this approach (applied here
93 to a small number of weed species and stages as a proof of concept) could help in the near future
94 for the large-scale characterization of the large panel of weed species potentially present in
95 agricultural fields.

96

97 **3. Materials and methods**

98 **3.1. Experimental treatments**

99 A greenhouse experiment was conducted in Dijon (France) using three annual weed species:
100 *Alopecurus myosuroides* Huds. (monocotyledonous C3 species preferentially germinating in
101 autumn), *Amaranthus hybridus* L. (dicotyledonous C4 species preferentially germinating in
102 spring and summer) and *Abutilon theophrasti* Medik. (dicotyledonous C3 species preferentially
103 germinating in summer). Five water treatments were applied, corresponding to 20%, 30%, 40%,
104 55% and 75% of field capacity. The five treatments were applied to the three species, except
105 the 40% treatment on *A. hybridus* (due to space limitation in the greenhouse). Eight plants were
106 grown per species × water treatment combination. Plant species and water treatments were
107 randomly arranged. The duration of the experiment was 62 days.

108

109 **3.2. Growing conditions**

110 Seeds were germinated in an incubator with a 16-h photoperiod and day/night temperatures
 111 adapted to each species (25/20°C for *A. myosuroides* and 30/25°C for *A. hybridus* and *A.*
 112 *theophrasti*). On 14 March 2017, germinated seeds were sown in the greenhouse into 1-L pots
 113 filled with a solid and inert substrate made up of 80 % of expanded clay and 20 % of attapulgite
 114 (volume proportions), with a bulk density at 0.67 +/- 0.01 g cm⁻³. The retention curve of the
 115 substrate is given in Supplementary Material Section A online. One seed was sown in each pot.
 116 The pots were placed on fixed tables and watered automatically with a complete nutrient-rich
 117 solution made up of N-P-K (10-10-10) and oligo-elements via tubes at a frequency allowing
 118 non-limiting watering. Twenty-three days later (on 6 April, when plants were between six and
 119 nine leaves), plants were transferred into an automated platform where the five water treatments
 120 were imposed. This platform (described in Jeudy et al., 2016) is based on conveyors that
 121 automatically transport pots towards a watering unit (consisting of a weighing terminal and a
 122 high-precision pump-watering station) (Supplementary Material Section B online). In our
 123 experiment, plants were conveyed three times per day to be weighed. When actual weight was
 124 lower than target weight, they were watered (Supplementary Material Section C online). There
 125 was no drain because irrigation did not exceed field capacity. Over all irrigation events,
 126 irrigation allowed to reach the pot target weight ± 0.13 % (calculated as the absolute difference
 127 between the target and the actual weight just after the irrigation event, divided by the target
 128 weight). The elapsed time between the irrigation of the first and the last pot (over 130 pots) was
 129 34 ± 9 minutes.

130 Throughout the experiment, the same complete nutrient-rich solution was used in order to avoid
 131 strong plant-nitrogen-limitation even when water supply was low. In the discussion (Section
 132 5.4), the comparison of our results to the literature suggests that this methodological approach
 133 allowed to minimize a potential nitrogen limitation.

134

135 Target weight was determined as:

136

$$137 \frac{[(SW_{100\%} - SW_{0\%}) \times \%WaterCapacity]}{100} + SW_{0\%} + EPotW + PlantW \quad [Equation 1]$$

138

139 $SW_{100\%}$ and $SW_{0\%}$ are substrate weight (in g). $SW_{100\%}$ is measured at field capacity, and $SW_{0\%}$ is
 140 the weight of dry substrate. $\%WaterCapacity$ is the target proportion of field capacity (in %,
 141 ranging from 20 to 75 %). $EPotW$ is empty pot weight (in g). $PlantW$ is fresh plant weight (in
 142 g). Plant weight was considered as negligible at the beginning of the experiment. It was adjusted

143 during the experiment for *A. theophrasti* (using plant weight data from the first sampling date;
144 see Section 3.3).

145 At each weighing session, the weight of each pot was recorded before and after watering. These
146 data were used to calculate the daily fraction of evapotranspirable soil water, currently named
147 ‘Fraction of Transpirable Soil Water’ (FTSW_d in %), for each species × water treatment
148 combination. The FTSW_d relates the actual plant-available soil water content to the total plant-
149 available soil water content for day *d* (Lebon et al., 2006). It was calculated as:

150

$$151 \text{ FTSW}_d = \frac{(sw_{100\%} - sw_{0\%}) + \sum_{d=1}^n (\text{WaterInput}_d) - \sum_{d=1}^n (\text{Evapotranspiration}_d)}{(sw_{100\%} - sw_{0\%})} \quad [\text{Equation 2}]$$

152

153 *WaterInput_d* (in g) is the daily amount of water provided by automatic watering at day *d*, and
154 *Evapotranspiration_d* (in g) is the daily amount of water lost by evapotranspiration at day *d*.

155 Note that the day the pots were transferred into the platform, FTSW was close to 100% for all
156 pots, and then differentiated water treatments started (Supplementary Material D). So, during
157 the first days, water input was nil. Water input and evapotranspiration were the same only when
158 the target weight was reached.

159 Throughout the experiment, artificial light was provided using 400 W lamps (HPS Plantastar,
160 OSRAM, Munich, Germany), in addition to natural light. Mean photoperiod was 14.5 ± 0.7 h.
161 Incident photosynthetically active radiation was 17.2 ± 2.1 mol m⁻² day⁻¹ (silicon sensors;
162 Solems, Palaiseau, France). Air temperature was $21.2 \pm 1.7^\circ\text{C}$ (PT100 sensors; Pyro-Contrôle,
163 Vaulx-en-Velin, France). Air relative humidity was 57.7 ± 3.0 % (AIDC HIH-4000-001;
164 Honeywell, Minneapolis, USA).

165

166 **3.3.Plant measurement and trait calculation**

167 Plant measurements were made at two sampling dates, and four plants were sampled per species
168 × water treatment × sampling date combination. At the first sampling date, all the species ×
169 water treatment combinations were sampled. *Abutilon theophrasti* and *A. myosuroides* were at
170 the vegetative stage, and *A. hybridus* was at the flowering stage. At the second date, only one
171 species (*A. theophrasti*) was sampled at the flowering stage. The first sampling was performed
172 21 days after beginning of water treatments (i.e. 45 days after sowing), leaving enough time for
173 the water treatments to stabilize (Supplementary Material Section D online) and plants to adapt.
174 The second sampling was performed 38 days after beginning of water treatments (i.e. 62 days
175 after sowing), when *A. theophrasti* reached the flowering stage.

176 At each sampling date, the following plant growth traits were measured. Plant height and plant
177 leaf area (LI-3100 Area Meter; LI-COR, Lincoln, NE, USA) were measured. Leaf, stem and
178 root biomass were independently determined after 48 h at 80°C. These plant growth traits were
179 used to calculate plant morphological traits that play a key role in competition for light (Colbach
180 et al., 2019): (1) leaf to aboveground biomass ratio (LBR) is the ratio of the leaf to aboveground
181 biomass. It reflects the efficiency for producing leaves for a given aboveground plant biomass,
182 with a higher value for leafier plants. (2) Specific leaf area (SLA) is the ratio of the leaf area to
183 the leaf biomass at the plant level. It is the efficiency for producing leaf area from a given leaf
184 biomass. High values indicate thin leaves, while low values mean thicker leaves. (3) Height to
185 biomass ratio (HBR) is plant height relatively to aboveground biomass. The higher height to
186 biomass ratio, the taller the plants are for a given biomass. We also calculated (4) Root to total
187 plant biomass ratio (RBR), i.e. root biomass relative to total plant biomass, reflecting plant
188 efficiency for producing root biomass from total plant biomass, with a higher value for plants
189 favoring root vs. aboveground growth. This trait is often considered to play a key role in the
190 interaction between competition for light and water (McCarthy and Enquist, 2007; Craine and
191 Dybzinski, 2013).

192

193 **3.4. Statistical analyses**

194 Soil-water availability was expressed in fraction of transpirable soil water, with FTSW_{mean} the
195 mean over FTSW_d values from the beginning of water treatment to sampling date. FTSW_{mean}
196 was compared between plant species and plant stages by analysis of variance (lm function of
197 R). As the three weed species were not sampled at both phenological stages, the relative effects
198 of species and stage could not be dissociated. So, the global effect of both species and stage
199 was analyzed.

200 The response of each morphological trait to FTSW_{mean} was analyzed by covariance analysis
201 (lm function of R). The following model was used:

202

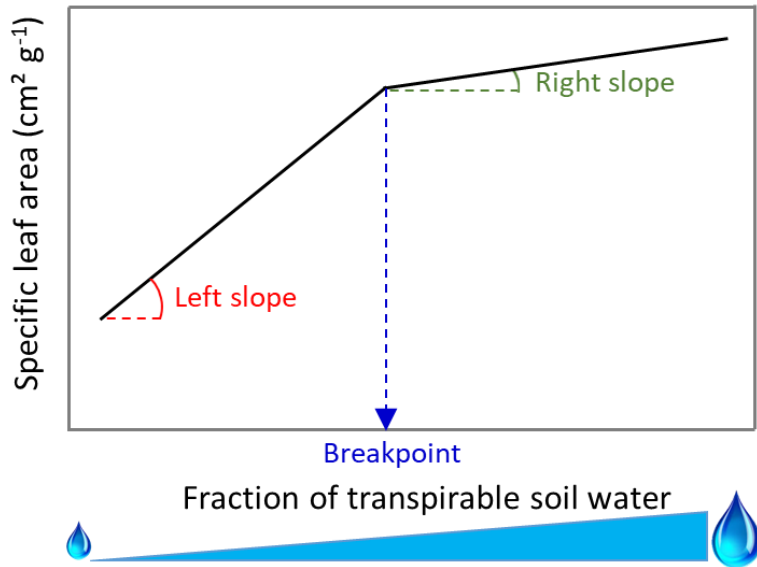
$$203 \text{ plant_trait}_{ps} = \text{constant} + c_s + a \times \text{FTSW}_{\text{mean}_{ps}} + b_s \times \text{FTSW}_{\text{mean}_{ps}} + \text{error}_{ps} \quad [\text{Equation 3}]$$

204

205 where plant_trait_{ps} was the morphological trait measured on plant p for a given species \times stage
206 combination s, and *constant*, *a*, *c_s* and *b_s* were regression slopes, with the latter two depending
207 on the species \times stage combination s. This model was applied to the four morphological traits.
208 For HBR, a \log_n transformation was applied to normalize residue distribution. For SLA, a
209 piecewise regression was performed using the segmented package in R (Muggeo, 2008), in

210 order to account for its two-phase response pattern (Figure 1). So, for HBR, RBR and LBR, the
 211 response of species \times stage combinations to water availability was compared on one slope
 212 value, while for SLA it was compared on two slope values and breakpoint (i.e. $FTSW_{\text{mean}}$ at
 213 which slope values change).

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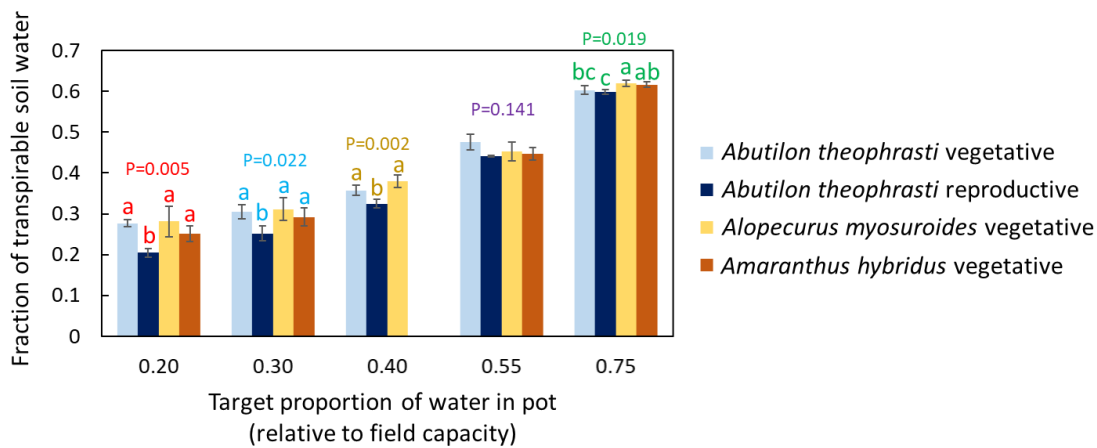
216 **Figure 1: Theoretical example of the two-phase-response-pattern of specific leaf area (SLA) to**
 217 **water availability (characterized by the fraction of transpirable soil water, FTSW).** It shows three
 218 parameters: breakpoint (i.e. FTSW at which slope value changes) and left and right slopes (i.e. slope of
 219 the regression when FTSW is lower and higher, respectively, than breakpoint value).

220

221 4. Results

222 4.1. Dynamics of soil-water availability

223 The five water treatments resulted in different soil-water status characterized by the mean
 224 fraction of transpirable soil water (FTSW) (Figure 2). For most water treatments (defined by
 225 the target proportion of field capacity), the mean daily FTSW (averaged over the period running
 226 from the beginning of water treatments to sampling date) varied with the plant species/stage
 227 (Figure 2). In general, FTSW was lower for *A. theophrasti* at the reproductive stage. This was
 228 due to the dynamics of FTSW that progressively decreased over time until stabilization
 229 (Supplementary Material Section D online) and to the later sampling date (39 instead of 22 days
 230 after the beginning of water treatments) for *A. theophrasti* at the reproductive stage, resulting
 231 in more days at low FTSW values. As a given water treatment mostly resulted in different
 232 FTSW values depending on species/stage, plant morphology was analyzed in response to FTSW
 233 in the following sections.



235

236 **Figure 2: Fraction of transpirable soil water (FTSW) averaged over the period running**
 237 **from the beginning of water treatments to sampling date, for each species/stage and water**
 238 **treatment combination.** P-values refer to variance analysis performed independently for each
 239 water treatment (defined by the target proportion of water in pot). Within each treatment, bars
 240 with the same letter show values that are not significantly different (least significant difference
 241 test).

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243

244 4.2. Response of plant growth to water availability

245 Water availability strongly influenced all the plant growth traits, i.e. biomass, leaf area and
 246 height (Table 1A and Supplementary Material Section E online). The response of all these traits
 247 to water availability varied with the plant species/stage (Table 1A). For all species \times stage
 248 combinations, plant leaf area was the most responsive variable (Table 1B).

249

250 **Table 1: Effects of water availability and species/stage on plant growth traits. A.** Partial R^2
 251 (calculated from the type III sum of square of Anova function of R) indicates the proportion of
 252 variance explained by each factor for each trait. **B.** Variation factor (calculated as the ratio of
 253 the maximum to minimum value) shows the variability for each trait and each species/stage.
 254 FTSW for fraction of transpirable soil water. *** for $P < 0.001$

255

Plant growth traits	Total biomass	Aboveground biomass	Leaf biomass	Root biomass	Leaf area	Height
A. Partial R^2						
FTSW	0.393***	0.374***	0.459***	0.448***	0.482***	0.480***
Species/stage	0.374***	0.378***	0.329***	0.351***	0.343***	0.308***
Interaction	0.212***	0.229***	0.182***	0.141***	0.150***	0.111***

Total R²	0.980	0.982	0.970	0.940	0.974	0.899
B. Variation factors for each species/stage						
<i>Abutilon theophrasti</i> vegetative	7.2	8.0	7.8	5.8	14.9	3.2
<i>Abutilon theophrasti</i> reproductive	15.1	18.4	12.3	9.8	23.0	5.9
<i>Alopecurus myosuroides</i> vegetative	4.9	4.9	4.8	4.9	12.9	2.6
<i>Amaranthus hybridus</i> reproductive	4.9	5.4	5.7	4.0	11.0	5.6

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4.3. Response of plant morphology to water availability

The four studied morphological traits varied with soil water availability and, for all of them, the response to water availability varied with the plant species/stage (Table 2A). Height to biomass ratio HBR and specific leaf area SLA were the traits that responded the most to soil-water availability for each species /stage (Table 2B).

Table 2: Effects of water availability and species/stage on morphological traits. A. Partial R² (calculated from the type III sum of square of Anova function of R) indicates the proportion of variance explained by each factor for each trait. **B.** Variation factor (calculated as the ratio of the maximum to minimum value) shows the variability for each trait and each species/stage. FTSW for fraction of transpirable soil water. As the specific leaf area shows a two-phase response pattern, the analysis was performed separately for FTSW values lower vs. higher than breakpoint (i.e. FTSW at which slope value changes). Grey cells indicate when FTSW had non-significant effects on the morphological trait. HBR was log_n-transformed for statistical analysis. ns for P>0.05; ** for P<0.01; *** for P<0.001.

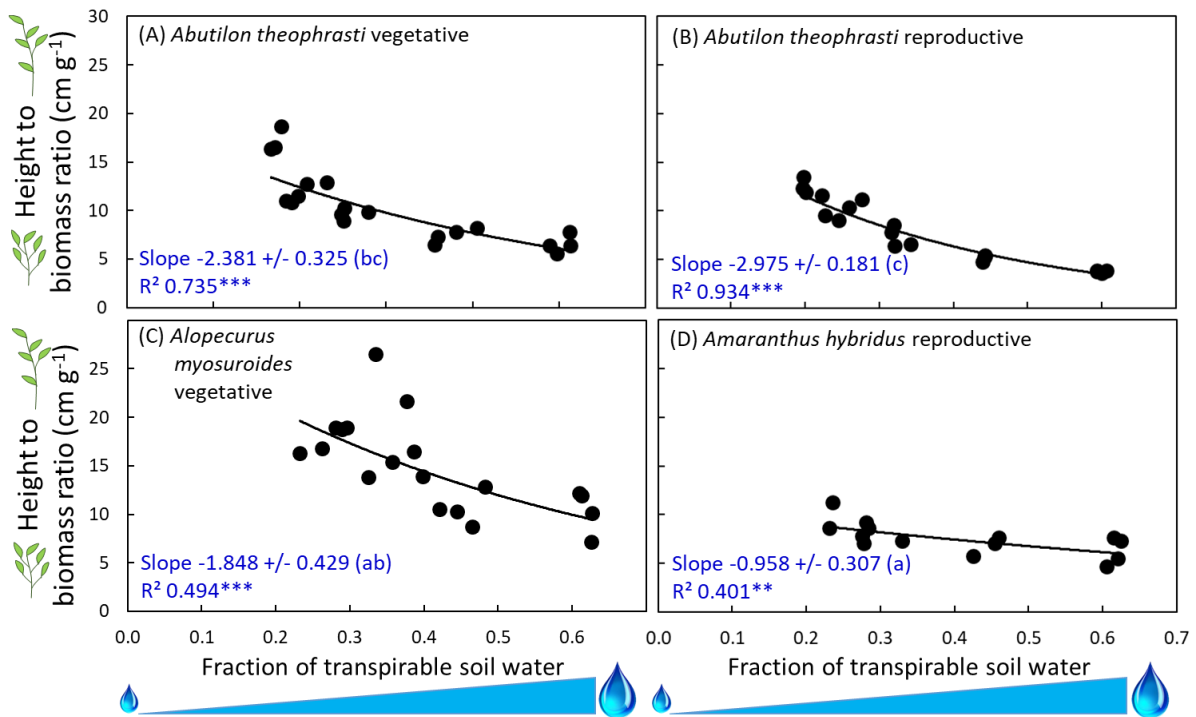
Morphological traits	Leaf to aboveground biomass ratio LBR	Height to biomass ratio HBR	Root to total plant biomass ratio RBR	Specific leaf area SLA	
				For FTSW >breakpoint	For FTSW <breakpoint
A. Partial R²					
FTSW	0.05**	0.32***	0.13***	<0.01ns	0.22***
Species/stage	0.40***	0.48***	0.38***	0.47***	0.28***
Interaction	0.12***	0.05***	0.10**	0.10ns	0.21**
Total R²	0.57	0.85	0.61	0.57	0.72
B. Variation factors for each species/stage					
<i>Abutilon theophrasti</i> vegetative	1.17	3.37	1.37	2.21	
<i>Abutilon theophrasti</i> reproductive	1.64	3.75	1.87	1.97	

<i>Alopecurus myosuroides</i> vegetative	1.33	3.69	1.71	3.42
<i>Amaranthus hybridus</i> reproductive	1.54	2.40	1.72	2.48

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4.3.1. Height to biomass ratio

278 For each species × stage combination, height to biomass ratio HBR increased exponentially
279 with decreasing soil water availability (Figure 3). In response to water limitation, both
280 aboveground biomass and plant height decreased, but the effect was larger for aboveground
281 biomass than for plant height (Table 1; Supplementary Material Section E online). *A.*
282 *theophrasti* was the most responsive species, followed by *A. myosuroides* and *A. hybridus* (see
283 slope values on Figure 3). For *A. theophrasti* (the only species with data at both vegetative and
284 reproductive stages), the phenological stage did not significantly affect the response slope.



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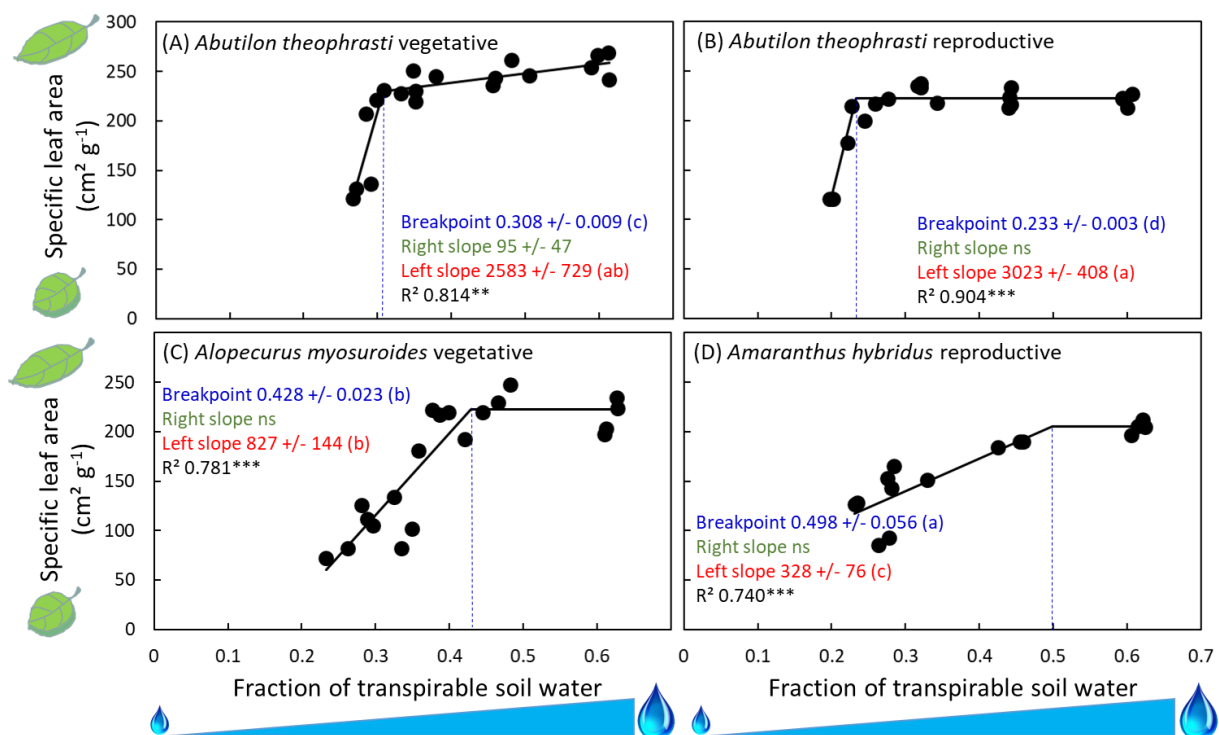
Figure 3: Response of height to biomass ratio (log_n-transformed) to soil-water availability (fraction of transpirable soil water) for each species × stage combination. The slope of the relationships (+/- standard error) and R² are shown (** for P<0.01 and *** for P<0.001). Slopes with the same letter show non-significant differences. Each symbol represents one plant.

4.3.2. Specific leaf area

292 Contrary to height to biomass ratio, specific leaf area SLA decreased with decreasing soil water
293 availability (Figure 4), meaning that plants produced smaller and thicker leaves in response to

294 water limitation. This was due to a stronger effect of water deficit on leaf area than on leaf
 295 biomass (Table 1; Supplementary Material Section E online). Broken lines were used to account
 296 for the two-phase response pattern of SLA to FTSW, providing three parameters on which the
 297 four plant species \times stage combinations were compared: breakpoint (i.e. FTSW at which slope
 298 value changes) and left and right slopes (i.e. slope of the regression when FTSW is lower and
 299 higher, respectively than breakpoint value)(Section 3.4). The SLA was constant during the first
 300 phase for three out of the four combinations (right slope on Figure 4). For *A. theophrasti* at the
 301 vegetative stage only, SLA decreased slightly with decreasing soil water availability. Soil water
 302 level from which SLA started to decrease sharply and the intensity of this SLA decrease
 303 (determined by the breakpoint and the left slope, respectively, on Figure 4) were used to
 304 discriminate species. As the breakpoint and the left slope were negatively correlated ($r=-0.99$;
 305 $P=0.012$; $n=4$), two contrasted patterns were identified. On the one hand, *A. theophrasti* at the
 306 reproductive stage maintained its SLA constant (non-significant right slope) until a FTSW value
 307 as low as 0.23, but below this threshold, SLA dropped very sharply (high left slope value). On
 308 the other hand, *A. hybridus* with SLA starting to decrease while soil water availability was much
 309 higher (FTSW at 0.50) but, below this threshold, SLA decrease was less steep (low left slope
 310 value).

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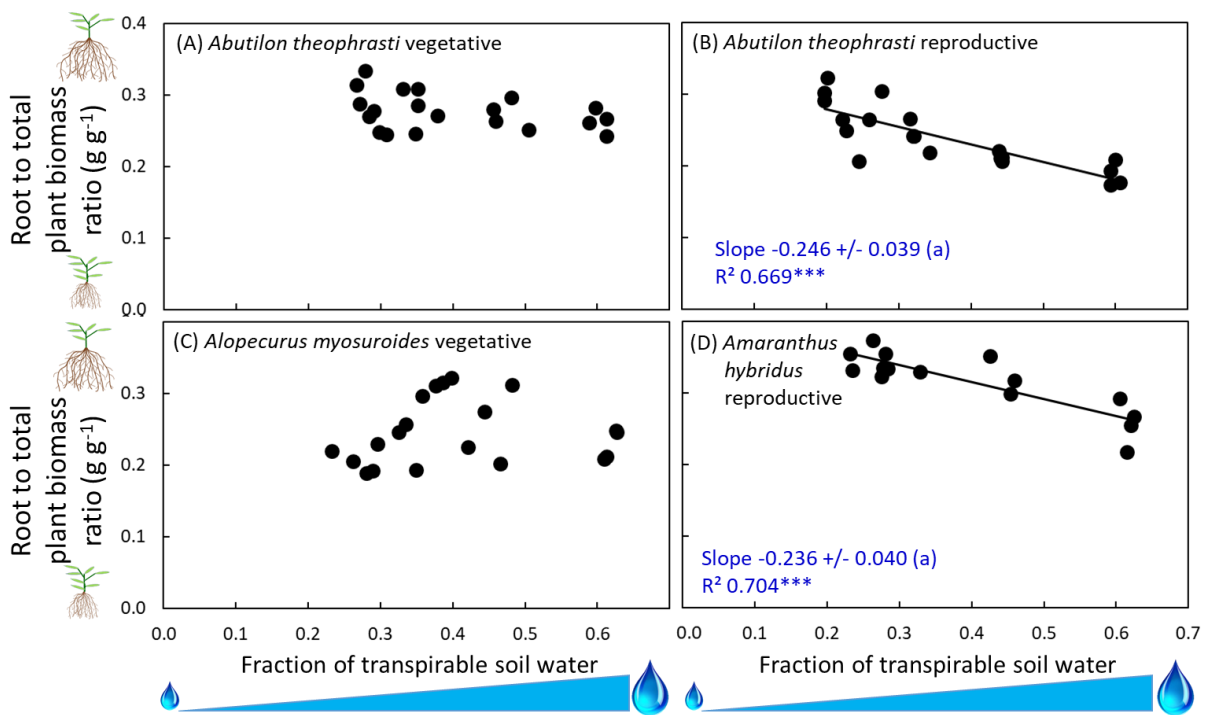
312
 313 **Figure 4: Response of specific leaf area to soil-water availability (fraction of transpirable**
 314 **soil water) for each species/stage combination. The slopes and breakpoint of the relationships**

315 (+/- standard error) and R^2 (** for $P < 0.01$ and *** for $P < 0.001$) are shown. Values with the
 316 same letter show non-significant differences. Each symbol represents one plant.

317
 318 **4.3.3. Root to total plant biomass ratio**

319 For two out of the four combinations of species \times stage (*A. theophrasti* at the vegetative stage
 320 and *A. myosuroides*), root to total plant biomass ratio RBR was independent of soil water
 321 availability (average value at 0.25 g g^{-1} on Figure 5). Only for *A. hybridus* and *A. theophrasti*
 322 at the reproductive stage, RBR increased linearly with increasing soil water limitation. This
 323 indicated that proportionally more biomass was invested to root vs. aboveground plant parts in
 324 response to water limitation. The intensity of this RBR increase (reflected by the slopes on
 325 Figure 5) was similar for both species.

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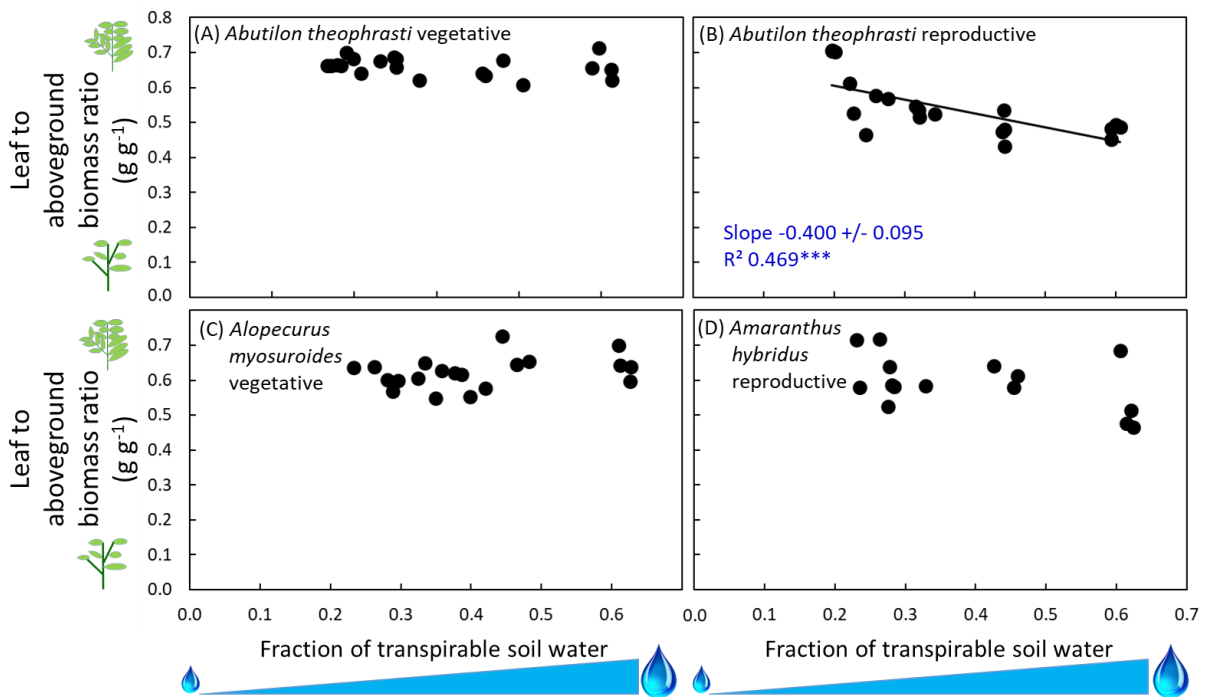
327
 328 **Figure 5: Response of root to total plant biomass ratio to soil-water availability (fraction**
 329 **of transpirable soil water) for each species/stage combination.** The slopes (+/- standard
 330 error) and R^2 (***) for $P < 0.001$) are shown when significant. Values with the same letter show
 331 non-significant differences. Each symbol represents one plant.

332
 333 **4.3.4. Leaf to aboveground biomass ratio**

334 Leaf to aboveground biomass ratio LBR (i.e. ratio of leaf to aboveground biomass) was
 335 independent of soil water availability in most situations (Figure 6). Only for *A. theophrasti* at
 336 the reproductive stage, LBR increased in response to water limitation, meaning that

337 proportionally more biomass was invested to leaf vs. stem and reproductive organs in response
338 to water limitation.

339



340

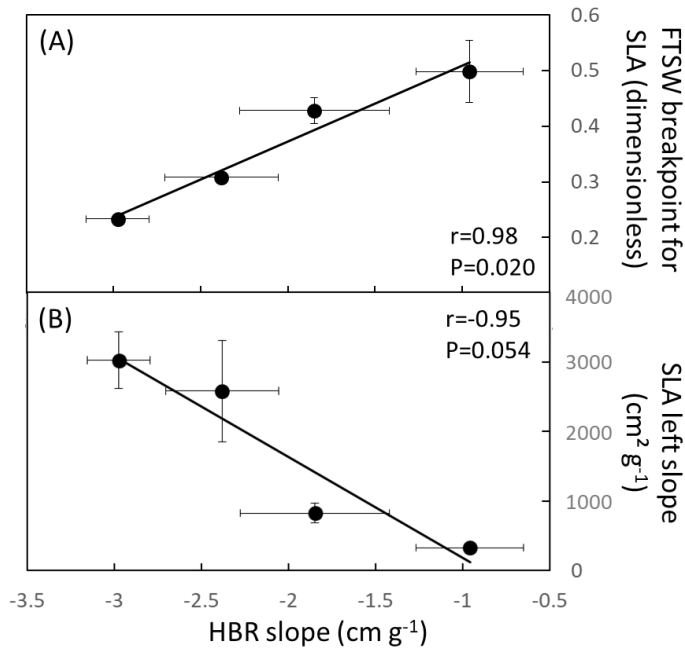
341 **Figure 6: Response of leaf to biomass ratio to soil-water availability (fraction of**
342 **transpirable soil water) for each species/stage combination. The slope (+/- standard error)**
343 **and R² (***) for P<0.001) are shown when significant. Each symbol represents one plant.**

344

345 4.3.5. Correlations among morphological parameters

346 To identify potential synergies/antagonisms among processes involved in plant morphological
347 response to water limitation, correlations among parameters were analyzed. We focused on the
348 three parameters for which we had values for the four species × stage combinations (SLA
349 breakpoint, SLA left slope and HBR slope). Interestingly, the more height to biomass ratio
350 increased in response to water limitation (low HBR slope), the more they were able to maintain
351 high SLA even at low FTSW (low SLA breakpoint), and the stronger the decrease of SLA to
352 water limitation (high SLA left slope) (Figure 7).

353



354

355 **Figure 7: Correlation between the slope of the response of height to biomass ratio (HBR)**
 356 **to soil-water availability (FTSW) and (A) the specific leaf area (SLA) breakpoint and (B)**
 357 **the left slope of the response of SLA to soil-water availability.** The parameter values (+/
 358 standard error) come from Figure 3 (for height to biomass ratio) and Figure 4 (for specific leaf
 359 area). Each symbol represents a species × stage combination.

360

361 5. Discussion

362 5.1. An efficient methodology to analyse the diversity of weed response to water availability

363 The response of weed species to water stress has rarely been studied. Here, we used an
 364 innovative approach by (1) focusing on morphological traits previously identified in a
 365 simulation study as playing a key role in light competition between arable crops and annual
 366 weeds (Colbach et al., 2019), and (2) growing weed species on an experimental platform
 367 allowing automatic and precise plant watering as well as quantification of soil water availability
 368 in each individual pot. Only Jeudy et al. (2016) used such a platform, that they combined with
 369 high-throughput phenotyping, in order to compare root distribution among species including
 370 both crop and weed species, in response to soil-nitrogen availability. The present study is the
 371 first one using an automated watering platform to quantify the response of weed species to soil
 372 water availability. The possibility of this platform (1) to automatically weight and water each
 373 pot individually with a high precision and several times a day, and (2) to quantify daily soil
 374 water availability in each individual pot was crucial. In most previous studies, the response of
 375 weed species to different water regimes was based on manual watering. For example, in some

376 studies a constant volume of water was supplied daily (Monaco et al., 2005). Moreover, in these
377 studies, water availability in each individual pot was not quantified. As a consequence, water
378 treatments were most often characterized qualitatively (for example, referring to ‘full’ vs.
379 ‘medium’ vs. ‘low’ water in Zhang and Wen (2009) or to the target proportion of water in pot
380 in Chahal et al. (2018)). Yet, our study shows that a given water treatment may result in different
381 amounts of soil water availability (described here by the fraction of transpirable soil water,
382 FTSW) depending on plant species/stage or sampling date. Moreover, FTSW values may
383 diverge from target proportion of water in pot. Finally, such platforms make it easier to water
384 pots several times a day, allowing a more constant soil water availability than with manual
385 watering (limiting pot watering to a maximum of once per day). Based on this innovative
386 approach, our study provided new insights on how competition for water and light may interact
387 in determining crop-weed dynamics in the field.

388

389 **5.2. Water availability strongly affected light competition traits**

390 All the studied morphological traits responded to water availability. For the best-documented
391 morphological traits, results agreed well with the literature. Decrease of specific leaf area in
392 response to water limitation is generally observed in annual plant species (Poorter et al., 2009)
393 including weeds (Monaco et al., 2005). This classical physiological adaptation in plants allows
394 them to decrease transpiring leaf area, thereby reducing plant water requirement under dry
395 conditions (Poorter et al., 2009).

396 Similarly, biomass allocation to roots vs. aboveground plant parts frequently increases with
397 water limitation, both in crop and in wild/weed species (Monaco et al., 2005; Acciaresi and
398 Guiamet, 2010; Eziz et al., 2017; Chahal et al., 2018). This phenomenon refers to the ‘functional
399 equilibrium’ or ‘optimal partitioning’ theories, considering that plants preferentially allocate
400 biomass to the compartment that acquires the most limiting resource (Brouwer, 1962). A
401 proportionally larger investment in root biomass in case of water limitation is often considered
402 as a way for plants to increase soil exploration and access to water (McCarthy and Enquist,
403 2007).

404 In our study, the preferential biomass allocation to [leaf] vs. [stem and reproductive organs] in
405 response to water limitation occurred for only *A. theophrasti* at the reproductive stage (not for
406 the other species/stages). Previous studies identified that the leaf to aboveground biomass ratio
407 either increased with or did not respond to water limitation (Lu et al., 2014; Chahal et al., 2018;
408 de Oliveira et al., 2018). Further studies with a larger number of plant species are needed to test

409 the importance of leaf to aboveground biomass ratio in the response of plant morphology to
410 water stress.

411 For height to biomass ratio, the scarcity of references in the literature made the comparison
412 difficult. As this trait is known to play a key role in competition for light, it is often analyzed in
413 response to light availability (Leishman and Westoby, 1994; Pakeman et al., 2015; Colbach et
414 al., 2020). We did not find any references quantifying its response to water limitation. The
415 observed increase of height to biomass ratio in response to water limitation can simply be
416 interpreted as the result a stronger impact of water limitation on aboveground biomass than on
417 plant height, without necessarily conducting to a physiological/competitive advantage for
418 plants.

419 Our study allowed ranking plant traits according to the magnitude of their response to water
420 limitation. Increased plant height per unit of aboveground biomass and production of
421 smaller/thicker leaves were the most noteworthy responses to water limitation. Not only these
422 phenomena occurred for all the studied plant species/stages, but also the magnitude of the
423 response of the corresponding morphological traits (height to biomass ratio and specific leaf
424 area, respectively) to water were the strongest. Conversely, the response of root to total plant
425 biomass ratio and leaf to aboveground biomass ratio to water limitation was significant for,
426 respectively, only two and one out of the four plant species \times stage combinations under study.
427 Moreover, the order of magnitude of the response of these morphological traits was lower than
428 for height to biomass ratio and specific leaf area. When focusing on the most documented traits
429 in the literature, our ranking results differed from Monaco et al. (2005) showing that root to
430 total plant biomass ratio was more responsive than specific leaf area. The focus of their study
431 on another weed species (*Isatis tinctoria*), other water treatments (50 vs. 100 mL of water
432 supply per day) and other environmental conditions (e.g. pot size, light intensity,
433 photoperiod...) probably explains these discrepancies, as reported by Poorter et al. (2012a) and
434 Poorter et al. (2012b).

435

436 **5.3. Species and stage-specificities**

437 Our study provides information regarding the interspecies variability of the morphological
438 response to water limitation in a few weed species. To avoid confounding effects with plant
439 stage and sampling date (and therefore duration of water limitation), the species effect could be
440 analyzed only by comparing *A. myosuroides* and *A. theophrasti* at the vegetative stage. Only
441 the response of specific leaf area SLA differed between species, with *A. theophrasti* maintaining

442 high SLA values even when soil water availability was low, which was not the case for *A.*
443 *myosuroides*.

444 The stage effect was analyzed by focusing on *A. theophrasti* (the only species studied at two
445 different stages). For this species, the phenological stage affected three out of the four
446 morphological traits. From the vegetative to the reproductive stage, specific leaf area became
447 less sensitive to water limitation, while root to total plant biomass ratio and leaf to aboveground
448 biomass ratio became sensitive to water limitation. Poorter et al. (2012c) hypothesized that this
449 delayed change of biomass allocation in response to water limitation could be a mechanism of
450 plant preservation. Indeed, they argued that changing biomass allocation too quickly might
451 result in a suboptimal growth after restoration of the water supply, as water availability often
452 depends on rain events that are unpredictable. Thus, in accordance with this hypothesis, our
453 results suggest that changes in biomass allocation would occur in the long term. Short-term
454 response to water limitation would primarily change plant height per unit of aboveground
455 biomass and specific leaf area.

456 To be noted that correlations among these short-term responses were identified, with plants
457 strongly increasing height per unit of aboveground biomass in response to water limitation
458 being able to maintain high specific leaf area, even at low soil water availability. Studies on
459 additional plant species would be necessary to confirm this interaction between morphological
460 changes.

461

462 **5.4. Disentangling the effects of nitrogen from those of water limitation**

463 In our experiment, plants were watered with a nutrient-rich solution in order to limit a possible
464 indirect effect of a nitrogen limitation that could be associated with a lower water supply.
465 Nonetheless, a nitrogen limitation cannot be excluded in our study (Supplementary Material
466 Section F online). A parallel study was conducted on *A. myosuroides* in order to analyse the
467 morphological response to nitrogen limitation, focusing on the same morphological traits
468 except root to total plant biomass ratio (Supplementary Material Section G online) (Perthame
469 et al., 2022). Height to biomass ratio was unresponsive to soil-nitrogen limitation in Perthame
470 et al. (2022), which contrasts with the strong response of this trait to water in the present study.
471 Moreover, leaf to aboveground biomass ratio decreased in response to nitrogen limitation in
472 Perthame et al. (2022), while this trait was unresponsive to water limitation in the present study.
473 Specific leaf area was the only trait responding in the same direction (i.e. decrease) to both
474 nitrogen and water limitation. However, the responsiveness was stronger to water than to
475 nitrogen. Moreover, the two-phase response pattern observed in the present study for water was

476 not identified when analysing the response to nitrogen. Thus, altogether these results strongly
477 suggest that, even if a nitrogen limitation cannot be totally excluded in our study, the water
478 effect was larger than a possible nitrogen effect. It is likely that the lower nitrogen supply in
479 treatments with a strong water limitation was sufficient to fulfil the lower nitrogen requirements
480 of water-stressed plants, thus limiting the putative confounding effects of water and nitrogen
481 deprivations.

482

483 **5.5. Practical implications**

484 In temperate and non-irrigated field conditions, water availability may vary, depending on
485 rainfall events. Given the strong influence of water on seed germination and emergence (Durr
486 et al., 2015), these events play a key role in determining which weed species emerge and when
487 in a given field during the cropping season. Situations of alternation among conditions of water
488 limitation also result in diverse crop-weed competition situations: either for water mainly, or
489 for light mainly under non-limiting water conditions (provided that nitrogen is not a limiting
490 factor). In this context, the strong effect identified in the present study of water limitation on
491 key morphological traits involved in competition for light, suggests that water
492 limitation/competition could affect light competition in the field. Consequences on crop-weed
493 communities could be expected.

494 Water limitation affects weed dynamics in the field (Souza et al., 2020). The present study
495 provides insight regarding the underlying mechanisms, with plant morphology possibly playing
496 a key role. Moreover, by showing species- and stage-specificities in the response of
497 morphological traits to water availability, our study provides explanations on why the
498 consequences of water limitation on crop-weed dynamics may depend on the starting date of
499 the water limitation, its intensity and its length, as well as on the weed species (that may respond
500 differently to water limitation). Our results also suggest that promoting weed ecological
501 regulation by competition requires taking into consideration competition not only for light but
502 also for water (Andrew et al., 2015), especially in areas with dry climates and/or subjected to
503 the context of climate change (Iglesias et al., 2012). However, the results from our comparative
504 ecology study are, as such, insufficient to identify management options that would be relevant
505 to regulate weeds in situations of water limitation. First, we studied only three weed species.
506 Second, interactions among traits should not be neglected. For example, plant species A with a
507 high ability to increase height to biomass ratio could be assumed to have a competitive
508 advantage over a neighboring plant species B with a lower ability. However, a better tolerance
509 of photosynthesis (per unit leaf area) to water stress of species B could counterbalance the

510 shading effect of species A. Third, many and diverse components interact in the agroecosystem
511 (e.g. management techniques, pedoclimate, biophysical processes, diversity of the weed flora,
512 long time-step resulting from the persistence of the weed seed bank in the soil).
513 Using a simulation model quantifying the effects of cropping systems on weed and crop
514 dynamics is essential to cope with this complexity. In particular, process-based models are
515 useful to synthesize existing knowledge, identify knowledge gaps, explore prospective
516 scenarios in different contexts in the long term, and design new cropping systems (Colbach,
517 2010; Renton and Chauhan, 2017). Among the existing models simulating weed dynamics
518 (Holst et al., 2007), FLORSYS is, to our knowledge, the only individual-based model quantifying
519 the effects of cropping systems on the dynamics of multispecies weed floras, in interaction with
520 pedoclimate (Colbach et al., 2014; Colbach et al., 2021). This model currently only considers
521 crop-weed competition for light (Munier-Jolain et al., 2013) and nitrogen (Moreau et al., 2021),
522 assuming that water resources are sufficient to sustain both crop and weed requirements. So,
523 using the approach developed in the present study, the next step will consist of investigating the
524 large diversity of response to water limitation among the numerous weed and crop species in
525 arable fields. Such information will be useful to (1) introduce competition for water into
526 FLORSYS, and (2) perform simulations with the new model version in order to identify
527 innovative weed management strategies that are both sustainable (e.g. low reliance on herbicide
528 use) and robust to climatic hazards (e.g. the weed management strategies are efficient even in
529 case of climatic hazards).

530

531 **6. Conclusions**

532 Weed response to water availability was analyzed using an original approach (1) focusing on
533 key species traits involved in competition for light that were derived from a mechanistic
534 simulation model and (2) using an experimental platform allowing automatic and precise
535 watering. Focusing on three weed species, this study allowed ranking traits according to their
536 responsiveness to water limitation and characterizing species- and stage-specificities in
537 responses. The strong effect of water limitation on key morphological traits involved in
538 competition for light suggests that water competition could strongly affect light competition in
539 the field, with consequences on crop-weed communities. In the near future, the methodological
540 approach presented here will be applied to the high-throughput characterization of the large
541 diversity of weed species. Knowledge gained from this approach will feed both comparative
542 ecology approaches on weed species and mechanistic simulation models that will be used to
543 better understand crop-weeds dynamics in different scenarios of water limitation.

544

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