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1 **The response of weed and crop species to shading. How to predict their morphology and**
2 **plasticity from species traits and ecological indexes?**

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36 21 **Highlights**

- 37
38 22 - 33 crop and 25 weed species were studied in various light availability conditions
39 23 - Potential plant morphology and shading response were measured on individual plants
40 24 - Ecophysiological parameters were linked to easily-measured species traits
41 25 - Ecological indicators of habitat preference (Ellenberg) were linked to parameters
42 26 - Shade response differed for legume vs non-legume, weed vs crop, C3 vs C4 species
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47 27 **Abstract**

48
49 28 To assess the competitive ability of plant species, ecologists describe many species from contrasting
50 29 habitats with traits that are proxies of ecophysiological functions whereas agronomists describe few
51 30 species from similar habitats with process-based parameters. Here, we combined both approaches and
52 31 compared many contrasting crop and weed species of temperate European arable crops in terms of
53 32 competition for light, to understand weed response to shading by crop canopies and to choose light-
54 33 competitive crop species and varieties. We (1) measured species parameters that drive light-
55 34 competition processes in 26 crop and 35 weed species of temperate European arable cropping systems,
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35 (2) related the parameter values to species features that are easier to measure or available in databases.
36 Early plant-growth parameters (relative growth rate RGR, initial leaf area) were measured in optimal
37 light and nutrient conditions in a greenhouse with automatic non-destructive measurements. Potential
38 plant morphology in unshaded conditions (specific leaf area SLA, leaf biomass ratio LBR, plant height
39 and width per unit biomass HM and WM, vertical leaf distribution) was measured in garden plots in
40 optimal light and nutrient conditions and harvested at 4-5 stages. Shading response was measured by
41 comparing potential morphology to that of plants grown under shading nets. We confirmed well-
42 known relationships (lower SLA and LBR in legumes vs non-legumes...), included new species
43 features (base temperature, photosynthetic pathway...), and established relationships for the new
44 shading-response parameters (weeds respond more to shade than crops, by increasing LBR, SLA, HM
45 and WM...). Some correlations reported in ecology (RGR vs SLA...) were not verified on our species
46 pool from arable temperate fields. Shade-response parameters explained species responses to habitat
47 described by Ellenberg indexes, e.g., when shaded, shade-loving species (low Ellenberg-L values)
48 increased SLA and HM to increase light interception.

49
50 **Keywords.** Functional trait; comparative ecology; morphological plasticity; ecophysiology; FLORSYS;
51 photosynthetically active radiation PAR; plant architecture

52 53 54 **1 Introduction**

55 Herbicide use must be reduced due to environmental and health issues (Waggoner *et al.*, 2013; Duke,
56 2020), which led to national and European legislation limiting herbicide use intensity (e.g., the
57 Ecophyto plan in France, <https://agriculture.gouv.fr/ecophyto>) and available molecules (e.g., the EU
58 Reach directive EC 1907/2006). This makes it more difficult to control weeds, which are by far the
59 main pest in organic farming compared with conventional farming (Muneret *et al.*, 2018). Crops are
60 thus more often confronted to competition with weeds. In temperate climates with high-input crop
61 management (especially high nitrogen fertilizers and irrigation when needed), light is generally the
62 main resource for which crop and weed plants compete (Wilson and Tilman, 1993; Perry *et al.*, 2003;
63 Munier-Jolain *et al.*, 2013). So, choosing light-competitive crop species and varieties is a major lever
64 for non-chemical weed management (Jha *et al.*, 2017; van der Meulen and Chauhan, 2017).

65 Regarding plant-plant competition for light, three main processes are crucial to determine the
66 competitive ability of plant species, once they have emerged: how fast they occupy empty space in the
67 field, how much space they occupy, and how they avoid or adapt to shade. Depending on the scientific
68 discipline, this contest has been investigated differently. Ecological studies investigate large ranges of
69 species, covering habitats as diverse as cold tundras and hot tropics, using species traits that are
70 proxies of ecophysiological functions (e.g. specific leaf area as a proxy of photosynthesis, Poorter and

71 Garnier, 2007). With these traits, plant species can be positioned along gradients of ecological trade-
72 offs (e.g. leaf economic spectrum, Wright *et al.*, 2004) and their competitive ability better understood.
73 As these traits are often easier to measure than the ecophysiological functions themselves, they can be
74 used to characterize a large number of species. Using these proxies instead of measuring the actual
75 functions is, however, only acceptable if valid hypotheses can be established regarding the link of the
76 traits with the estimated ecophysiological functions.

77 Conversely, agronomic studies develop process-based models for a small number of species to
78 describe in detail how crop canopies or even single plants within these canopies intercept, absorb and
79 use light. These mechanistic models consist of equations and other mathematical formalisms including
80 parameters with a biological meaning. As these parameters are closer to the studied processes, they
81 often reflect intrinsic properties of plant species (Tardieu, 2003; Tardieu and Tuberosa, 2010) and are
82 therefore ideal to compare plant species. However, their measurement is often expensive and time-
83 consuming, making it impossible to simultaneously characterize a large number of species.

84 In the present paper, the objective was to combine both approaches and to compare a large range of
85 contrasting crop and weed species of temperate European arable crops in terms of the main
86 competitive process of this environment, i.e. competition for light, to understand weed response to
87 shading by crop canopies and to choose light-competitive crop species and varieties. To do so, we
88 (1) measured and analysed the diversity of detailed species parameters that drive processes related to
89 competition for light, (2) determined species functional groups in terms of light-competition
90 parameters, (3) related the parameter values which are difficult to measure to species features that are
91 easier to access (i.e. easier to measure or referenced in existing databases), which makes it easier in the
92 future to characterize more species. These steps constitute a framework to simplify the assessment of
93 new species for their competitive ability for light. Using parameters based on a mechanistic modelling
94 approach rather than directly measured variables (whose value is strongly influenced by environment
95 conditions) is essential to disentangle the correlated effects of sun light on biomass production from
96 that of shade on plant morphology adaptation; it allows characterising and comparing species,
97 irrespective of the experimental conditions, and establish generic functional rules extrapolable to other
98 situations (Granier *et al.*, 2002; Moreau *et al.*, 2017). Ultimately, these parameters will allow to model
99 plant morphology and plasticity in multispecies canopies. In a companion paper, we investigated
100 which species parameters are linked to the weed impact on crop production and biodiversity (Colbach
101 *et al.*, 2019).

102 Here, parameters are components of equations driving processes as a function of environmental
103 conditions and are independent of the environment. They have biological meaning and can be either
104 measured on plants in a given environment (e.g. initial leaf area after emergence) or estimated by
105 fitting an equation to data measured in different environments (e.g. change of specific leaf area SLA
106 with shading intensity). We chose parameters that discriminate species for their ability to compete for
107 light, relatively to the three main processes mentioned above. These processes concern initial growth

108 which determines how fast plants occupy space, potential morphology which determines how much
109 space plants occupy, and response to shading. These parameters were derived from a 3-dimensional
110 individual-based modelling approach used to simulate competition for light in crop-weed canopies in
111 the weed dynamics model FLORSYS (Munier-Jolain *et al.*, 2013; Munier-Jolain *et al.*, 2014) (Table 1).
112 Munier-Jolain's method has the major advantage to separate the effect of radiation on biomass
113 accumulation from that of shading response by working on relative changes.
114 Linking parameters to species traits and other features assumes that inter-species variability is higher
115 than intra-species variability (Roche *et al.*, 2004). Species features consisted here of (1) species
116 taxonomy, i.e. clade; (2) species traits according to Violle (2007), related to seeds, leaves as well as
117 plant lifespan, (3) qualitative species traits referring to plant development and growth, i.e. plant growth
118 form, hypogeal vs epigeal growth, photosynthetic pathway, and ability to symbiotically fix dinitrogen,
119 and (4) ecological habitat preferences, described by Ellenberg indexes. These were chosen based on
120 hypotheses on their links with ecophysiological functions, either based on previous observations, or on
121 analogies and deductions based on these same observations (Table 2).

122 **2 Material and methods**

123 **2.1 Principle**

124 Parameters driving initial growth (initial leaf area, relative growth rate RGR) were measured in
125 optimal light and nutrient conditions in a greenhouse with automatic non-destructive measurements.
126 Potential morphology parameters describing morphology in unshaded conditions were measured on
127 individual plants grown in garden plots and harvested at 4-5 stages during plant cycle in optimal light
128 and nutrient conditions. Plants were sufficiently distanced to avoid any competition, whether for light,
129 nutrients or water. Shading response parameters were measured by comparing potential morphology to
130 that of plants grown under shading nets in these same gardens. The nets made it possible to know the
131 exact shade experienced by each target plant, and their shade was assumed to have the same effect as
132 shade due to neighbour plants.

133 Species traits and other features were either measured during the experiments (e.g. seed weight), taken
134 from previous experiments or databases (e.g. seed lipid content) or based on expert opinion (e.g. plant
135 form). The functional relationships between species parameters and species features were established
136 with linear models of species parameter values as a function of features or other parameters. The tested
137 correlations were based on biological hypotheses (e.g. leaf distribution depends on plant form) and
138 results from literature (Table 2). For instance, we assumed that short-living plants grew faster and had
139 a larger initial leaf area, analogically to faster growth and larger leaf biomass ratio (e.g., ratio of leaf
140 biomass to total or above-ground plant biomass) in short-living leaves (Reich *et al.*, 1997; Garnier and
141 Navas, 2012; Reich, 2014). Similarly, we assumed that initial plant leaf area (instead of initial plant
142 biomass) increased with seed mass because heavier seeds include more reserves and/or a larger

embryo (Fayaud *et al.*, 2014), or that initial leaf area and relative growth rate could increase with seed lipid content as this type of reserve stores more energy (Lüttge, 2013).

2.2 Plant material

35 weed species and 26 crop species from temperate European arable cropping systems were investigated in the present study (Appendix 1 and Appendix 2). Both crop and weed species were chosen to be frequent but contrasting in terms of species features. Sixteen species were tested in two different years, with several seasons per year for five of these (section B.4 online). For wheat, pea and faba bean, two or three varieties were investigated. Species were chosen to be contrasting in terms of clade, emergence or sowing period, length of life cycle and plant structure. Crop species included both cash crops and cover crops.

Weed seeds originated from our in-house seed collection if available, or were bought from Herbiseed (Twyford, UK) at the few occasions where the collection could not provide seeds for the experiment (section A.1 in supplementary material online). Crop seeds of commercial varieties were bought from the local cooperative, and from the in-house variety collection for varieties that were selected by the INRA Dijon genetists' team. Between seed harvest and the experiments, seeds were stored in a cold and dry room. Prior to the experiment, eight samples of 100 randomly chosen seeds were dried for 48 hours at 80°C and weighted to determine seed mass for each species or variety.

2.3 Early growth

2.3.1 Experimental conditions

The experiment was conducted in an unheated greenhouse at Dijon, Burgundy, France (47°19'2.624"N, 5°4'26.883"E, 257m asl) without artificial light. Several series of experiments with 8 to 12 species were carried out, from 2009 to 2012, each lasting for three to four weeks. As far as possible, species were tested during their usual emergence season, i.e. winter species in autumn, spring species in spring and summer species in early summer. Temperature was recorded every 20 minutes with PT100 (ARIA) sensors. Seeds were put onto filter paper inside watered Petri dishes inside growth chambers at optimal temperature and light conditions (details in section A.4 online). Once germinated, seeds were planted 2 cm deep in pots (13 cm x 13 cm x 13 cm) filled with dry potting soil (NFU 44-551 consisting of peat, wood fibers and clay, with 1.2 kg/m³ of 14-16-18 NPK fertilizer and pH 6.5) over clay pebbles, with one plant per plot. For each species or variety, 20 pots were prepared. The greenhouse was equipped with an automatic conveyor belt which moved the pots continuously to provide the most similar thermal and light conditions to all plants.

2.3.2 Measurements and statistics

The conveyor belt weighted and photographed the pots daily. Water was added daily when needed to keep pots at 2.3 g water/g dry soil. Two pictures were taken from above of each plant twice a day to estimate leaf area. Two control pots without plants were added, each with a 10 cm by 10 cm green cardboard placed horizontally, which was used as a standard to calibrate the images during analysis. Leaf area was estimated from the pictures using Visilog® (Noésis).

Every week after plant emergence, five pots were randomly sampled per species or variety and the plants were taken out to calibrate leaf area values estimated from the images. The height and width of each plant was measured with a ruler, leaf area was measured with a leaf area meter (LI-3100 Area Meter; Li-Cor, Lincoln, NE, USA) and biomass weighted after plants were dried for 48 hours at 80°C. Three weeks after emergence, the remaining 10 plants were similarly measured and weighted. The leaf area measured with the leaf area meter was used to correct the values estimated with image analysis to take account of overlapping leaves that images would not detect (further details in section [B.1.1](#) online).

For the ten plants monitored throughout the experiment, a linear regression was fitted to the \log_n -transformed leaf area LA_p (cm²) vs thermal time TT_p (°C days, with species-dependent base temperatures) since plant emergence for each plant p using the `lm()` function of R (R Core Team, 2016). The slope of this regression is the relative growth rate RGR_p (cm² cm⁻² °C⁻¹ days⁻¹) and the constant is the \log_n -transformed leaf area at emergence $LA0_p$ (cm²) (Storkey, 2004):

$$[1] \quad \log_n(LA_p) = RGR_p \cdot TT_p + \log_n(LA0_p)$$

Using thermal time rather than the number of days (as did Grime and Hunt, 1975) produces an RGR independent of growing conditions and is essential to compare species with different thermal requirements (see for instance Granier *et al.*, 2002 for the advantages of thermal time). Measurements taken after the end of the initial exponential growth period were discarded (further details in section [B.1.2](#) online). The parameter values for the species or variety were the average over all those pots for which the R^2 of the previous linear regression exceeded 0.66 and weighted by the inverse of the relative standard-error of each pot (i.e. $se_LA0_p/LA0_p$ and se_RGR_p/RGR_p , with se_LA0_p and se_RGR_p the standard-errors estimated when fitting equation [1]).

Sixteen species were tested in different seasons and years, with 2-5 dates per species (section [A.1](#) online). An analysis of variance was run on $LA0_p$ and RGR_p , with species and month/year nested within species as factors using `lm()`, followed by a comparison of means according to Tukey of month/year per species, using `lsmeans()` and `cld()` (section [B.4](#) online).

2.4 Potential plant morphology and response to shading

The experimental and computational approaches were developed by Munier-Jolain et al (2014) who analysed plant morphology in five contrasting shading conditions over time. Here, we simplified and adapted the method to worked with only two shading conditions (unshaded and highly shaded).

2.4.1 Experimental conditions

The second series of experiments was carried out in garden plots at INRA Dijon from 2009 to 2016. The soil was 0.33 g/g clay, 0.49 g/g silt, and 0.17 g/g sand, with pH=8.3 and 0.31 g/g organic matter. The area was divided into four blocks. The soil was covered with a permeable opaque plastic sheet to avoid emergence of plants other than those sown for the experiment. A 3-m-high metallic cage was erected over half the area of all the blocks, and covered with a shading net to intercept at least 60% of the incident photosynthetically active radiation (PAR). Outside, only the area unshaded by the cage was used for the experiment. Temperature was measured with Testo sensors (175-T1) placed 1 m above ground and protected from the sun, with two sensors inside and two outside the cage. Incident PAR was measured every 10 minutes with quantum sensors (silicium sensors; Solems, Palaiseau, France) at 60, 90 and 110 cm above soil surface inside and outside the shading cage. The shading index inside the cage was calculated as 1 – the slope of a linear regression fitted to incident PAR inside vs. outside the cage during the experiment (details in section D.1.5 online). Shading index was 0.82 in the 2010 and 2012 experiments, 0.60-0.61 in the other experiments. Section 2.4.3 explains how this index was used to estimate comparable shading response parameters. For each species or variety, seeds were sown into 4 x 4 x 4 cm peat clods (Jiffy pastilles, Puteaux SA) inside plastic seedling trays, preparing 100 clods with 2-3 seeds per clod. The clods were watered and put into lightened growth chambers at 4°C for those species that needed to be vernalized, or directly into an unheated greenhouse without artificial light. Plant stage was monitored on the BBCH scale, i.e. a generic scale applying to both mono and dicotyledonous weed species to identify their growth stages (Hess *et al.*, 1997). Once seedlings had reached the 2-leaf stage (stage 2 on the BBCH scale), superfluous plants were eliminated to keep only one plant per clod, and clods were transplanted into the garden plots. Half of the plants (at least 16, if possible 32) were placed inside the shaded cage, and the remaining outside, in the unshaded area. Plants were placed inside holes in the plastic sheet, with at least 50 cm between plants to avoid shading and root interference. In each experimental series, up to 10 species or varieties were tested simultaneously, with at least one plant in each block of each light treatment. In case of climbing or twining species, a circular meshed trellis was set up for each plant. The plots were regularly hand-weeded, and watered if necessary. To avoid N stress, 50 kg N/ha were added at the end of winter during the years the experiments were conducted.

244 **2.4.2 Measurements**

245 For each species or variety, four to eight plants were sampled before transplanting, and then for each
246 light treatment at five sampling dates, i.e. 2 leaves, 4 leaves, 8 leaves for dicots or tillering for
247 monocots, flowering onset and flowering end. Sampling dates in unshaded and shaded conditions
248 could differ, because of lower temperature and light conditions inside the shading cage.

249 A lateral picture of each sampled plant was taken with a Canon EOS 450D and analysed with Matlab
250 scripts to determine the distribution of leaf area vs relative plant height. Then, plant height and width,
251 leaf area and biomass were measured. For the latter two, leaves (including petioles), stems and
252 reproductive parts were discriminated.

254 **2.4.3 The parameters of plant morphology and shading response**

255 The parameters for characterizing plant morphology and response to shading (Table 1.B and C) were
256 derived from Munier-Jolain et al (2014) and were calculated for each sampling date of the garden-plot
257 experiment as well as for one measurement of the initial-growth experiment (\sim BBCH = 0). As the
258 latter worked with unshaded conditions, shading response was not assessed.

259 Four parameters assess the species efficiency in producing leaf area, leaf biomass, plant height and
260 plant width in unshaded conditions, i.e. specific leaf area (SLA₀), leaf biomass ratio (LBR₀), specific
261 plant height (HM₀) and specific plant width (WM₀). Two other parameters (b_{HM} and b_{WM})
262 evaluate how far plant height and width depend on plant biomass, ranging from 0 (height and width
263 are constant) to 1 (height and width increase linearly with plant biomass). Two further parameters
264 assess leaf area distribution along plant height, with high RLH₀ values indicating top-heavy plants and
265 high b_{RLH} values indicate that leaves are grouped together instead of distributed along the whole
266 plant height. Five other parameters evaluate the species response to shading, positive values indicating
267 that shaded plants increase their specific leaf area, leaf biomass ratio, plant height and width per unit
268 biomass (SLA_{mu}, LBR_{mu}, HM_{mu}, WM_{mu}, respectively) and shift their leaves towards
269 (RLH_{mu}).

271 **2.4.4 Calculating parameters**

272 For each stage, species (or variety) and morphological variable, a non-linear equation based on
273 Munier-Jolain et al (2014) was fitted to each variable v (e.g. specific leaf area SLA) measured on all
274 shaded and unshaded plants vs the shading index SI (MJ/MJ):

$$275 \text{ eq. 1. } v = v_0 \cdot \exp(v_{\mu} \cdot SI)$$

276 where v_0 was the potential plant morphology in unshaded conditions and v_{μ} the shading response.
277 The shading index was 0 in unshaded conditions and corresponded to the ratio of the PAR measured
278 inside to that outside the shaded cage (usually approximately 0.60). In the example of the specific leaf
279 area SLA, a positive SLA_{mu} value indicates that plants increase their specific leaf area when shaded

280 by reducing leaf thickness. The v_0 values can also be calculated directly as the average over the four
281 (or more) plants sampled in unshaded conditions, which makes their estimation less dependent on
282 shading conditions but reduces the number of plant samples.

283 The equation for determining the parameters related to plant height and width was somewhat more
284 complicated. Specific plant height HM depends on the plant height H, the total above-ground biomass
285 BM and the shape parameter b_{HM} :

$$\text{eq. 2.} \quad HM = H / BM^{b_{HM}}$$

287 To calculate all three parameters, HM_0 , b_{HM} and HM_{μ} , eq. 1 was modified as follows:

$$\text{eq. 3.} \quad H = HM_0 \cdot \exp(v_{HM} \cdot SI) \cdot BM^{b_{HM}}$$

289 This equation was fitted to plant height H vs shading index SI and plant biomass BM, using data of
290 both shaded and unshaded plants. To make HM_0 less dependent on shading conditions, it was
291 recalculated as the average of HM over all unshaded plants, using the b_{HM} value estimated with eq.
292 3. The same principle was used for b_{WM} , WM_{μ} and WM_0 .

293 The last two variables, median leaf area height RLH and leaf distribution b_{RLH} were not measured
294 directly on individual plants, but estimated by fitting an S-shaped non-linear regression to the relative
295 cumulated leaf area RCLA ($\text{cm}^2 \cdot \text{cm}^{-2}$) vs relative plant height rh ($\text{cm} \cdot \text{cm}^{-1}$) (Munier-Jolain *et al.*,
296 2014):

$$\text{eq. 4.} \quad RCLA = \frac{1 - RLH^{b_{RLH}}}{1 - 2 \cdot RLH^{b_{RLH}}} \cdot \left(1 - \frac{1}{1 + \left(\frac{1}{RLH^{b_{RLH}} - 2} \right) \cdot rh^{b_{RLH}}} \right)$$

298 RLH is the relative plant height ($\text{cm} \cdot \text{cm}^{-1}$) below which half of the plant's leaf area is located, and
299 b_{RLH} (dimensionless) is a shape parameter. Values close to 1 indicate a uniform leaf area
300 distribution, and larger values correspond to a leaf area concentrated around RLH. The RLH_0 and
301 b_{RLH} corresponding to leaf area distribution in unshaded conditions were calculated as the averages
302 over RLH and b_{RLH} estimated with eq. 4 over all unshaded plants. The shading response RLH_{μ}
303 was estimated by fitting eq. 1 to RLH from all plants vs shading intensity SI.

304 It was not possible to carry out measurements at exactly the same stages for all species because of
305 experimental constraints. Moreover, not all samplings could be carried out when plants were missing
306 because of predation or insufficient emergence. To make species comparable, parameters were
307 interpolated over plant stages, using the BBCH scale. Parameter values were then estimated for 11
308 stages (from BBCH 0 to 10) for each species using local non-parametric regressions (details in section
309 **D.3** online). This method has the advantage of not assuming any general shape of the relationship
310 between parameter and time.

311 Here, linear smoothing was used if there were less than six sampling dates, quadratic local polynomial
312 otherwise. Constraints were added, based on biological knowledge: shading response at plant
313 emergence (BBCH=0) was nil ($\mu = 0$), monocotyledonous plants consisted of only leaves at
314 emergence (LBR0 = 1), leaves of totally mature plants (BBCH=10) were dry (SLA0 = 0, LBR0 = 0)

315 and did not respond to shading (μ_{SLA} and $\mu_{LBR}=0$). Additional restrictions ensured that
1 316 parameter values were logical from a biological point of view. For instance, specific leaf area SLA
2 317 must be > 0 , leaf biomass ratio LBR must be in $[0, 1]$ etc. Predictions were also capped by minimum
3 318 and maximum measured values to avoid extremely small or large values in case of extrapolation for
4 319 late stages when only a few early stages were measured.

8 320 eq. 1 and eq. 3 were log-transformed before fitting with PROC REG of SAS. eq. 4 was fitted with
9 321 PROC NLIN. Non-parametric interpolation was carried out with PROC LOESS.

11 322

13 323 **2.5 Effects of species features on plant morphology and shading**

15 324 **response parameters**

17 325 The data from these two series of experiments as well as data from a field experiment estimating
18 326 morphology and plasticity parameters (Munier-Jolain *et al.*, 2014) were pooled in order to establish
19 327 functional relationships between parameters and species features (taxonomy, quantitative and
20 328 qualitative, traits, habitat indicators) that are easy to measure or can be found in literature and trait
21 329 databases (Appendix 3). The initial growth parameters (initial leaf area, relative growth rate) were
22 330 analysed as a function of 11 species features: seed mass and lipid content, clade (monocot or dicot),
23 331 emergence type (epigeal or hypogeal), legume vs. non-legume, C3 vs C4, crop vs. weed species, plant
24 332 lifespan and ecological habitat preferences. Lifespan data for weeds were taken from a database in the
25 333 decision support system DECID'Herb (Munier-Jolain *et al.*, 2005a); for crops, lifespan was estimated
26 334 from simulations with the crop model STICS (Brisson *et al.*, 1998) or based on expert opinion. For
27 335 annuals, we considered minimum and maximum plant lifespan durations. In addition, we
28 336 discriminated perennials from annuals with a short (strict spring and summer annuals), a long (strict
29 337 winter annuals) or an indeterminate lifespan (species that emerge in both autumn and spring). These
30 338 categories were useful for including interactions with quantitative features in the analyses. For habitat
31 339 preferences, we used base water potential and temperature for germination as indicators of
32 340 hydrothermal requirements, and three Ellenberg indicators (N, L, R) for nitrogen, light and pH habitat
33 341 preferences (Ellenberg, 1974; Ellenberg *et al.*, 1992). If the latter were missing, they were estimated
34 342 from other ecological indicators (details in section [A.3](#) online). Interactions between clade and
35 343 emergence type on one hand, seed weight on the other hand were also included.

36 344 For the analysis of the potential morphology and shading response parameters, further features (plant
37 345 growth form, distinguishing prostrate, erect, rosette and climbing or twining, section [A.2.1](#) online),
38 346 parameters (e.g. potential HM when analysing shading response HM_{μ}) as well as plant stage (in
39 347 BBCH scale, and distinguishing early, mid and late life) were added (Table 3). Interactions between
40 348 stage and plant growth form were also included. Features were chosen for their biological relevance to
41 349 the studied parameters (see introduction). When features supply similar information, precise

350 quantitative features were preferred (e.g. species base temperature was preferred to Ellenberg
1 351 preference index for temperature).

3 352 First, correlations among parameters were investigated with a Principal Component Analysis (PCA),
4 353 followed by a Ward ascendant hierarchy classification to cluster crop and weed species into functional
5 354 groups, using the PCA() and hclust() functions of the FactoMineR package of R. To identify which
6 355 species features were linked to parameters, the species features were projected onto the PCA axes.
7 356 Moreover, two-by-two correlations were analysed among parameters and features as well as between
8 357 parameters and features, using both Pearson correlation coefficients (cor() function of R) and linear
9 358 regressions (lm function of R).

10 359 Then, the effect of species features on parameters was analysed with linear models using PROC
11 360 GLMSELECT of SAS (version 9.4) which was developed to select from a very large number of
12 361 effects (Cohen, 2006) and has been successfully used in various disciplines (e.g., Van der Borghet *et*
13 362 *al.*, 2011). Features were removed sequentially (backward selection), by removing effects that at each
14 363 step produce the smallest value of the Schwarz Bayesian information criterion (SBC) statistic and
15 364 stopping when removing any effect increased the SBC statistic again. The final model was chosen
16 365 among the successive models as the one that yielded the lowest predicted residual sum of square with
17 366 cross validation. For potential plasticity and shading response, forward selection was used as
18 367 backward selection tended to produce over-fitted models. We moreover eliminated any feature whose
19 368 effect was not significant at $p=0.05$. Using a method including cross-validation leads to more robust
20 369 relationships and avoids fitting regressions that are based on a single extreme species behaviour. The
21 370 detailed results on all parameters can be found in supplementary material online (section [E.1](#)). Here,
22 371 only a few examples and a schematic summary were presented.

372 **3 Results**

373 First, we looked how the analysed parameters varied among species (section 3.1), whether they were
374 correlated (section 3.2) and how they differed between crop and weed species (section 3.3). Next, we
375 analysed which species features influenced parameters of initial growth (section 3.4), potential
376 morphology and shading response (section 3.5).

377 **3.1 Which parameters varied most among species?**

378 Initial leaf area LA0 varied more than a 100-fold, from 0.01 cm² for *Matricaria perforata* to 3.98 cm²
379 for *Pisum sativum* cv. Enduro (Table 1.A). It varied more among species than relative growth rate
380 RGR which varied from 0.0093 (*Pisum sativum* cv. Enduro) to 0.0592 cm²/cm²/°Cdays (*Zea mays*).

381 Plant width per unit biomass WM0 and, to a lesser degree, height per unit biomass HM0 were the
382 potential-morphology parameters for which species differed most over all stages (largest coefficient of
383 variation in Table 1.B). Conversely, species were more similar in terms of leaf biomass ratio (LBR0)
384 and leaf area distribution (RLH0).

385 Shading response varied the most among species for specific leaf area (i.e. SLA_{mu}) and height per
386 unit biomass (HM_{mu}) and the least for leaf biomass ratio (LBR_{mu}) (Table 1.C). Shaded plants
387 produced larger (and usually thinner) leaves (i.e. SLA_{mu} > 0), and increased both their height and
388 width per unit biomass (HM_{mu} and WM_{mu} > 0). Some species decreased their leaf biomass ratio
389 when shaded (e.g. *Brassica napus*, LBR_{mu}= -0.51 in average over all stages), others invested more
390 biomass into leaves (e.g. *Digitaria sanguinalis*, average RLH_{mu} = 0.28). Shading effect on leaf area
391 distribution also varied with the species: some shifted their leaves upwards (e.g. *Galium aparine*,
392 RLH_{mu} = 0.62 averaged over all stages), other moved them downwards (e.g. *Abutilon theophrasti*,
393 average RLH_{mu} = -0.54).

394 Parameters describing potential morphology and shading response also varied with plant age (Figure
395 1). In unshaded conditions, leaf biomass ratio LBR was the parameter that changed the most during
396 plant life (Figure 1.C), decreasing from 1 (i.e. plants consisting of only leaves) in young plants to
397 approximately 0.20 (i.e. only 20% of biomass attributed to leaves) in average in fully mature plants,
398 but with a huge variability ranging from 0 (leaf-less plants) to more than 0.75 (75% of biomass
399 attributed to leaves at that stage). In addition, specific leaf area SLA decreased (i.e. leaves became
400 smaller, Figure 1.A) and median leaf area height RLH increased (i.e. plants became top-heavier,
401 Figure 1. I) with plant age. The variability among species made it more difficult to identify general
402 tendencies for the other parameters (Figure 1.E and G).

403 Shading response generally increased with plant stage, i.e. parameter values became increasingly
404 positive or negative (Figure 1.B, D, F, H, I). Shading response of specific leaf area SLA was the
405 shading response that changed most during plant life, with plants progressively increased their SLA
406 more when shaded (Figure 1.B). The same applied to specific plant height and width (Figure 1.D and
407 F), i.e. older plants increased their plant heights and widths more when shaded. As written above, the
408 change in shading response with plant age depended very much on the species for the two remaining
409 parameters. Some species increasingly attributed more biomass to leaves (Figure 1.D) and/or shifted
410 their leaves upwards when shaded (Figure 1.H); the opposite applied to other species.

3.2 Which parameters were correlated?

413 Few parameters were correlated (Figure 2), indicating that our set of parameters provided
414 complementary information. The most correlated parameters were shade response in terms of specific
415 leaf area (SLA_{mu}) and plant height per unit biomass (HM_{mu}) (Pearson correlation coefficient $r =$
416 0.55), i.e. plants that tended to produce larger leaves when shaded also grew taller per unit biomass
417 when shaded. Height and width per unit biomass were also positively correlated ($r=0.42$). Finally,
418 LBR₀ was negatively correlated to both LBR_{mu} (arrows are opposed on Figure 2.C, $r=-0.33$) and
419 SLA_{mu} (arrows are opposed on Figure 2.A, $r=-0.38$), i.e. potentially leafy plants reduced their leaf
420 biomass ratio when shaded, and their leaves became smaller (also line [8] in Table 5). Other

421 correlations were only visible in linear regressions including species features (Table 6). The taller a
422 species was per unit biomass and the top-heavier it was in unshaded conditions, the less it was able to
423 grow taller and top-heavier when shaded (HM_mu and RLH_mu). The expected trade-off between
424 relative growth rate RGR and specific leaf area SLA0 could not be observed on the principal
425 component analysis (Figure 2), and only slight correlations could be identified for four stages using
426 linear regressions (see example in Figure 3, details in section [B.3.1](#) online).

3.3 Did crop and weed species differ?

429 Weed species differed from crop species in several parameters (Table 1): their leaf area at emergence
430 was smaller but they presented a larger specific leaf area in unshaded conditions (SLA0), they were
431 wider per unit biomass (higher WM0), and both plant height and width depended more on plant
432 biomass (higher b_HM and b_WM). Weeds responded much more to shade than crops, further
433 increasing their SLA (higher SLA_mu), their leaf biomass ratio (higher LBR_mu), their plant height
434 and width per unit biomass (higher HM_mu and WM_mu).

435 However, when clustering species based on parameters of initial growth, plant morphology and
436 shading response for the different plant stages (Figure 2.B and D), crop and weed species belonged to
437 the same clusters. The only exception was cluster C consisting of the earliest stages of five weed
438 species only, i.e. *Abutilon theophrasti* (ABUTH), *Avena fatua* (AVEFA), *Chenopodium album*
439 (CHEAL), *Digitaria sanguinalis* (DIGSA) and *Polygonum persicaria* (POLPE). The species and plant
440 stages of this cluster were characterized by taller and wider plants per unit biomass in unshaded
441 conditions (HM0 and WM0 in upper right quadrant of Figure 2.B), with a strong impact of plant
442 biomass on plant height and width (b_HM, b_WM in the same upper right quadrant). All the other
443 clusters comprised both crops and weeds, and usually species changed clusters when growing older.
444 *Ambrosia artemesiifolia* (AMBEL), *Panicum miliaceum* (PANMI), oilseed rape (BRSNN), sunflower
445 (HELAN), two pea varieties (China and Enduro) and maize (ZEAMX) were the only species
446 remaining in the same cluster throughout their plant life, albeit in different ones. Wheat varieties
447 always belonged to the same clusters, whereas pea and field bean varieties were spread over different
448 clusters, pointing to a larger intra-species variability in the studied parameters.

449 When other species features were included in the analysis as in sections 3.4 and 3.5, the crop vs weed
450 status was rarely significant. The difference between crops and weeds only remained significant for
451 LA0 (Table 4), b_WM, RLH0 and LBR_mu (Table 6). Indeed, crop and weed species notably differed
452 in several features (Table 3). For instance, there were no legumes among weeds and their leaf nitrogen
453 content was much lower than in crops. Crop plants were potentially taller and narrower than weeds,
454 they were more often winter annuals and perennials, their seeds were heavier but lipid-poorer, they
455 required less warmth and moisture to grow but more light, and there were fewer C4 species and fewer
456 species with epigeal pre-emergent growth among them.

None of the analysed species parameters could be easily related to one or a small number of species traits and other features, using Principal Component Analysis (Figure 2.A and C). Consequently, linear regressions were used in the next sections to relate parameters to species features.

3.4 Which features influenced initial growth?

Among the 16 species or varieties that were run in different months or years (details in section B.4 online), only one species presented a significantly different initial leaf area LA0, i.e. *Zea mays* leaf area was approximately four times larger in July 2012 than in March 2010. This magnitude is though small compared to the interspecies variation in LA0 which varied more than 400 times among species (Table 1). Once data was aggregated over all seasons for each species, standard-error was approximately half the average leaf area ($se = 0.565 \cdot LA0^{1.01}$, section B.2 online). The relative growth rate RGR varied for two species with month/year (*Solanum nigrum*, *Z. mays*) but the variation was small (2 and 1.3 times), particularly compared to the inter-species variation (13 times).

Initial leaf area increased with increasing base temperature and seed weight (Table 4). It was also higher for epigeal vs hypogeal species, and for crop vs weed species. RGR was higher for non-legume vs legume species. It also increased with increasing seed weight and base temperature but decreased with increasing initial leaf area, particularly for hypogeal species. The effect of the other features was not significant. Even when all other features were disregarded, RGR and Ellenberg N were not correlated at all in non-legume species ($p = 0.4996$, section B.3.1 online).

3.5 Which features influenced potential morphology and shading response?

3.5.1 Leaf biomass ratio as a case study

Plant stage and growth form. In young plants, leaf biomass ratio in unshaded conditions (LBR0) was the highest for rosette-shaped and erect plant species (regressor values of 1.81 and 1.07 in lines [3] and [4] in Table 5) and the lowest for prostrate and climbing or twining plant species (values of 0.12 and 0 in lines [2] and [5]). LBR0 decreased with plant stage, i.e. young plants consisted mostly of leaf biomass and old plants mostly of stem biomass (Figure 1.C). The decrease was the fastest for rosette-shaped and erect plants (regressor values of -0.953 and -0.843 for *stage* in lines [3] and [4] in Table 5) and the slowest for prostrate and climbing or twining species (values of -0.752 and -0.558 in lines [2] and [5]). So, in old plants ($stage = 10$), rosette-shaped plants presented the lowest leaf biomass ratio ($1.81 - 0.953 \cdot 10 = -7.72$) and climbing or twining species the highest leaf biomass ratio ($0 - 0.558 \cdot 10 = -5.58$).

Shading response generally increased with plant stage, i.e. parameter values became increasingly positive or negative (Figure 1.D). Generally, older plants tended to attribute less biomass to leaves when shaded, particularly climbing or twining species (-0.0477 in line [5] is more negative than the

493 three regressor values of lines [2] to [4] in Table 5). However, there was a lot variability in shading
1 494 response with many species increasing their leaf biomass ratio (approximately 50% of values above
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3 495 zero at stages 8-10 in Figure 1.D).

4 496 **Other plant morphology features.** In unshaded conditions, species with potentially wide plants (i.e.
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6 497 with a large maximum plant width) attributed less biomass to leaves than narrower species (-0.00651
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8 498 in line [7] of Table 5). When shaded, potentially tall plants (i.e. with a large maximum plant height)
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10 499 increased leaf biomass ratio less (-0.000663 in line [6]). The same applied to species with a large leaf
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12 500 biomass ratio in unshaded conditions (-0.519 in line [8]).

13 501 **Plant lifespan.** In unshaded plants, leaf biomass ratio was highest for perennials and indeterminate
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15 502 annuals and lowest for summer and winter annuals (1.078 and 0.722 in lines [9] and [11] are larger
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17 503 than 0 and -0.002 in lines [10] and [12] of Table 5). When shaded, the same ranking persisted, i.e.
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19 504 perennials and indeterminate species attributed even more biomass to leaves (0.376 and 0.174 in lines
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21 505 [9] and [11]) than the other two types (0 and -0.024 in lines [10] and [12]).

22 506 **Taxonomy, dinitrogen fixation and photosynthetic pathway.** In unshaded conditions, dicots
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24 507 generally attributed more biomass to leaves than monocots (0.0877 in line [13] of Table 5). But when
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26 508 shaded, they attributed less biomass to leaves than monocots (-0.145 in line [13]). In unshaded
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28 509 conditions, C4 species presented a lower proportion of leaf biomass than non-legume C3 species (-
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30 510 0.622 in line [14]). There was no significant difference in shading response between C3 non-legumes
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32 511 and C4 species (blank cell in line [14]). Legumes also attributed less biomass to leaves than C3 non-
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34 512 legumes (-1.603 in line [15]) but legumes and non-legumes did not differ in terms of shading response
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36 513 (blank cell in line [15]).

37 514 **Ecological habitat preferences.** The behaviour of non-legumes also depended on their nitrogen
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39 515 requirement (Ellenberg N): species that preferred nitrogen-rich habitats (i.e. high Ellenberg-N values)
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41 516 had a lower leaf biomass ratio in unshaded conditions (-0.146 in line [16] of Table 5) and reduced it
42
43 517 even more when shaded (-0.0131 in line [16]), than species preferring nitrogen-poor habitats. The
44
45 518 other habitat preferences only influenced shading response. Heliophile species which prefer sunny
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47 519 open habitats (i.e. high Ellenberg-L values) increased leaf biomass ratio more (0.0741 in line [17])
48
49 520 than species preferring shaded habitats (i.e. low Ellenberg-L values). Hygrophilic (i.e., "moisture-
50
51 521 loving") species (i.e. high base water potential) attributed less biomass to leaves (-0.0539 in line [18])
52
53 522 when shaded than species that were adapted to drier habitats.

54 523 **Seed and leaf traits.** In unshaded conditions, heavy-seeded species attributed less biomass to leaves
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56 524 than light-seeded ones (-0.236 in line [19] of Table 5). But, when shaded, they attributed more
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58 525 biomass to leaves (0.0632 in line [19]). Leaf traits only influenced shading response. Species with
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60 526 denser leaves (i.e. higher dry matter content) attributed less biomass to leaves when shaded than
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62 527 species with less dense leaves (-0.000726 in line [20]). And species with nitrogen-rich leaves (i.e. high
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64 528 leaf nitrogen content) increased leaf biomass ratio more than species with nitrogen-poor leaves
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66 529 (0.00223 in line [21]).

530 **3.5.2 The other parameters**

1 531 The same kind of linear regressions were carried out for all species parameters as a function of species
2 532 features (section E.1 online). These were summarized into profiles linking species traits and other
3 533 features to contrasting morphologies and shading responses (Table 6). For instance, in unshaded
4 534 conditions, a large specific leaf area (i.e. larger usually thinner leaves) was found in young plants, non-
5 535 perennial species with a prostrate growth form, potentially tall and narrow plants; they tended to be
6 536 dicots, C3 non-legumes that preferred N-poor, acid and/or warm habitats (Table 6.A). Conversely, a
7 537 low specific leaf area (i.e. small and usually thick leaves) was more frequent in old plants, perennial
8 538 plants with a climbing or twining growth form, potentially short and wide plants; they tended to be
9 539 monocots, legumes or C4 species, and they preferred basic and/or cool habitats.

10 540 The species traits and other features found in these contrasting morphologies and shading responses
11 541 varied considerably with the analysed parameters. Some tendencies could though be identified. For
12 542 instance, short-living species (i.e. summer annuals) tended to improve efficiency of biomass to
13 543 increase leaf area and to occupy space in both shaded and unshaded conditions, i.e. they presented a
14 544 larger specific leaf area, their plant height depended more on plant biomass and when shaded, they
15 545 became taller per unit biomass, they invested more biomass in stems but their leaf area was distributed
16 546 more uniformly along plant height. A few of these correlations could also be seen on the Principal
17 547 Component Analysis, mainly the higher shading response of summer annuals (Figure 2.A). There was
18 548 no common tendency in terms of resource deficiency, i.e. different parameter values were found in
19 549 species adapted to N-poor, cool or dry habitats.

20 550

21 551 **3.5.3 The importance of interactions**

22 552 Overall, the variability (R^2) explained by the species features in the multiple regressions varied from
23 553 0.09 to 0.85 (mean 0.39), depending on the analysed parameter (Table 7). If regressions were carried
24 554 out separately for crops and weeds, R^2 was higher for the former (average 0.60) vs the latter (0.44).
25 555 The R^2 was also higher for monocots (average 0.60) vs dicots (0.45) in case of separate regressions.
26 556 The explained variability could be increased further by adding interactions, e.g. between plant stage
27 557 and species traits, thus pinpointing correlations that were only visible at either early or late stages. This
28 558 would though have increased the number of regressors even more, with a high risk of overfitting the
29 559 model and thus decreasing its genericity.

30 560 In the complete model, the R^2 reflected the precision of the various measurements. It was highest for
31 561 leaf biomass ratio based on only weight measurements, and lowest for specific height HM and width
32 562 WM which were based on plant height and width (Table 7). Measuring the latter two is notoriously
33 563 difficult, particularly in climbing and twining species.

564 **4 Discussion**

1
2 565 The present experiments measured parameters for initial growth, plant morphology in unshaded
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4 566 conditions and plant response to shading in more than 50 annual crops and weeds from temperate
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6 567 arable cropping systems and belonging to 17 different botanical families. In terms of plant
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8 568 morphology, the study showed that species widely differed in terms of plant volume, with specific
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10 570 plant heights and widths HM0 and WM0 greatly varying among species, but they were similar in
11
12 571 terms of leaf biomass ratio and leaf area distributions. Similarly, some shading response strategies
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14 572 were common to all species (e.g. specific leaf area SLA increased in shaded species) whereas
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16 573 opposing responses were observed for other morphology variables (e.g. either attribute more biomass
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18 574 to stems or to leaves).

17 574 In terms of functional relationships linking parameters to easily accessible species features, the study
18
19 575 (1) confirmed a few well-known relationships (e.g. lower specific leaf area SLA and leaf biomass ratio
20
21 576 LBR in legumes vs non-legumes, increase of initial leaf area with seed weight) (Table 2), (2) included
22
23 577 new species features into these relationships (e.g. relative growth rate RGR increased with species
24
25 578 base temperature, C4 had a lower LBR than C3 species), and (3) demonstrated a series of original
26
27 579 relationships for the newly proposed shading-response parameters (e.g. weeds respond more to shade
28
29 580 than crops and do this by increasing LBR and SLA and by producing taller and wider plants for a
30
31 581 given plant biomass; prostrate and rosette-shaped plants etiolate more than erect and climbing or
32
33 582 twining species).

34 584 **4.1 Are our results consistent with previous studies?**

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36 585 Many of our results linking species parameters to species features were consistent with previous
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38 586 reports and/or hypotheses (Table 2) and we often confirmed relationships that were first demonstrated
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40 587 on a small number of species (e.g., Fayaud *et al.*, 2014) or on other species (e.g., den Dubbelden and
41
42 588 Verburg, 1996). Recent studies also demonstrated that changes in light quality modify plant
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44 589 morphology even if the amount of photosynthetically active radiation remains unaltered (McKenzie-
45
46 590 Gopsill *et al.*, 2019; Schambow *et al.*, 2019). Such results support the pertinence of our parameters
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48 591 which discriminate the effect of light on biomass accumulation from that of shading on morphology.
49
50 592 Here, we will focus on understanding discrepancies between our results and previous literature reports.
51
52 593 Some are only slight. For instance, height per unit biomass was reported to be larger for climbing vs
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54 594 self-supporting legume species (den Dubbelden and Verburg, 1996). This was true here only in older
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56 595 plants whereas the opposite ranking was observed for young plants.

54 596 As we worked with original parameters, it was often difficult to find literature studies to compare to
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56 597 our results. This was particularly true for shading response. The rare studies that investigated
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58 598 morphological plasticity in similar species did not measure shading intensity and calculated specific

599 height differently (with a constant b_{HM} parameter, Pakeman *et al.*, 2015). It is thus impossible to
1 600 compare results.

3 601 The best documented variable is specific leaf area SLA. The LEDA trait data base (Kleyer *et al.*,
4 602 2008) reported larger values for the species used here (275 ± 71 cm²/g over sources and species in the
5 603 data base compared to 179 ± 70 cm²/g over stages and species in our study), without any correlation
6 604 between the two types of data ($p=0.6468$ for Spearman correlation, section **F.1.1** online). Indeed, we
7 605 measured SLA in unshaded conditions using all plant leaves and including petioles, whereas some
8 606 previous studies often only considered the top leaf limbs and did not specify shading conditions. But
9 607 SLA has been shown to vary along plant height, because of self-shading (Ishida *et al.*, 1999), and we
10 608 similarly showed that SLA usually increased with shading. When comparing our results to Storkey's
11 609 (2004) who also worked in unshaded conditions and calculated SLA over all plant leaves, our data
12 610 were correlated (Spearman $r = 0.63$, section **F.1.2** online). Our SLA values are still lower than
13 611 Storkey's, probably because he excluded petioles from his measurements (J. Storkey, pers. comm.
14 612 2018).

23 613 These methodological differences probably also explain why we did not observe the frequently
24 614 reported correlation between relative growth rate RGR and specific leaf area SLA (Poorter and
25 615 Remkes, 1990; Reich *et al.*, 1997; Poorter and Van Der Werf, 1998; Storkey, 2004), except very
26 616 slightly at vegetative stage. Another explanation could be that our RGR (cm²/cm²/°Cday) was based
27 617 on plant leaf area growth and not on plant biomass growth as the literature RGR (g/g/days). The two
28 618 are only equivalent if temperature, leaf biomass ratio and specific leaf area are constant over time,
29 619 which is not the case (see section 3.5.1). But Storkey's (2004) who used the same approach as we did
30 620 (but also included radiation effects) found the same magnitude in terms of relative growth rate RGR
31 621 and initial leaf area LA0, and the species were ranked similarly (Pearson correlation coefficient = 0.31
32 622 and 0.82 for RGR and LA0, respectively). Storkey's RGR and LA0 were in average respectively 40%
33 623 and 50% larger than ours, because they included stem area in their calculation of RGR, and they
34 624 started leaf area measurements only a few days after emergence.

43 625 Most probably, we could not find a trade-off between RGR and SLA in the present study because we
44 626 focused on crops and weeds (which cohabit in the same type of habitat) whereas ecological studies
45 627 cover a larger range of habitats and species types (or 100-400 cm²/g in Poorter and Remkes, 1990; e.g.
46 628 SLA measured here at stage 5 ranged from approximately 75-300 cm²/g compared to 60-600 cm² in
47 629 Reich *et al.*, 1997). Storkey (2004) who worked with species similar to ours could only observe the
48 630 RGR-SLA correlation when discriminating monocots vs dicots and spring vs autumn growth seasons.
49 631 Other studies focusing on crops were also unable to identify an RGR-SLA trade-off and explained this
50 632 by their limited species pool as well as a domestication effect which could have distorted the
51 633 relationship (Tribouillois *et al.*, 2015).

634 These differences in methods and species pools probably also explain other discrepancies between our
1 635 results and previous reports from literature. For instance, we did not observe the expected negative
2 636 correlation between the leaf dry matter content LDMC and the specific leaf area SLA (Wilson *et al.*,
3 637 1999; Roche *et al.*, 2004; McIntyre, 2008; Tribouillois *et al.*, 2015) or the positive correlation between
4 638 RGR or SLA and Ellenberg N (Poorter and Remkes, 1990). Indeed, the latter was observed with
5 639 biomass-based RGR and single-leaf SLA on a species pool whose Ellenberg N indices varied from 1
6 640 to 8. Our species ranged from 5 to 9 and in that range Poorter & Remkes' data did not show any
7 641 notable correlation either (section **F.2** online). The same was true for many other correlations with
8 642 Ellenberg indicator values reported in literature (Table 2).
9
10 643 In conclusion, the identification of functional relationships depends on measurement conditions,
11 644 methods as well as on the investigated species pool. Our results clearly show the limits of transposing
12 645 results from comparative ecology, which focuses on a wide range of habitats, to agricultural fields.
13 646 The trade-offs among plant traits identified on large sets of wild species are not necessarily valid when
14 647 analysing plant strategies of species from a narrower range of habitats.
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25 649 **4.2 Disentangling species differences from environmental effects**

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27 650 The present study combined the method developed by Munier-Jolain et al (2014) to characterize plant
28 651 morphology in heterogeneous crop:weed canopies with the method developed by Gardarin et al (2010;
29 652 2011) to link difficult-to-measure species parameters to easily accessible species features. Munier-
30 653 Jolain's parameters were essential to separate the effect of radiation on biomass accumulation from
31 654 that of shading response. Indeed, shaded plants are usually smaller and lighter than unshaded plants,
32 655 but the shading-response parameters used here check whether plants change their rules for allocating
33 656 biomass and determining morphology.
34
35 657 These parameters are very expensive to measure in terms of time, space and labour. But their nature
36 658 makes their values largely independent of the experimental conditions (see e.g. section 2.3.2
37 659 explaining this for relative growth rate RGR) and thus makes it possible to compare species tested in
38 660 different years or outside growth chambers, albeit some methodological precautions. To minimize the
39 661 risk of confusing species and year effects, the experimental setup in the garden plots aimed to ensure
40 662 optimal water and nitrogen conditions, and the initial growth phase was studied in greenhouse where
41 663 plants were protected from frost damage. Working in garden plots has the disadvantage that the
42 664 amount of available light varies with the years (see section **E.6** online), but it has the major advantage
43 665 over climate chambers of having natural light (in terms of magnitude, quality and daily variation), and
44 666 allowing us to space plants sufficiently to avoid shading from neighbours. By sampling plants at key
45 667 stages (instead of fixed dates), we moreover accounted for differences in temperature not only between
46 668 shaded and unshaded conditions, but also among experimental years and seasons. Moreover, we
47 669 recently started to test our species in quite different conditions (University of Rostock, North-Eastern
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670 Germany) and the first results show that the parameter values estimated there on the same French
671 populations are very close to those measured in France (Bürger and Colbach, 2018).

672 In contrast to most ecological studies (e.g. the trade-off between RGR and SLA, Table 2), we analysed
673 most of the parameters implicated in competition for light, and this for a large number of species. We
674 moreover analysed these parameters in multiple regressions instead of two-by-two analyses and did
675 this using a large number of contrasting species. This was essential as previous studies established
676 many simultaneous two-by-two correlations, without being able to conclude which was actually
677 relevant as many explanatory species features were themselves correlated, particularly when working
678 with small species pools (see review by Bartelheimer and Poschlod, 2016). We had the same problem
679 here: the difference in parameters between crop vs weed species was often due to differences in other
680 species properties, e.g. legumes could only be crops and C4 species were more frequently weeds. But,
681 even if it had been our objective, it would have been next to impossible to apply a complete species
682 sampling plan decorrelating the crop vs weed status from other species because of the effect of crop
683 breeding.

684 Our multiple regressions made it possible to identify minor correlations that are impossible to see in
685 2-by-2 analyses, similar to Tribouillois et al (2015), or to identify the traits and processes that explain
686 differences between species types. For instance, we observed large differences in parameter values
687 between the analysed crop and weed species. Even though our species choice did not aim at testing the
688 crop vs. weed status of species, the observed differences were consistent with hypotheses on
689 domestication, i.e. crops were selected to ensure a fast establishment, homogenous populations and a
690 large seed production to the detriment of other abilities. Conversely, weeds responded much more to
691 shade, by increasing leaf area and plant width per unit biomass. This is logical insofar as weeds
692 usually grow below crop canopies and must thus be able to tolerate shade. But most of this difference
693 was actually related to other feature differences, as shading response depended very little on the crop
694 vs weed character of the species, once other features were included in the analysis.

695 Our approach made it possible to explain species responses to habitat that are characterized in ecology
696 by integrative indicators such as Ellenberg indicators. For instance, heliophilic species (i.e. high
697 Ellenberg-L values) had a high light requirement because they were potentially smaller and narrower
698 per unit biomass, and when shaded, they were bad at outgrowing neighbours (i.e. increasing height
699 and width per biomass) and had to increase leaf biomass ratio to compensate for their smaller leaves.
700 In addition to habitat preferences, we were able to demonstrate other novel relationships, e.g. the lower
701 leaf biomass ratio of C4 vs. C3 species, or the correlation with seed and emergence traits whose effect
702 was not solely limited to initial growth but persisted throughout plant life (e.g. correlation between
703 seed lipid content or leaf nitrogen content and specific leaf area). Many of these correlations between
704 parameters and species features are easy to understand and predict (e.g., the larger photosynthetic
705 efficiency of C4 allows them to reduce their leaf biomass ratio), but there have been, to our
706 knowledge, no experimental demonstrations presented to date as summarized in Table 2. For others,

707 we have no biological assumption yet, far less a demonstration of a biological cause. For instance,
708 basidophile species here presented a lower leaf area and plant width per unit biomass and responded
709 less to shading in terms of plant height and width than acidophile species, even though the experiment
710 was carried out on an alkaline soil.

4.3 Practical conclusions for experiments and parameter estimation

713 As already mentioned above, the parameters studied here are difficult to measure. The present study
714 attempted to propose a few solutions to this bottleneck. For instance, additional analyses (section E.3
715 online) showed that experiments could be limited for the first three stages and further behaviour could
716 be predicted from these earlier measurements and species traits. The necessary species features are
717 either easy to measure (e.g. seed mass) or can be found in trait databases (e.g. the TRY database,
718 <http://www.try-db.org>).

719 Parameters could also be solely estimated from species features to add new species to models such as
720 FLORSYS weed dynamics simulation model (whose parameters were the conceptual basis of the
721 present study, Munier-Jolain *et al.*, 2013; Munier-Jolain *et al.*, 2014). This approach was validated by
722 Gardarin (2008) in greenhouse experiments who compared the predicted emergence of weeds to
723 observations, using either measured or estimated parameters, as well as by Colbach *et al* (2016) who
724 compared observed weed densities from multiannual and multisite field trials to simulations with the
725 FLORSYS model including parameter-feature functions for pre-emergent parameters. Incidentally, the
726 latter evaluation study also validated the relevance of the present morphology and shading-response
727 parameters for predicting crop yield and multiannual weed dynamics as the FLORSYS simulations were
728 run with many species and parameters measured in the experiments presented here.

729 As the R^2 of the statistical models estimating parameters from species features were sometimes low,
730 using separate models for crops vs weeds, or dicots vs monocots, would improve the level of
731 explained parameter variability (section 3.5.3). This is tantamount to including more interactions, with
732 a risk of overfitting the model. The use of the GLMSELECT function which uses cross-validation to
733 identify the best model is thus essential to avoid making effects depend on a single data point and to
734 reduce the risk of confusing effects. The latter was essential as our data set was imbalanced, e.g. there
735 were no legume weeds and few C3 crop species, and probably thanks to domestication, our crop
736 species were generally taller with heavier seeds. Cross-validation was even more crucial as we
737 identified here several novel correlations for which we have as yet no demonstration of a biological
738 link (e.g. decrease in specific leaf area SLA with increasing Ellenberg-R which reflects species
739 preference for basic soils).

740 Predicting parameters from a few detailed measurements combined with accessible species features, or
741 with e.g. crop-only functions would be helpful for parameters that could not be precisely predicted
742 here with the complete models such as those of Table 5. This would be particularly the case for the

743 parameters that are essential to simulate crop production and weed impacts with models such as
744 FLORSYS, e.g. potential plant width per unit biomass and its shading response (Colbach *et al.*, 2019).

746 **4.4 Practical implications for crop and weed management**

747 The effect of domestication on crops was visible both in the analysed light-competition parameters as
748 well as in the species features that were linked to these parameters, with crops tending to be faster,
749 larger and more homogeneous (i.e. lower standard-errors on parameter values, lower sensitivity of
750 plant width to plant biomass b_{WM}) aiming at homogenous canopies with a large biomass production.
751 Conversely, weeds were more plastic, reflecting their adaptation to survive and grow inside earlier-
752 emerging crop canopies. But the present study demonstrated these species types to overlap, with a
753 large variability.

754 Table 4 and Table 6 could be used to choose (cash or cover) crop species or varieties based on their
755 light-competition abilities according to the targeted objectives and the production situation. For
756 instance, epigeal heavy-seeded summer crops could ensure a faster crop establishment whereas
757 oligotrophic, non-legume C3 dicots would maximise light interception.

758 However, neither biomass production nor crop-weed competition can be inferred from a single
759 parameter, and it is impossible to conclude on the performance of parameter combinations from these
760 tables. This is only possible after integrating the parameters into a simulation model such as FLORSYS
761 as we did in the companion paper (Colbach *et al.*, 2019). There, we were able to determine ideal crop-
762 parameter combinations in terms of weed control, showing for instance that the same parameter values
763 promote crop and weed species in mixed canopies and that successful species present a larger specific
764 leaf area and are taller and wider per unit biomass, particularly when shaded. Integrating the
765 parameters into a model also allows checking their consistencies indirectly, by comparing model
766 simulations to independent field observations. This evaluation demonstrated that the model based on
767 the present parameters produces predictions consistent with field observations (Colbach *et al.*, 2016).

769 **5 Conclusion**

770 By combining ecological and agronomical approaches, the present study was able to produce new
771 insights on crop:weed competition for light. From agronomy, we borrowed the idea of using detailed
772 parameters linked to ecophysiological processes. We could thus explain species responses to habitat –
773 which are characterized in ecology by integrative indices – via differences in plant morphology and,
774 particularly, the ability to respond to shade by, e.g., increasing leaf area or plant height for a given
775 biomass. From comparative ecology, we borrowed the notion of species traits and trade-offs among
776 traits, showing, e.g., that plants with a lower specific leaf area compensate with a higher leaf biomass
777 ratio. By combining both approaches, we were able to establish functional relationships that link
778 process-close but difficult-to-measure species parameters to easy-to-measure integrative species traits.

779 This, combined with the use of novel traits that have not yet been used in comparative ecology,
780 identified new insights on which plant traits drive shading response. As we focused on species that
781 cohabit in the same type of habitat (i.e. crops and weeds in temperate arable fields), the investigated
782 species were more similar and the range of explored species traits much smaller than in ecological
783 studies. This, together with our process-close parameters (e.g. leaf-area based RGR, discriminating
784 shade response from biomass production), explains why classic correlations (e.g., relative growth rate
785 RGR vs specific leaf area SLA) reported in ecology were not observed. Relationships established in
786 ecology on a large range of wild species from very contrasting habitats do thus not necessarily apply
787 to domesticated species or species evolving in a single type of habitat.

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8 Tables

Table 1. Species parameters for characterizing initial growth, potential plant morphology and response to shading. Median, minimum and maximum values over all species as well as means per crop and weed species (values of a row followed by the same letter are not significantly different at $p=0.05$)

Parameter name	Relative advance of growth stage at the time of parameter measurement	Unit	Median [min,max] [§]	Variation ^{&}	Crops	Weeds
A. Initial growth (without shading or self-shading)						
RGR	Relative growth rate	cm ² ·cm ⁻² ·°Cday ⁻¹	0.0186 [0.0093, 0.0592]	0.52	0.0231 A	0.0207 A
LA0	Leaf area at emergence	cm ²	0.260 [0.01, 3.97]	1.48	1.194 A	0.220 B
B. Potential morphology (morphology variables in unshaded conditions)						
SLA0	Specific Leaf Area (ratio of leaf area to leaf biomass [§])	cm ² ·g ⁻¹	153 [10, 1204]	0.49	168 B	187 A
LBR0	Leaf biomass ratio (ratio of leaf biomass to total above-ground biomass)	none	0.75 [0, 1]	0.23	0.7 A	0.69 A
HM0	Specific (allometric) plant height (ratio of plant height to total above-ground plant biomass to the power of b_HM)	cm·g ⁻¹	20 [1.2, 838]	1.08	30 A	37 A
b_HM	Shape parameter for impact of plant biomass on plant height (0 = none, 1 = positive correlation)	none	0.27 [0.0005, 0.99]	0.55	0.28 B	0.32 A
WM0	Specific (allometric) plant width (ratio of plant width to total above-ground plant biomass to the power of b_WM)	cm·g ⁻¹	22 [0.82, 3464]	2.68	27 B	115 A
b_WM	Shape parameter for impact of plant biomass on plant width (0 = none, 1 = positive correlation)	none	0.37 [0.02, 1.7]	0.58	0.37 B	0.41 A
RLH0	Median relative leaf area height (relative plant height below which 50% of leaf area are located)	cm cm ⁻¹	0.48 [0.2, 0.81]	0.21	0.49 A	0.5 A
b_RLH	Shape parameter for leaf area distribution along plant height	none	2.7 [0.24, 58]	0.78	8.66 A	2.66 B
C. Response to shading (variation in morphology variables with shading intensity)						
SLA_mu	Response of specific leaf area to shading	none	0.48 [-0.56, 1.72]	0.36	0.44 B	0.55 A
LBR_mu	Response of leaf biomass ratio to shading	none	-0.01 [-0.66, 1.02]	0.19	-0.041 B	0.037 A
HM_mu	Response of specific height to shading	none	0.43 [-0.53, 2.27]	0.39	0.36 B	0.52 A
WM_mu	Response of specific width to shading	none	0.27 [-1.53, 1.87]	0.31	0.23 B	0.32 A
RLH_mu	Response of median relative leaf area height to shading	none	0.01 [-1, 1.39]	0.25	0.009 A	0.012 A

[§] For B and C, over all stages.

[&] standard-deviation/mean, except for shading response where standard-deviation because of negative values of mean close to zero

[§] Biomass is always dry (leaf or plant) mass.

062 Table 2. Summary of relationships between species features and parameters reported in literature, the underlying hypotheses and possible adaptations for our study (SLA: specific leaf area, RGR: relative growth rate,
063 LBR and RBR: respectively, leaf and root biomass ratio, LAR: leaf area ratio; HM specific plant height; for further details see Table 1). Green and red cells show relationships respectively consistent and inconsistent
064 with our own observations, yellow cells show cases where we did not find any relationship in contrast to literature, blank cells show correlations that we did not study

Species features	Related parameters	Effect [§]	Hypothesis	Reference	Adaptation in our study
Taxonomy and N2 fixation					
1 Clade (Dicots vs monocots)	RBR	-	Dicots attribute less biomass to roots	(Moreau <i>et al.</i> , 2014)	Look at clade effect on all parameters
2 Ability to symbiotically fix N2 (legumes)	SLA, LBR, LAR HM	- +	Legumes invest more in below-ground structures	(den Dobbelden and Verburg, 1996)	Also look at photosynthetic pathway (C3 vs C4)
Species traits					
6 Plant growth form: climbing vs self-supporting	RGR SLA LBRt HM	0 + ns - +	Climbing species have high SLA to compensate for low LBR Climbing species have longer stems	(den Dobbelden and Verburg, 1996)	Also look at other plant forms
10 Leaf life-span	Initial leaf biomass, RGR	-	High growth rate and initial leaf size compensate for short lifespan	(Reich <i>et al.</i> , 1997; Garnier and Navas, 2012; Reich, 2014)	Use plant life-span
13 Leaf dry matter content LDMC	SLA	+	Trade-off between conservative (low SLA and RGR) and acquisitive strategies (high RGR and SLA)	(Wilson <i>et al.</i> , 1999; Roche <i>et al.</i> , 2004; Wright <i>et al.</i> , 2004; McIntyre, 2008; Tribouillois <i>et al.</i> , 2015)	Analyse all parameters
	Resource capture	-	LDMC is a marker of a conservation strategy (low efficiency in resource capture)	(Lavorel and Garnier, 2002)	Analyse shading response
18 Leaf nitrogen content LNC	RGR	+	LNC is a marker of resource acquisitive species.	(Lavorel and Garnier, 2002; Tribouillois <i>et al.</i> , 2015)	Analyse all parameters
21 Epigeal vs hypogeal pre-emergent growth	Initial plant leaf biomass	+	The emerging cotyledons of epigeal species contribute to leaf mass and area immediately after emergence	(Fayaud <i>et al.</i> , 2014)	Analyse initial plant leaf area
23 Seed mass	Initial plant leaf biomass	+	Heavier seeds include more reserves and/or a larger embryo	(Seibert and Pearce, 1993; Fayaud <i>et al.</i> , 2014)	Analyse initial plant leaf area
	SLA	-	Small-seeded species devote more biomass to leaves but have denser leaves	(Seibert and Pearce, 1993)	
	LBR, RGR	-			
28 Seed lipid content	Faster germination, larger plants	+	This type of reserve stores more energy		Analyse all parameters
Ecological habitat preferences (base values or Ellenberg indicator values as proxies)					
32 Thermophily	Insect growth rate	+	Higher growth rate compensates for higher temperature requirement	(Angus <i>et al.</i> , 1981; Trudgill <i>et al.</i> , 2005; Gardarin <i>et al.</i> , 2011)	Analyse all parameters, use base temperature and water potential instead of Ellenberg T and M
	Germination rate	+	Higher temperature requirements allow annuals to detect gaps in existing vegetation	(Washitani and Takenaka, 1987)	
	SLA	+	Frost resistant species have smaller (and usually thicker) leaves	(Palta and Li, 1979)	
38 Hygrophyly	RGR, SLA, germination speed	+	Drought-resistant species invest more into roots, higher growth rates compensates for higher moisture requirements	(Bartelheimer and Poschlod, 2016)	
40 Heliophily	RGR, SLA	-	High SLA compensates for low light availability in shaded habitats	(Bartelheimer and Poschlod, 2016)	Analyse all parameters as a function of Ellenberg N, L and R
42 Nitrophily	SLA	+	In nutrient-rich habitats, species mainly compete for light, which selected for high SLA and RGR to the detriment of below-ground processes	(Poorter and Remkes, 1990; Bartelheimer and Poschlod, 2016)	
	RGR	+			
	RBR	-	Nitrophilic species invest less biomass into roots	(Fichtner and Schulze, 1992; Moreau <i>et al.</i> , 2014)	
	LBR	-			
49 Preferences for soil pH	RGR, SLA	+	Calciphile species could prefer nitrate over ammonium and higher temperature requirements, calcifuge species could be better adapted to acidic habits with their low nutrient availability and higher toxicity	(Bartelheimer <i>et al.</i> , 2014; Bartelheimer and Poschlod, 2016)	
Morphology					
53 SLA	RGR	+		(Poorter and Remkes, 1990; Reich <i>et al.</i> , 1997; Poorter and Van Der Werf, 1998; Storkey, 2004)	
56 LA0	RGR	-		(Storkey, 2004)	

065 § 0 = no effect, + = positive correlation or increase, - = negative correlation or decrease

1066 Table 3. Differences in species traits between crop and weed species. Comparison of lsmeans after
 1067 analysis of variance of trait as a function of crop vs weed character. R² cells were coloured from white
 1068 (0) to green (highest partial R²). For the list of references referring to the traits, see section A.2 online

Trait	Crops	Weeds	R ²	p
Taxonomy, N2 fixation and photosynthetic pathway				
Dicot species (proportion)	0.742	0.788		0.1356
Legume species (proportion)	0.57	0	0.39	<0.0001
C4 species (proportion)	0.038	0.182	0.05	<0.0001
Species traits				
Plant shape				
Prostrate	0.09	0.12		0.1638
Rosette	0.23	0.3	0.01	0.0358
Erect	0.51	0.48		0.3866
Climbing or twining	0.15	0.06	0.02	<0.0001
Max plant height (cm)	125.5	88.2	0.1	<0.0001
Max plant width (cm)	91.6	97.2		0.1049
Life-cycle: proportion of				
Summer annuals	0.2	0.57	0.15	<0.0001
Winter annuals	0.43	0.42		0.795
Indeterminate annuals	0.17	0	0.09	<0.0001
Perennials	0.19	0	0.1	<0.0001
Lifespan in annuals				
Minimum (months)	5.2	4.3	0.03	<0.0001
Maximum (months)	6.6	5.4	0.04	<0.0001
Seed traits				
Mass (mg)	75.46	5.86	0.17	<0.0001
Lipid content (g/g)	0.09	0.18	0.1	<0.0001
Epigeal preemergent growth (proportion)	0.406	0.788	0.15	<0.0001
Leaf traits				
Dry matter content (g/g)	167.3	174		0.0969
Nitrogen content (g/g)	44.6	27.5	0.35	<0.0001
Ecological habitat preferences				
Base temperature (°C)	2.78	4.36	0.07	<0.0001
Base water potential (MPa)	-1.51	-0.98	0.1	<0.0001
Ellenberg L	7.2	6.9	0.06	<0.0001
Ellenberg R	7.1	6.7	0.03	<0.0001
Ellenberg N in non-legumes	6.9	6.8		0.4284

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Table 4. Effect of species traits on initial-growth parameters. Linear regressors estimated with GLMSELECT of SAS on 45 annual crop and weed species. Blank cells show effects that are not significantly different from zero at p=0.05

Explanatory traits and variables	Analysed parameters	
	Initial leaf area (cm ²) [§]	Relative growth rate (cm ² /cm ² /°Cdays)
Selection mode	backward	backward
<i>R</i> ²	0.63	0.63
<i>Number of species</i>	49	49
Intercept	-2.37	0.000892
Initial leaf area [§] (cm ²)		-0.00375
Weed (instead of crop)	-0.841	
Epigeal vs hypogeal species	0.756	
Seed weight [§] (mg/seed)	0.445	0.00348
Base temperature (°C)	0.0641	0.00249

[§] log_n-transformed

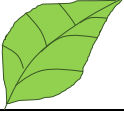













1079 Table 5. Effect of species traits on potential leaf biomass ratio and its response to shading. Linear regressors estimated with GLMSELECT using forward
 1080 selection N=672. Blank cells show effects that are not significantly different from zero at p=0.05. Continuous variables are in italics.











Species traits	In unshaded conditions Shading response	
	LBR0 (g/g) [§]	LBR_mu
[1] Weed vs crop species		0.384
Plant growth form and <i>plant stage (BBCH)</i>		
[2] Prostrate	0.12 - 0.752 · stage	-0.0321 · stage
[3] Rosette	1.81 - 0.953 · stage	-0.0245 · stage
[4] Erect	1.07 - 0.843 · stage	-0.0219 · stage
[5] Climbing or twining	0 - 0.558 · stage	-0.0477 · stage
Potential plant dimensions		
[6] <i>Maximum plant height</i>		-0.000663
[7] <i>Maximum plant width</i>	-0.00651	
Morphology parameters		
[8] Leaf biomass ratio		-0.529
Life-cycle duration		
[9] Perennials	1.078	0.376
[10] Winter annuals	-0.002	-0.024
[11] Indeterminate annuals	0.722	0.174
[12] Summer annuals	0	0
Taxonomy, N2 fixation and photosynthetic pathway		
[13] Dicot vs Monocot	0.877	-0.145
[14] C4 vs C3 (in non-legume species)	-0.622	
[15] Legume vs non-legume (in C3 species)	-1.603	
Habitat requirements		
[16] <i>Ellenberg N</i> (nitrogen) if non-legume	-0.146	-0.0131
[17] <i>Ellenberg L</i> (light)		0.0741
[18] <i>Base water potential</i> (MPa)		-0.0539
Seed and leaf traits		
[19] <i>Seed mass</i> log10(mg)	-0.236	0.0632
[20] <i>Leaf dry matter content</i> (g/g)		-0.000726
[21] <i>Leaf nitrogen content</i> (g/g)		0.00223

1081 [§] LBR was transformed to 10^{LBR} before analysis

084 Table 6. Summary of effects of species features on morphology and plasticity parameters based on linear regression as
 085 in Table 5 (with details in section E.1 online).

086 A. Unshaded conditions

Parameters	Contrasted morphologies	Species types				
		Crop or weed, plant stage, and life-cycle duration	Plant growth form ^{&} , maximum plant dimensions, morphology	Taxonomy, N ₂ fixation and photosynthetic pathway	Habitat preference [§]	Seed and leaf traits [§]
Specific leaf area (SLA0)		Young plant, annuals,	Prostrate, tall and narrow	Dicots, non-legume, C3	N-poor, acid, warm	
		Old plant, perennial,	Climbing or twining, short and wide	Monocots, legume, C4	N-rich [#] , Basic, cool	
Leaf biomass ratio (LBR0)		Young plants, perennial	Climbing or twining, narrow	Dicots, non-legume, C3	N-poor	Small seeds
		Old plants, summer or winter annual	Prostrate, wide	Monocots, legume, C4	N-rich	Heavy seeds
Specific plant height (HM0)		Young plant	Erect or rosette, tall, stemmy		N-poor for non-legumes, shaded, warm	Lipid-poor seeds
		Old plant	Prostrate, climbing or twining, short, leafy		N-rich for non-legumes, sunny, cool	Lipid-rich seeds
Impact of plant biomass on plant height (b _{HM})		Young plant, summer annual	Rosette or erect, tall per unit biomass	Dicots	Sunny, basic	Lipid-poor seeds
		Old plant, indeterminate annual	Climbing or twining, short per unit biomass	Monocots	Shaded, acid	Lipid-rich seeds
Specific plant width (WM0)			Tall	Non-legume, C4	Shaded, acid	N-rich leaves
			Short	Legume, C3	Sunny, basic	N-poor leaves
Impact of plant biomass on plant width (b _{WM})		Weed	Wide, wide per unit biomass			
		Crop	Narrow, narrow per unit biomass			
Median leaf area height (RLH0) ^t		Weed, old plant, perennial			N-poor, basic, cool, moist	Small seeds, hypogeal growth, non-dense leaves
		Crop, young plant, summer annuals			N-rich, acid, warm, dry	Heavy seeds, epigeal growth, dense leaves

Parameters	Contrasting changes	Species types				
		Crops or weeds, plant stage, and life-cycle duration	Plant growth form ^{&} , maximum plant height and width, morphology	Taxonomy, N2 fixation and photosynthetic pathway	Habitat preference [§]	Seed and leaf traits [§]
Change in specific leaf area when shaded (mu_SLA)		Old plants, summer annuals			N-rich, shaded	Lipid-rich seeds, N-rich leaves
		Young plants, indeterminate annuals			N-poor, sunny	Lipid-poor seeds, N-poor leaves
Change in Leaf biomass ratio when shaded (mu_LBR)		Weeds, young plants, perennials	Tall, stemmy	Monocots	N-poor, sunny, dry	Heavy seeds, non-dense or N-rich leaves
		Crops, old plants, summer or winter annuals	Short, leafy	Dicots	N-rich, shaded, moist	Light seeds, dense or N-poor leaves
Change in Specific plant height when shaded (mu_HM)		Old plants, summer annuals	Rosette or prostrate, tall and narrow, short per unit biomass	Legume, C3	Shaded, acid	Light seeds, hypogeal, dense leaves
		Young plants, perennials	Erect, climbing or twining, short and wide, tall per unit biomass	Non-legume, C4	Sunny, basic	Heavy seeds, epigeal, non-dense leaves
Change in Specific plant width when shaded (mu_WM)		Old plants	Narrow		Acid	
		Young plants	Wide		Basic	
Change in Median leaf area height when shaded (mu_RLH)		Old plants, perennials or winter annuals	Rosette, bottom-heavy	Dicots	Shaded	Lipid-poor or light seeds, non-dense leaves
		Young plants, summer or indeterminate annuals	Prostrate, top-heavy	Monocots	Sunny	Lipid-rich or heavy seeds, dense leaves

090 [§] Ellenberg N (nitrogen), L (light), R (pH), base temperature and water potential
 091 [§] Seed mass and lipid-content, leaf dry matter content, leaf nitrogen content, epigeal or hypogeal growth
 092 [&] Erect, prostrate, rosette, climbing or twining
 093 [#] Only for non-legumes
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Table 7. Variability in plant-morphology parameters explained by species features. R² of different linear models linking parameters to features using forward with with PROC GLMSELECT of SAS

Parameters	Model type				
	All species	Weeds only	Crops	Monocotyledonous species only	Dicotyledonous species only
Number of species	61	25	36	15	46
Potential morphology (in unshaded conditions)					
Specific Leaf Area SLA0	0.42	0.30	0.55	0.49	0.55
Leaf biomass ratio LBR0	0.86	0.83	0.88	0.89	0.86
Specific plant height HM0	0.26	0.25	0.68	0.3	0.32
Sensitivity of plant height to biomass b_HM	0.59	0.63	0.85	0.79	0.59
Specific plant width WM0	0.22	0.26	0.45	0.24	0.40
Sensitivity of plant width to biomass b_WM	0.29	0.32	0.48	0.96	0.20
Median relative leaf area height RLH0	0.35	0.37	0.65	0.67	0.28
Shape of leaf area distribution b_RLH	0.62	0.45	0.71	0.93	0.68
Shading response of					
Specific Leaf Area SLA_mu	0.45	0.48	0.75	0.44	0.53
Leaf biomass ratio LBR_mu	0.41	0.51	0.54	0.54	0.44
Specific plant height HM_mu	0.42	0.53	0.58	0.61	0.41
Specific plant width WM_mu	0.09	0.21	0.23	0.46	0.1
Median relative leaf area height RLH_mu	0.39	0.56	0.58	0.48	0.41

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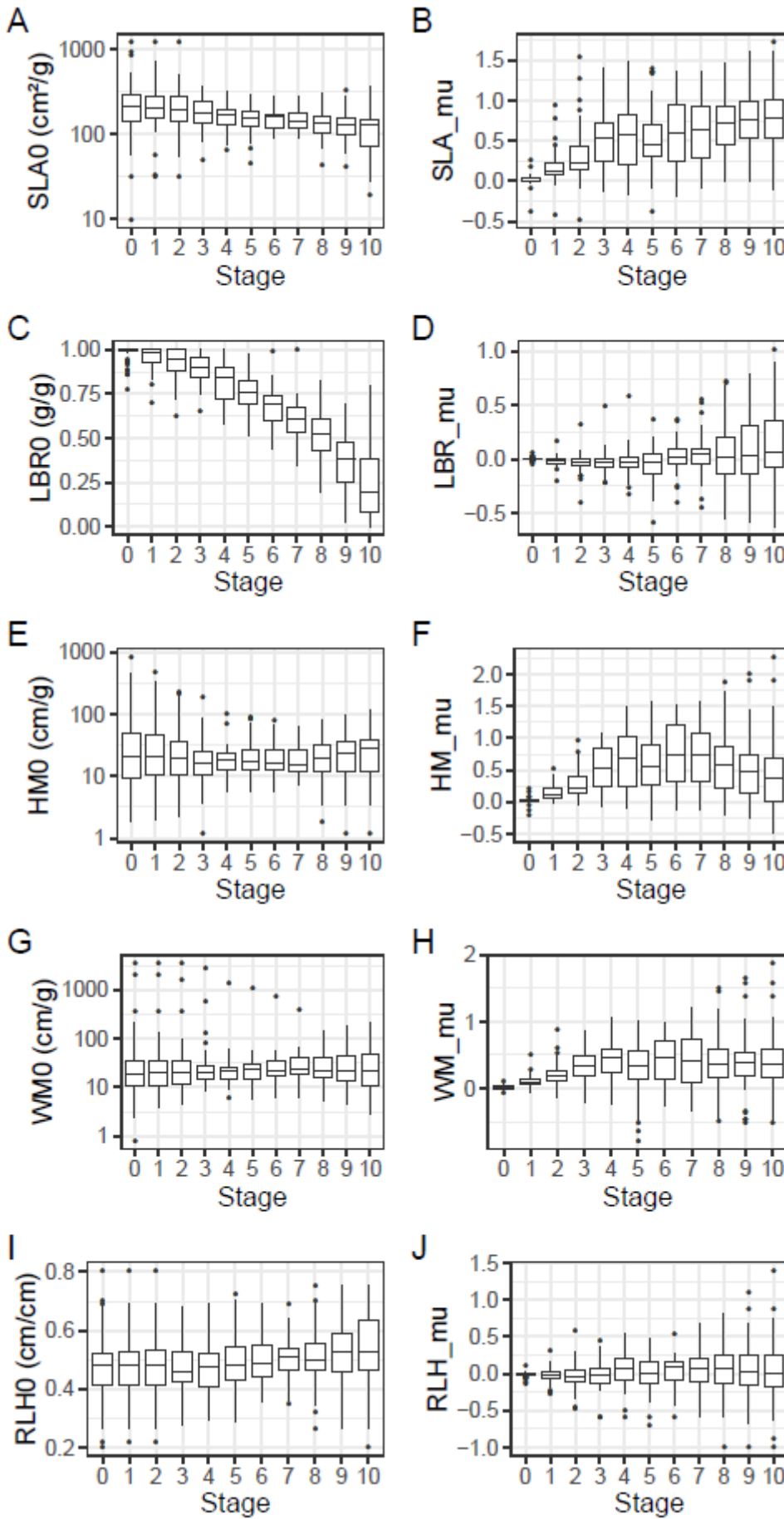
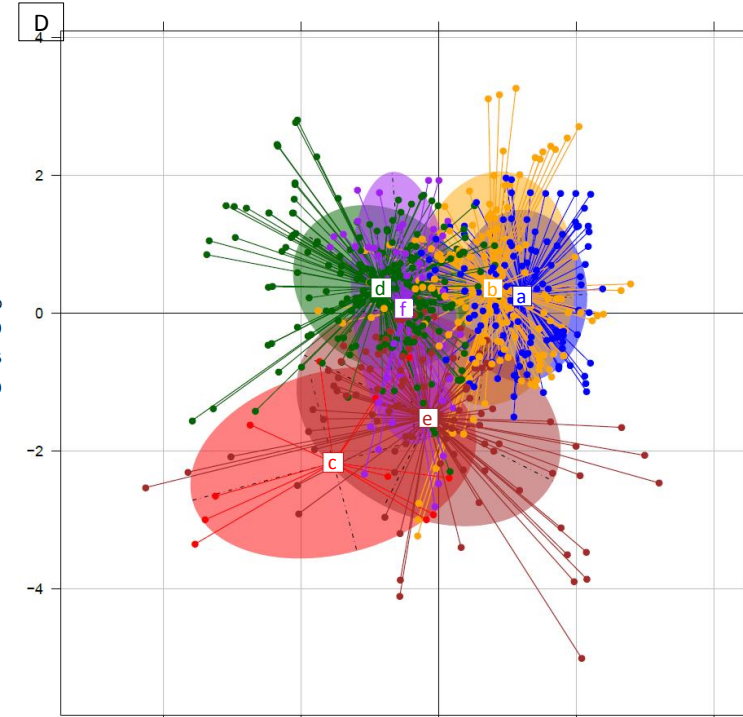
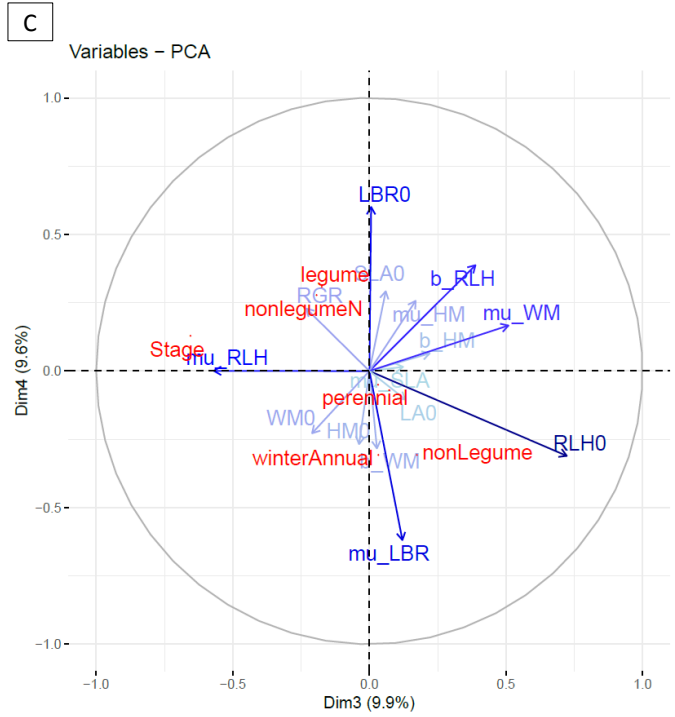
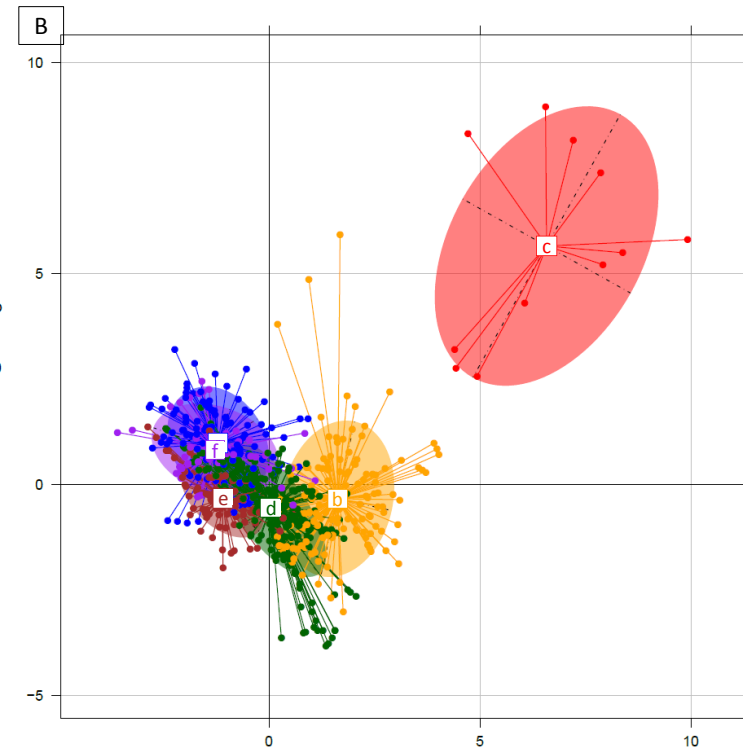
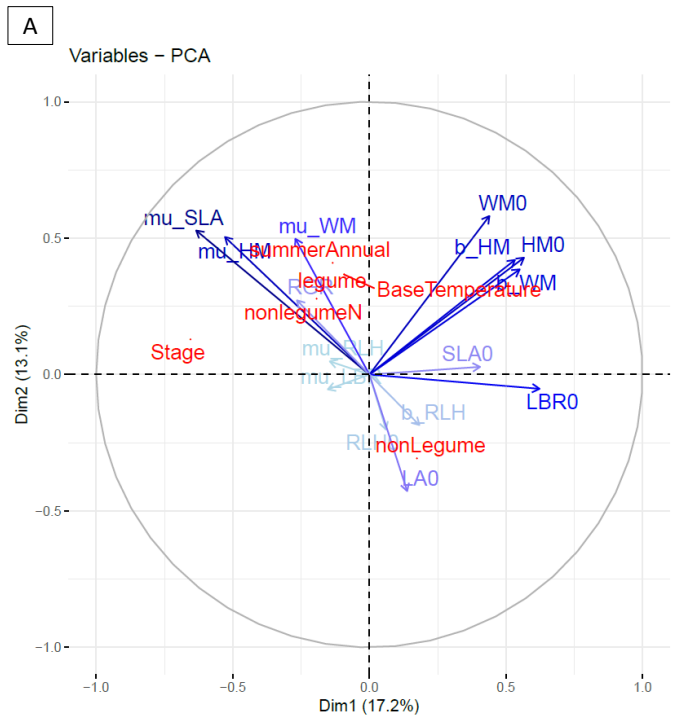


Figure 1. Variation in potential morphology parameters and shading response parameters with plant stage for 25 weed and 33 crop species x varieties. Boxes show 25%, 50% and 75% percentiles, whiskers are located at 1.5 IQR from the boxes, with IQR the distance between the first and third quantiles; dots show outliers. For the meaning of the parameters, see Table 1

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Species	Clusters listing species x stages					
	a	b	c	d	e	f
ABUTH	3-10	1-2	0			
ALOMY	2-3			0-1 4-8	9-10	
AMARE	7-8			0-6	9-10	
AMBEL				0-10		
AVEFA		3	0-2	4	5-10	
AVESG	5	0-4		6	7-10	
BRSNN				0-10		
CAPBP	7-9	1-6		0	10	
CHEAL	7-10	5-6	0-3			
DATST	6-8			0-5	9-10	
DIGSA			0-1			2-10
ECHCG	4-10			0-3		
FESRU	5-10	0-4				
GALAP		0-2		3-10		
GERDI		0-1		2-7	8-10	
GUIAB	5-10	0-4				
HELAN				0-10		
LENCU	7-10	0-6				
LENNI	6-10			0-5		
LOTCO		0-5			6-10	
LTHSA	7-10			0-2	3-6	
MATIN				0-5	6-10	
MEDLU	5-10	0-4				
MEDSA		0-6			7-10	
MERAN	3-10			0-2		
PANMI						0-10
PHCTA		0-4		5-8	9-10	
PIBSXcv886-1	10			0-8	9	
PIBSXcvChina				0-10		
PIBSXcvEnduro				0-10		
POAAN	4-10	0-2		3		
POLAV	6-10			0-5		
POLCO	4-10			0-3		
POLPE	3-10	1	0			
RAPSR	8-10	0-4		5-7		
SENVU		0-3 6-10			4-5	
SOLNI				0		1-10
SONAS	3-10			0-2		
STEME		0-4		5-8	9-10	
TRFAL		0-6			7-10	
TRFPR		0-5		6-8		9-10
TRFRE	3-10	0-2				
TRKFG		0-2		3-10		
TRZAXcvCaphorn				0-6	7-10	
TRZAXcvCézanne				0-6	7-10	
TRZAXcvOrvantis				0-6	7-10	
TTLSS				0-6	7-10	
VERHE				0-8	9-10	
VERPE		0-5			6-10	
VICFXcvDiana	7-8	0-2		3-6	9-10	
VICFXcvGladice		0-7			8-10	
VICSA		0-4		5-8	9-10	
ZEAMY						0-10

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105 3 Figure 2. Typology of crop and weed species based on a Principal Component Analysis on the morphology and shading-response parameters. Correlation circles with
106 4 parameters in blue (see Table 1 for meaning), with the five most important species features projected in red for the first two (A) and the last two axes (C). Individuals are
107 5 species x stage combinations clustered into groups, following a Ward ascendant hierarchy classification for the first two (B) and the last two axes (D). Species names are
108 6 EPPO codes, with weeds highlighted in yellow and crops in green, and the main cluster of each species in bold (Nathalie Colbach © 2019)

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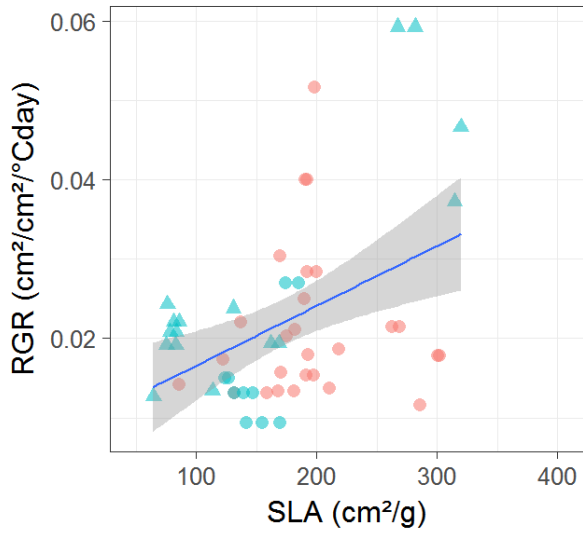


Figure 3. Variation in relative growth rate (RGR) with specific leaf area estimated for BBCH stage 4 from experiments (\blacktriangle = monocots, \bullet = dicots, \blacktriangle = hypogeal, \bullet = epigeal). Line shows fitted linear regression ($y = 0.0090 + 7.55 \cdot 10^{-5} x$, $R^2 = 0.19$, $p = 0.0013$)

10 Appendix

Appendix 1. List of weed species tested in the present experiments (further trait values can be found in section A.2 online)

Family	Species	EPPO code	Seed mass (mg) [§]	Used in analysis of Greenhouse	Used in analysis of Garden plots
Poaceae	<i>Alopecurus myosuroides</i>	ALOMY	2.3	2009	&
	<i>Avena fatua</i>	AVEFA	18.5	2009, 2010	2010
	<i>Digitaria sanguinalis</i>	DIGSA	0.63	2012	2012
	<i>Echinochloa crus-galli</i>	ECHCG	2.24	2010, 2011	2011
	<i>Panicum miliaceum</i>	PANMI	4.3	2012	2012
	<i>Poa annua</i>	POAAN	0.3	2010, 2012	2012
	<i>Setaria viridis</i>	SETVI	1.4	2012	
Amaranthaceae	<i>Amaranthus retroflexus</i>	AMARE	0.38	2010, 2011	2011
	<i>Chenopodium album</i>	CHEAL	0.56	2010, 2011	2011
Apiaceae	<i>Aethusa cynapium</i>	AETCY	1.4	2011	
Asteraceae	<i>Ambrosia artemisiifolia</i>	AMBEL	4.59	2010, 2011	2011
	<i>Ammi majus</i>	AMIMA	0.50	2010	
	<i>Lapsana communalis</i>	LAPCO	0.90	2010	
	<i>Matricaria perforata</i>	MATIN	0.27	2012	2012
	<i>Matricaria recutita</i>	MATCH	0.3	2010, 2011	
	<i>Senecio vulgaris</i>	SENVU	0.26	2010	2010
	<i>Sonchus asper</i>	SONAS	0.3	2010, 2011	2011
Brassicaceae	<i>Capsella bursa-pastoris</i>	CAPBP	0.14	2009	2009
	<i>Raphanus raphanistrum</i>	RAPRA	6.35	2012	
	<i>Sinapis arvensis</i>	SINAR	1.97	2009	
Caryophyllaceae	<i>Stellaria media</i>	STEME	0.4	2009, 2010	2009
Cucurbitaceae	<i>Sicyos angulatus</i>	SIYAN	102.2	2010	
Euphorbiaceae	<i>Euphorbia helioscopia</i>	EPHHE	2.5	2010	
	<i>Mercurialis annua</i>	MERAN	1.87		2011
Geraniaceae	<i>Geranium dissectum</i>	GERDI	2.12	2009	2009
Malvaceae	<i>Abutilon theophrasti</i>	ABUTH	8.12	2012 [§]	2012
Plantaginaceae	<i>Veronica hederifolia</i>	VERHE	3.52		2009
	<i>Veronica persica</i>	VERPE	0.67	2009, 2010	2009
Polygonaceae	<i>Fallopia convolvulus</i>	POLCO	6.52	2010	2011
	<i>Polygonum aviculare</i>	POLAV	1.52	2010, 2011	2011
	<i>Polygonum persicaria</i>	POLPE	1.9	2010, 2011	2011
Rubiaceae	<i>Galium aparine</i>	GALAP	7.37	2010	&
Solanaceae	<i>Datura stramonium</i>	DATST	7.2	2010	2012
	<i>Solanum nigrum</i>	SOLNI	0.8	2010, 2011	2011
Violaceae	<i>Viola arvensis</i>	VIOAR	0.57	2009, 2010	

[§] Dry mass per seed

[§] Year the experiments were carried out

& (Munier-Jolain *et al.*, 2014)

Appendix 2. List of crop species tested in the present experiments (further trait values can be found in section A.2 online)

Family	Species	Cultivar	EPO code	Seed mass (mg) [§]	Used in experiments in	
					Greenhouse	Garden plots
Poaceae	<i>Avena strigosa</i>	Pratex	AVESG	18.11		2015
	<i>Festuca rubra</i>	Greenlight	FESRU	0.86		2015
	<i>Sorghum bicolor</i>		SORVU	23.0	2010	
	<i>Triticum aestivum</i>	Caphorn	TRZAX	42.1	2009	2009
	<i>Triticum aestivum</i>	Cézanne	TRZAX	45.5	2009	2009
	<i>Triticum aestivum</i>	Orvantis	TRZAX	42.1	2009	2009
	<i>xTriticosecale</i>	Matinal	TTLSS	43.6	2009	2009, 2015
	<i>Zea mays</i>		ZEAMX	252	2010, 2012	2012
Asteraceae	<i>Guizotia abyssinica</i>	Azofix	GUIAB	2.51	2010	2015
	<i>Helianthus annuus</i>		HELAN	41.1	2010	2012
Boraginaceae	<i>Phacelia tanacetifolia</i>	Angelia	PHCTA	1.98	2010	2015
Brassicaceae	<i>Brassica napus</i>		BRSNN	4.4		&
	<i>Raphanus sativus</i>	Cardinal	RAPSR	12.1	2010	2015
	<i>Sinapis alba</i>		SINAL	6.5	2010	
Fabaceae	<i>Glycine max</i>		GLXMA	185	2010	
	<i>Lathyrus sativus</i>	N-fix	LTHSA	162		2016
	<i>Lens culinaris</i>	Anicia	LENCU	31.0		2016
	<i>Lens nigricans</i>	Lentifix	LENNI	17.1		2015
	<i>Lotus corniculatus</i>	Leo	LOTCO	1.13		2016
	<i>Medicago lupulina</i>	Virgo	MEDLU	1.71		2016
	<i>Medicago sativa</i>	Galaxy	MEDSA	2.00		2016
	<i>Pisum sativum</i>	China	PIBSX	153	2010	2010
	<i>Pisum sativum</i>	Enduro	PIBSX	187	2010	2010
	<i>Pisum sativum</i>	886/1	PIBSX	131	2010	2010
	<i>Trifolium alexandrinum</i>	Tabor	TRFAL	3.64	2010	2016
	<i>Trifolium pratense</i>	Trevviso	TRFPR	2.20		2016
	<i>Trifolium repens</i>	Aberdai	TRFRE	0.66		2015
	<i>Trigonella foenum-graecum</i>	Fenusol	TRKFG	16.9		2015
<i>Vicia faba</i>	Diana	VICFX	270		2016	
<i>Vicia faba</i>	Gladice	VICFX	426	2010	2010	
<i>Vicia sativa</i>	Nacre	VICSA	50.4		2016	

[§] Dry mass per seed; [§] Year the experiments were carried out; [&] (Munier-Jolain *et al.*, 2014)

Appendix 3. Sources used to estimate trait values other than those measured in the present experiments.

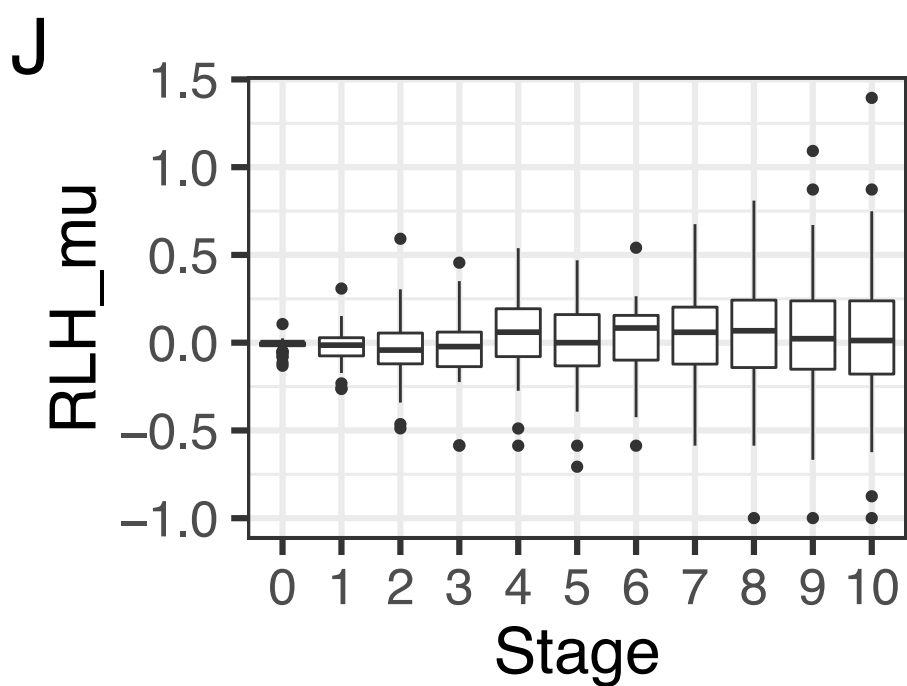
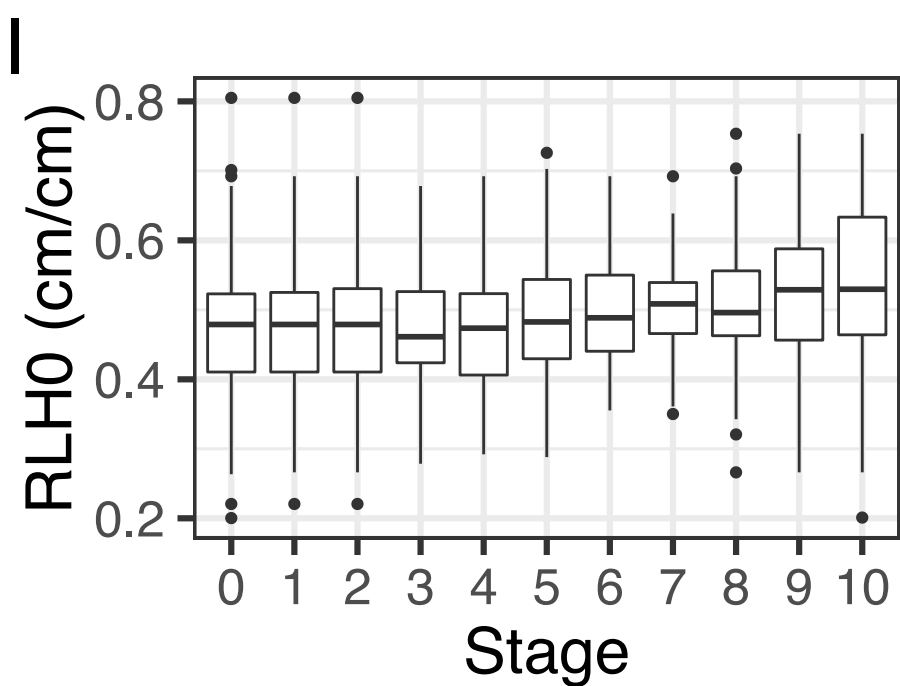
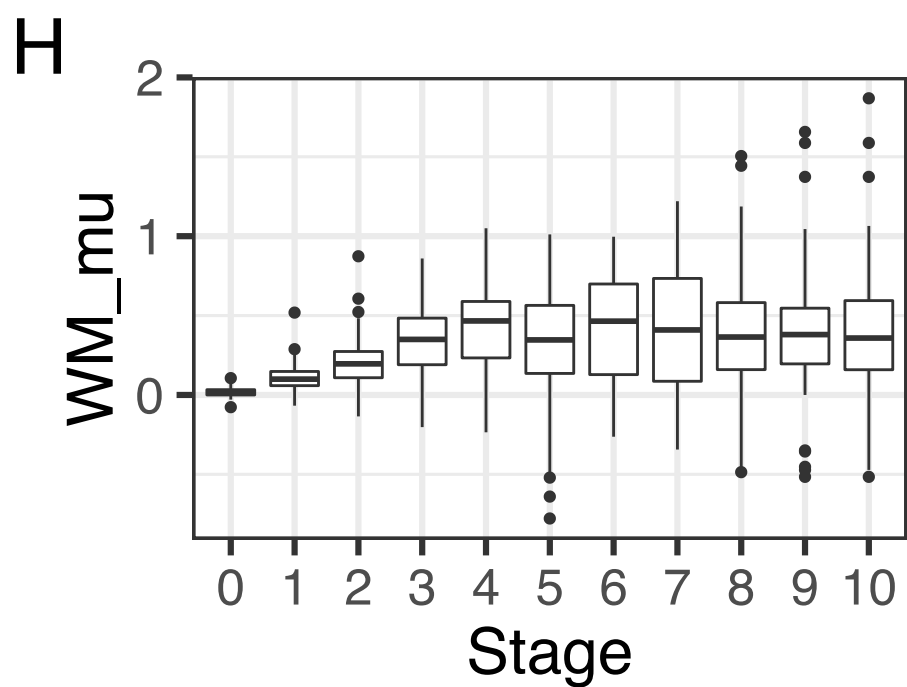
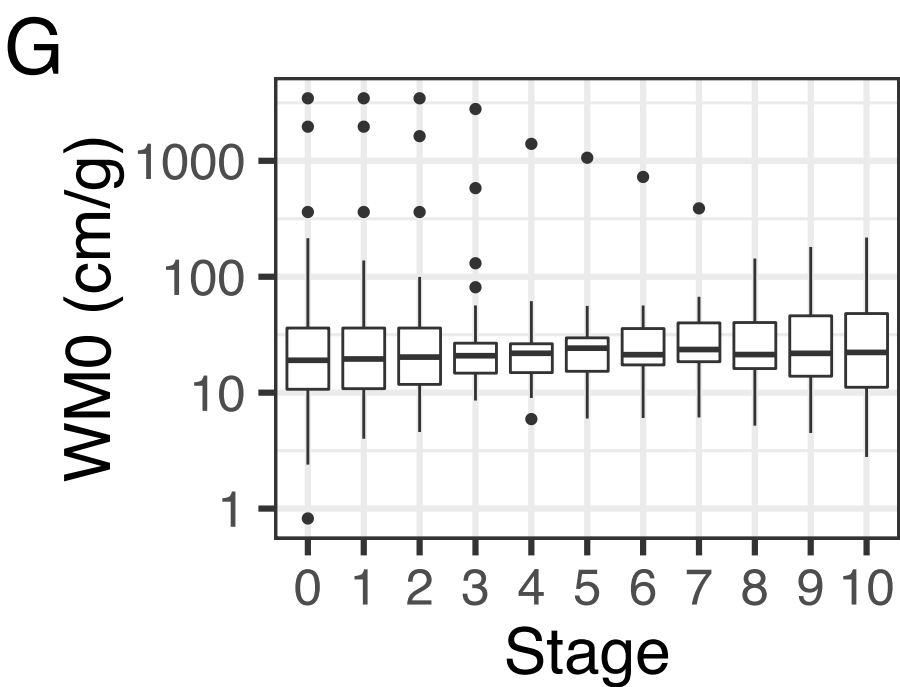
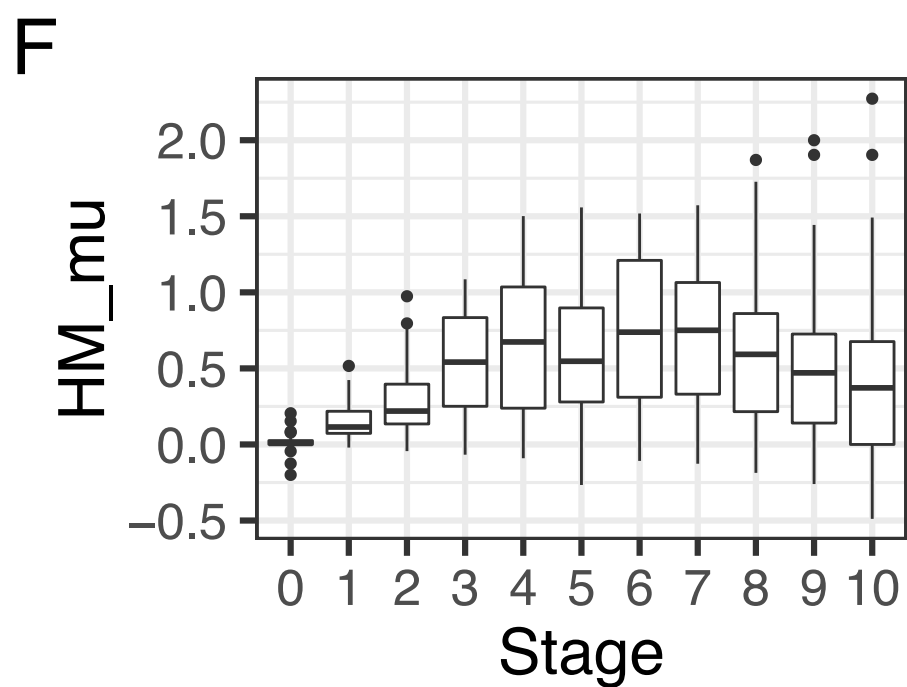
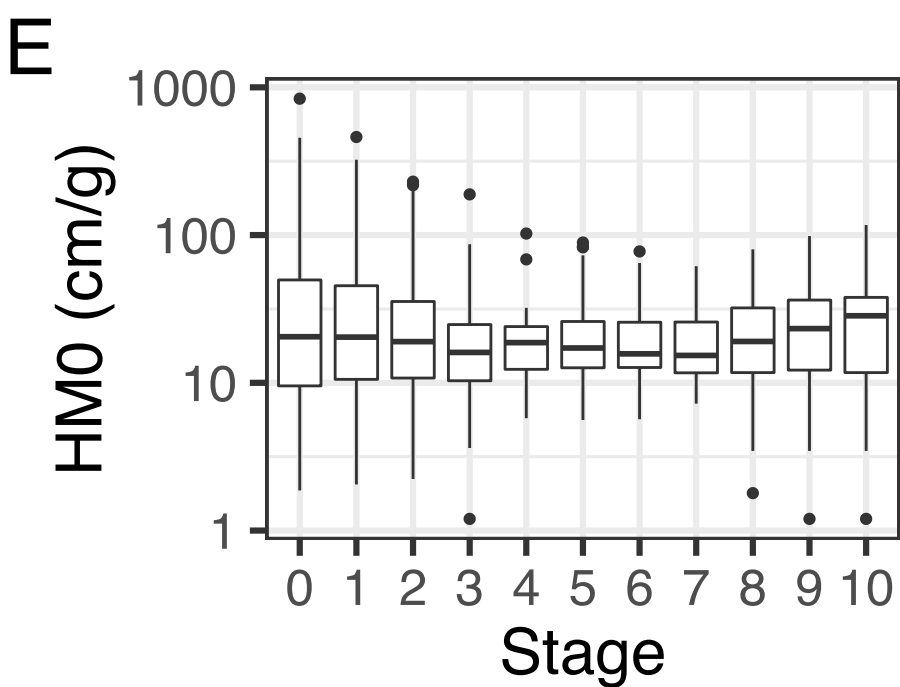
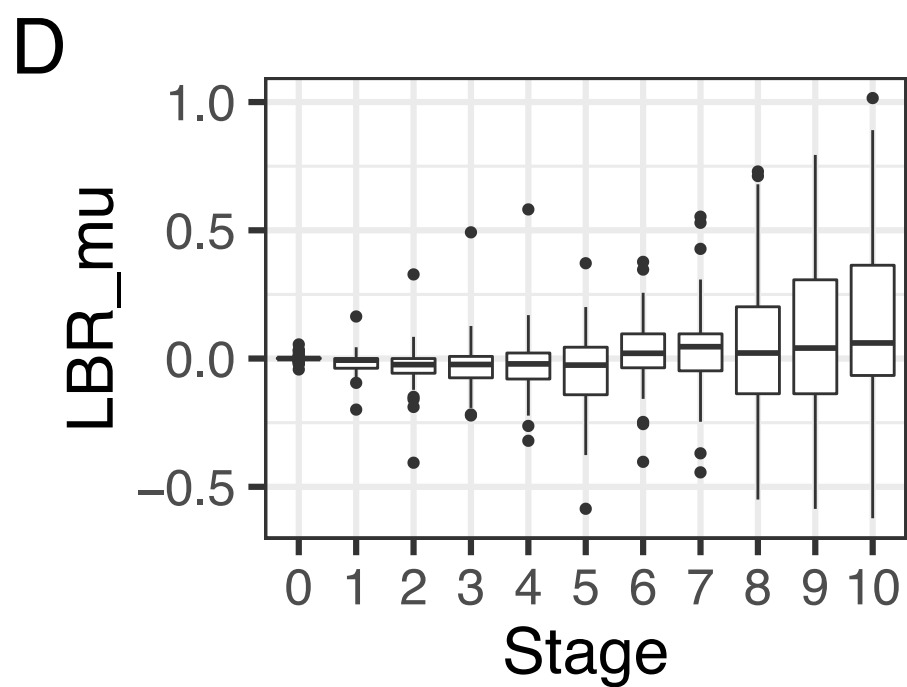
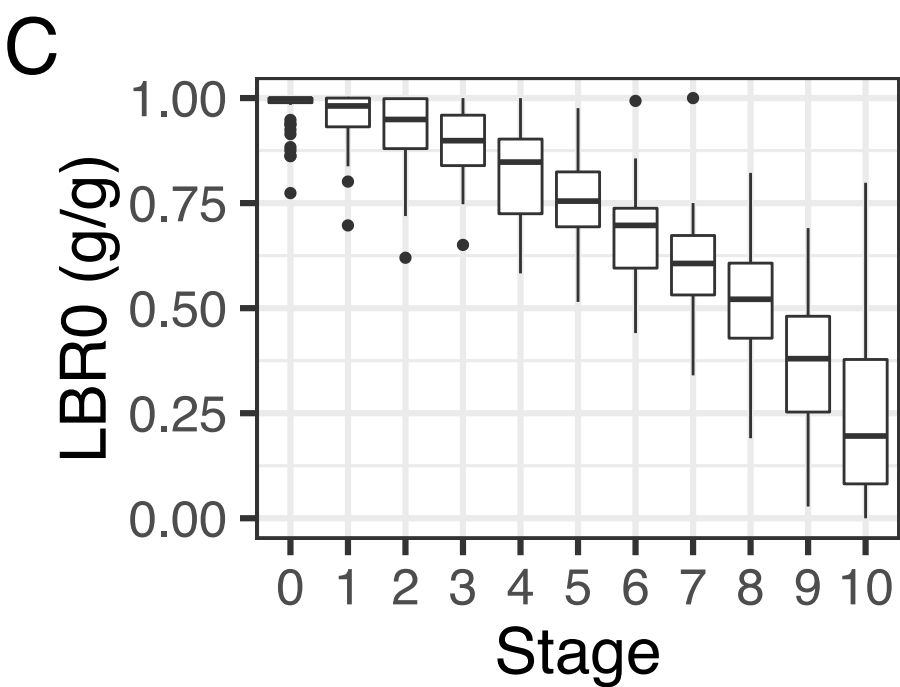
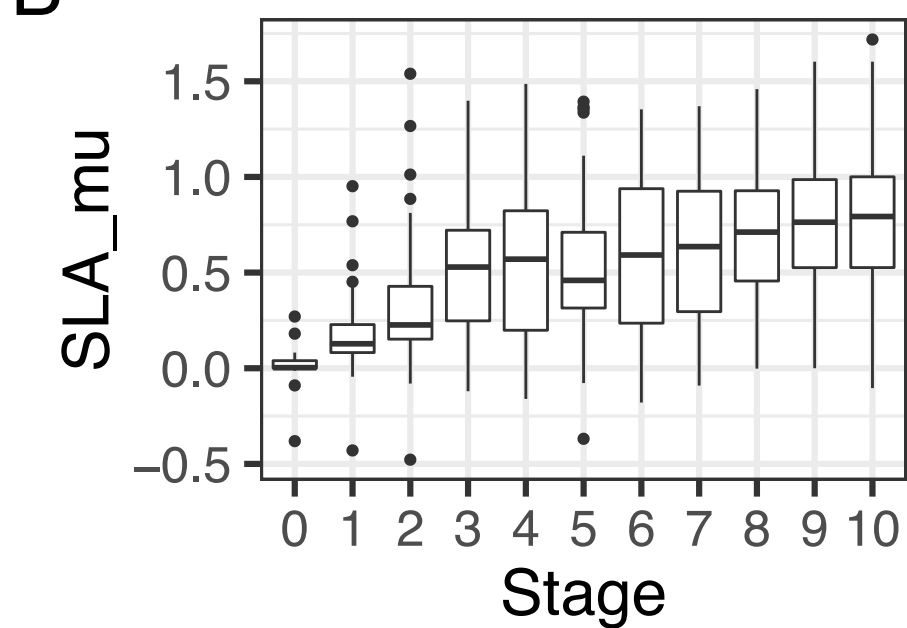
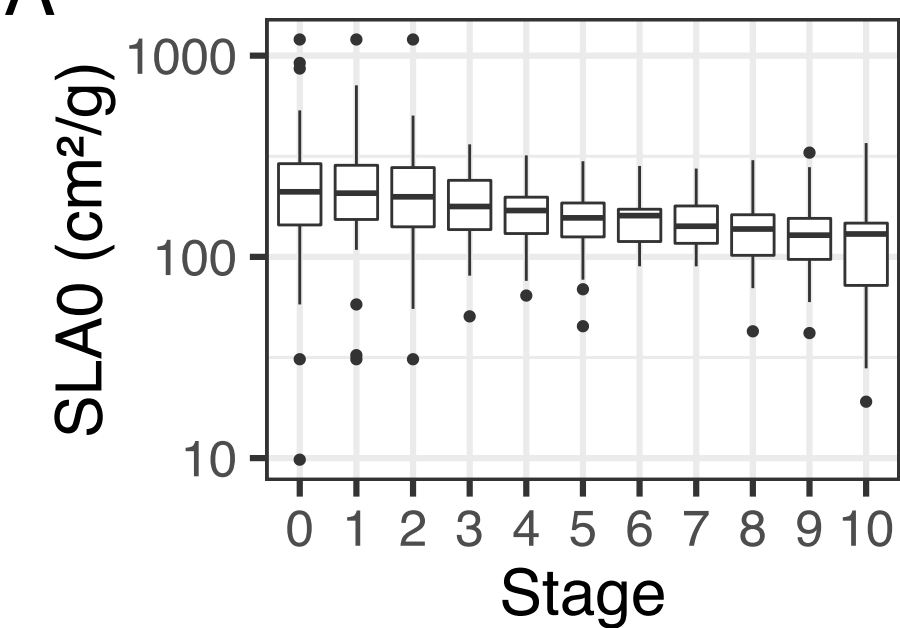
A. Trait data bases & web sites

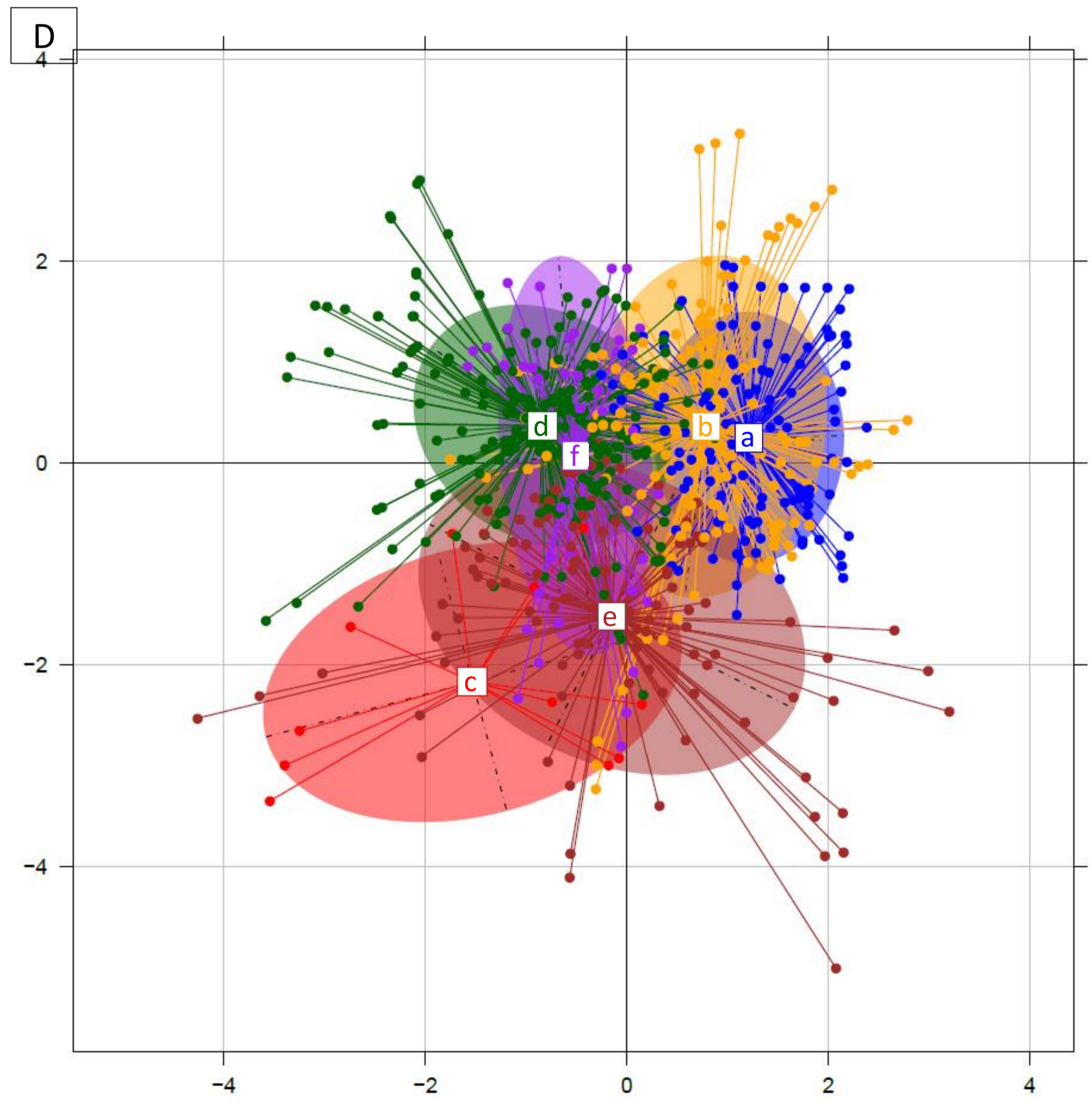
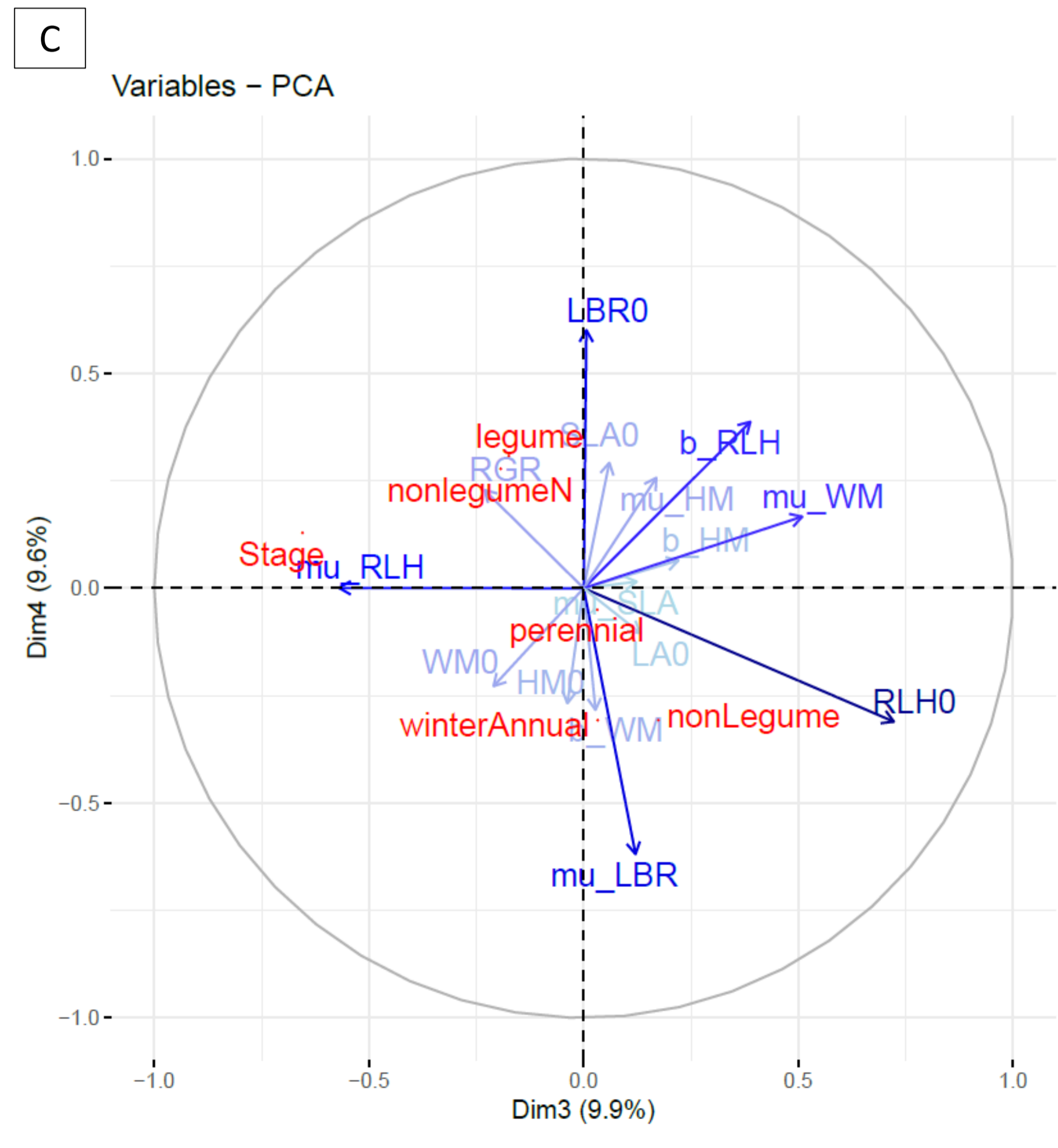
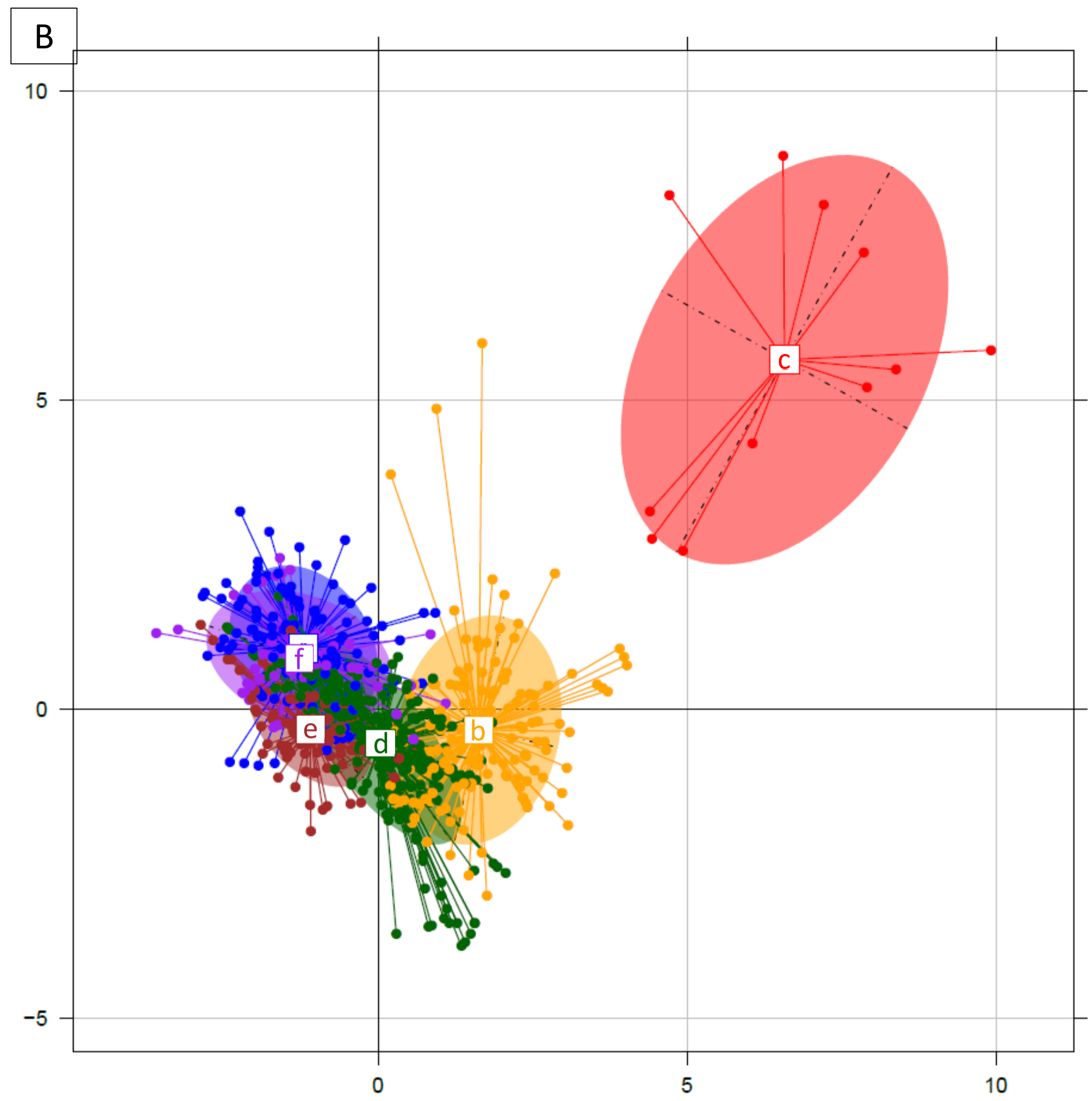
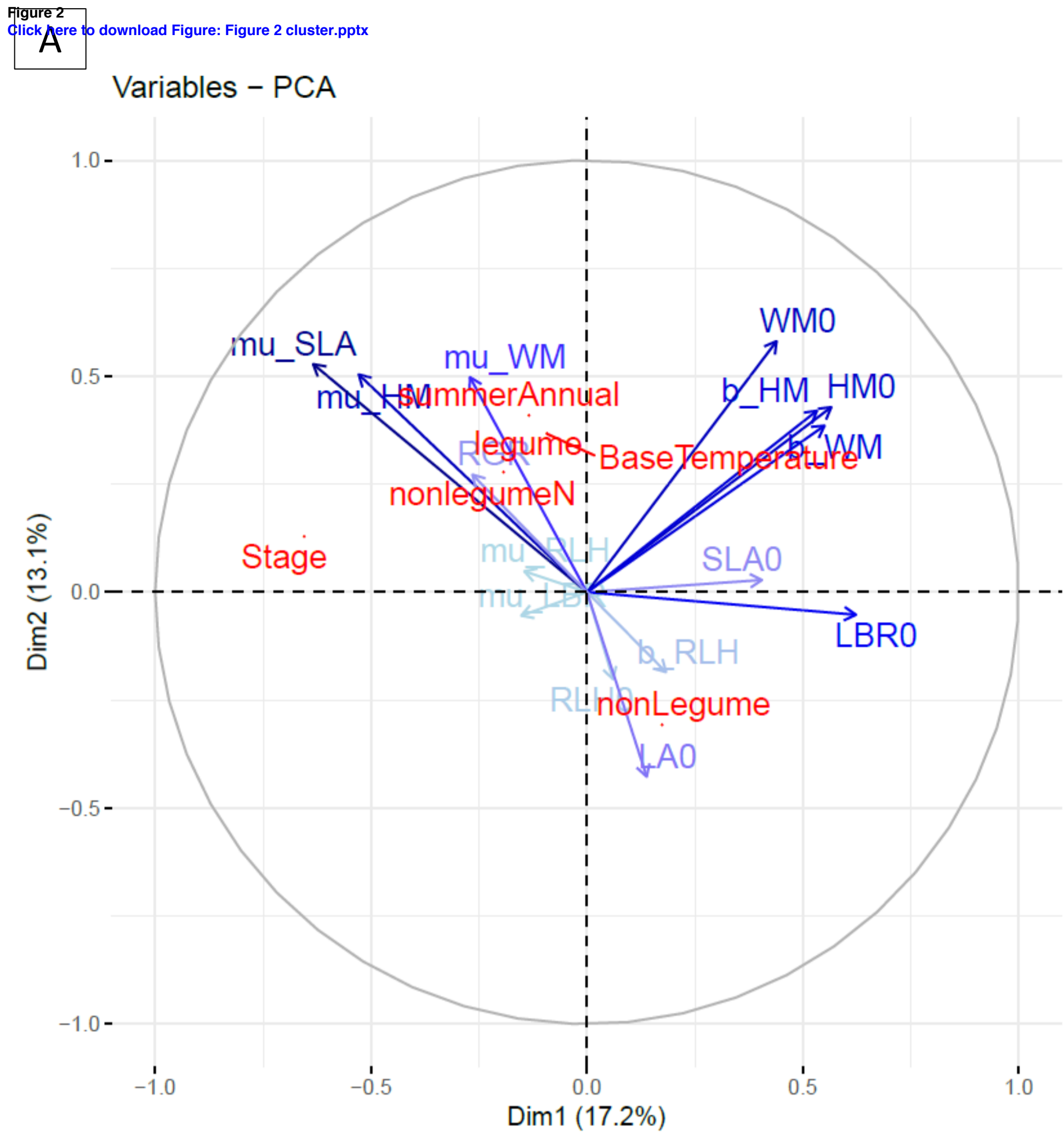
- <http://www.tela-botanica.org/bdtfx-nn-27521-synthese>
- (<http://data.kew.org/>
- <http://www.leda-traitbase.org>
- http://www2.dijon.inra.fr/hyppa/hyppa-f/abuth_fh.htm
- <http://www.try-db.org>

B. Literature

(Larsen, 1977; Bruckler, 1983b; 1983a; Hur and Nelson, 1985; Gummerson, 1986; Bouaziz and Bruckler, 1989; Fournier, 1990; Benvenuti and Macchia, 1993; Van Der Weide, 1993; Chauvel, 1996; Marshall and Squire, 1996; Brisson *et al.*, 1998; Grundy *et al.*, 2000; Colbach *et al.*, 2002a; Colbach *et al.*, 2002b; Granier *et al.*, 2002; Batlla *et al.*, 2003; Munier-Jolain *et al.*, 2005b; McGiffen *et al.*, 2008; Sartorato and Pignata, 2008; Alghamdi, 2009; Masin *et al.*, 2010; Gardarin *et al.*, 2011; Kattge *et al.*, 2011; Nasab, 2011; Fayaud *et al.*, 2012; Guillemain *et al.*, 2013; Dürr *et al.*, 2015; Gardarin and Colbach, 2015; Rolletschek *et al.*, 2015; Bretagnolle *et al.*, 2016; Gardarin *et al.*, 2016; Tribouillois *et al.*, 2016; Scherner *et al.*, 2017)

Figure 1
[Click here to download Figure: Figure 1 boxplot.pdf](#)





Species	Clusters listing species x stages					
	a	b	c	d	e	f
ABUTH	3-10	1-2	0			
ALOMY	2-3			0-1 4-8	9-10	
AMARE	7-8			0-6	9-10	
AMBEL				0-10		
AVEFA		3	0-2	4	5-10	
AVESG	5	0-4		6	7-10	
BRSNN				0-10		
CAPBP	7-9	1-6		0	10	
CHEAL	7-10	5-6	0-3			
DATST	6-8			0-5	9-10	
DIGSA			0-1			2-10
ECHCG	4-10			0-3		
FESRU	5-10	0-4				
GALAP		0-2		3-10		
GERDI		0-1		2-7	8-10	
GUIAB	5-10	0-4				
HELAN				0-10		
LENCU	7-10	0-6				
LENNI	6-10			0-5		
LOTCO		0-5			6-10	
LTHSA	7-10			0-2	3-6	
MATIN				0-5	6-10	
MEDLU	5-10	0-4				
MEDSA		0-6			7-10	
MERAN	3-10			0-2		
PANMI						0-10
PHCTA		0-4		5-8	9-10	
PIBSXcv886-1	10			0-8	9	
PIBSXcvChina				0-10		
PIBSXcvEnduro				0-10		
POAAN	4-10	0-2		3		
POLAV	6-10			0-5		
POLCO	4-10			0-3		
POLPE	3-10	1	0			
RAPSR	8-10	0-4		5-7		
SENVU		0-3 6-10			4-5	
SOLNI				0		1-10
SONAS	3-10			0-2		
STEME		0-4		5-8	9-10	
TRFAL		0-6			7-10	
TRFPR		0-5		6-8		9-10
TRFRE	3-10	0-2				
TRKFG		0-2		3-10		
TRZAXcvCaphorn				0-6	7-10	
TRZAXcvCézanne				0-6	7-10	
TRZAXcvOrvantis				0-6	7-10	
TTLSS				0-6	7-10	
VERHE				0-8	9-10	
VERPE		0-5			6-10	
VICFXcvDiana	7-8	0-2		3-6	9-10	
VICFXcvGladice		0-7			8-10	
VICSA		0-4		5-8	9-10	
ZEAMX						0-10

Figure 3
[Click here to download high resolution image](#)

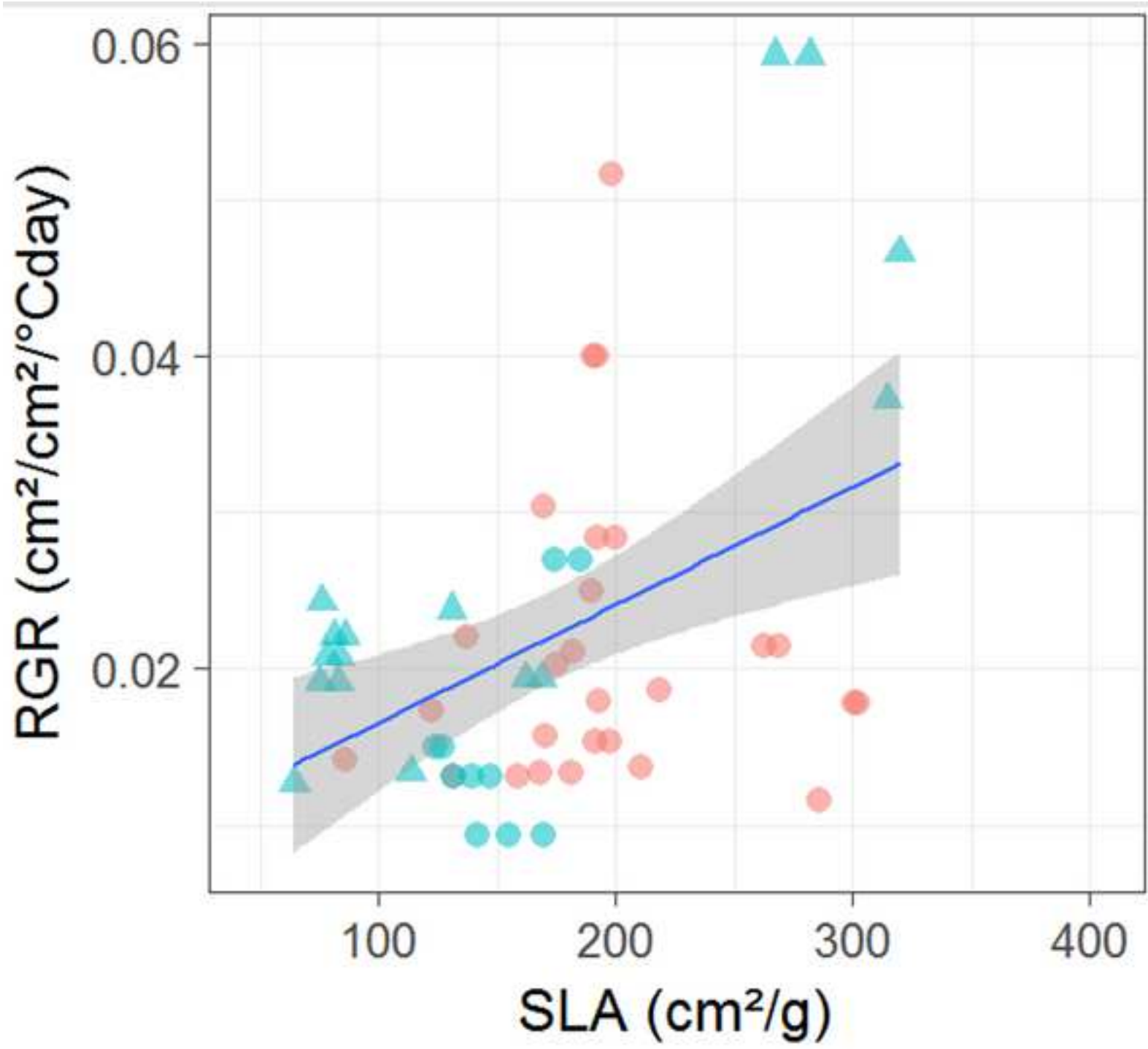


Table 1

Parameter name	Relative advance of growth stage at the time of parameter measurement	Unit	Median [min,max] [§]		Variation ^{&}	Crops	Weeds
A. Initial growth (without shading or self-shading)							
RGR	Relative growth rate	cm ² ·cm ⁻² ·°Cday ⁻¹	0.0186	[0.0093,0.0592]	0.52	0.0231 A	0.0207 A
LA0	Leaf area at emergence	cm ²	0.260	[0.01,3.97]	1.48	1.194 A	0.220 B
B. Potential morphology (morphology variables in unshaded conditions)							
SLA0	Specific Leaf Area (ratio of leaf area to leaf biomass [§])	cm ² ·g ⁻¹	153	[10,1204]	0.49	168 B	187 A
LBR0	Leaf biomass ratio (ratio of leaf biomass to total above-ground biomass)	none	0.75	[0,1]	0.23	0.7 A	0.69 A
HM0	Specific (allometric) plant height (ratio of plant height to total above-ground plant biomass to the power of b_HM)	cm·g ⁻¹	20	[1.2,838]	1.08	30 A	37 A
b_HM	Shape parameter for impact of plant biomass on plant height (0 = none, 1 = positive correlation)	none	0.27	[0.0005,0.99]	0.55	0.28 B	0.32 A
WM0	Specific (allometric) plant width (ratio of plant width to total above-ground plant biomass to the power of b_WM)	cm·g ⁻¹	22	[0.82,3464]	2.68	27 B	115 A
b_WM	Shape parameter for impact of plant biomass on plant width (0 = none, 1 = positive correlation)	none	0.37	[0.02,1.7]	0.58	0.37 B	0.41 A
RLH0	Median relative leaf area height (relative plant height below which 50% of leaf area are located)	cm cm ⁻¹	0.48	[0.2,0.81]	0.21	0.49 A	0.5 A
b_RLH	Shape parameter for leaf area distribution along plant height	none	2.7	[0.24,58]	0.78	8.66 A	2.66 B
C. Response to shading (variation in morphology variables with shading intensity)							
SLA_mu	Response of specific leaf area to shading	none	0.48	[-0.56,1.72]	0.36	0.44 B	0.55 A
LBR_mu	Response of leaf biomass ratio to shading	none	-0.01	[-0.66,1.02]	0.19	-0.041 B	0.037 A
HM_mu	Response of specific height to shading	none	0.43	[-0.53,2.27]	0.39	0.36 B	0.52 A
WM_mu	Response of specific width to shading	none	0.27	[-1.53,1.87]	0.31	0.23 B	0.32 A
RLH_mu	Response of median relative leaf area height to shading	none	0.01	[-1,1.39]	0.25	0.009 A	0.012 A

[§] For B and C, over all stages. [&] standard-deviation/mean, except for shading response where standard-deviation because of negative values of mean close to zero [§] Biomass is always dry (leaf or plant) mass

Table 2

Species features	Related parameters	Effect [§]	Hypothesis	Reference	Adaptation in our study
Taxonomy and N ₂ fixation					
Clade (Dicots vs monocots)	RBR	-	Dicots attribute less biomass to roots	(Moreau <i>et al.</i> , 2014)	Look at clade effect on all parameters
Ability to symbiotically fix N ₂ (legumes)	SLA, LBR, LAR HM	- +	Legumes invest more in below-ground structures	(den Dobbelden and Verburg, 1996)	Also look at photosynthetic pathway (C3 vs C4)
Species traits					
Plant growth form: climbing vs self-supporting	RGR SLA LBRt HM	0 + ns - +	Climbing species have high SLA to compensate for low LBR Climbing species have longer stems	(den Dobbelden and Verburg, 1996)	Also look at other plant forms
Leaf life-span	Initial leaf biomass, RGR	-	High growth rate and initial leaf size compensate for short lifespan	(Reich <i>et al.</i> , 1997; Garnier and Navas, 2012; Reich, 2014)	Use plant life-span
Leaf dry matter content LDMC	SLA	+	Trade-off between conservative (low SLA and RGR) and acquisitive strategies (high RGR and SLA)	(Wilson <i>et al.</i> , 1999; Roche <i>et al.</i> , 2004; Wright <i>et al.</i> , 2004; McIntyre, 2008; Tribouillois <i>et al.</i> , 2015)	Analyse all parameters
	Resource capture	-	LDMC is a marker of a conservation strategy (low efficiency in resource capture)	(Lavorel and Garnier, 2002)	Analyse shading response
Leaf nitrogen content LNC	RGR	+	LNC is a marker of resource acquisitive species.	(Lavorel and Garnier, 2002; Tribouillois <i>et al.</i> , 2015)	Analyse all parameters
Epigeal vs hypogeal pre-emergent growth	Initial plant leaf biomass	+	The emerging cotyledons of epigeal species contribute to leaf mass and area immediately after emergence	(Fayaud <i>et al.</i> , 2014)	Analyse initial plant leaf area
Seed mass	Initial plant leaf biomass	+	Heavier seeds include more reserves and/or a larger embryo	(Seibert and Pearce, 1993; Fayaud <i>et al.</i> , 2014)	Analyse initial plant leaf area
	SLA	-	Small-seeded species devote more biomass to leaves but have denser leaves	(Seibert and Pearce, 1993)	
	LBR, RGR	-			
Seed lipid content	Faster germination, larger plants	+	This type of reserve stores more energy		Analyse all parameters
Ecological habitat preferences (base values or Ellenberg indicator values as proxies)					
Thermophily	Insect growth rate	+	Higher growth rate compensates for higher temperature requirement	(Angus <i>et al.</i> , 1981; Trudgill <i>et al.</i> , 2005; Gardarin <i>et al.</i> , 2011)	Analyse all parameters, use base temperature and water potential instead of Ellenberg T and M
	Germination rate	+	Higher temperature requirements allow annuals to detect gaps in existing vegetation	(Washitani and Takenaka, 1987)	
	SLA	+	Frost resistant species have smaller (and usually thicker) leaves	(Palta and Li, 1979)	
Hydrophily	RGR, SLA, germination speed	+	Drought-resistant species invest more into roots, higher growth rates compensates for higher moisture requirements	(Bartelheimer and Poschlod, 2016)	
Heliophily	RGR, SLA	-	High SLA compensates for low light availability in shaded habitats	(Bartelheimer and Poschlod, 2016)	Analyse all parameters as a function of Ellenberg N, L and R
Nitrophily	SLA	+	In nutrient-rich habitats, species mainly compete for light, which selected for high SLA and RGR to the detriment of below-ground processes	(Poorter and Remkes, 1990; Bartelheimer and Poschlod, 2016)	
	RGR	+			
	RBR	-	Nitrophilic species invest less biomass into roots	(Fichtner and Schulze, 1992; Moreau <i>et al.</i> , 2014)	
Preferences for soil pH	LBR	-			
	RGR, SLA	+	Calciphile species could prefer nitrate over ammonium and higher temperature requirements, calcifuge species could be better adapted to acidic habits with their low nutrient availability and higher toxicity	(Bartelheimer <i>et al.</i> , 2014; Bartelheimer and Poschlod, 2016)	
Morphology					
SLA	RGR	+		(Poorter and Remkes, 1990; Reich <i>et al.</i> , 1997; Poorter and Van Der Werf, 1998; Storkey, 2004)	
LA0	RGR	-		(Storkey, 2004)	

[§]0 = no effect, + = positive correlation or increase, - = negative correlation or decrease

Table 3

Trait	Crops	Weeds	R ²	p
Taxonomy, N ₂ fixation and photosynthetic pathway				
Dicot species (proportion)	0.742	0.788		0.1356
Legume species (proportion)	0.57	0	0.39	<0.0001
C4 species (proportion)	0.038	0.182	0.05	<0.0001
Species traits				
Plant shape				
Prostrate	0.09	0.12		0.1638
Rosette	0.23	0.3	0.01	0.0358
Erect	0.51	0.48		0.3866
Climbing or twining	0.15	0.06	0.02	<0.0001
Max plant height (cm)	125.5	88.2	0.1	<0.0001
Max plant width (cm)	91.6	97.2		0.1049
Life-cycle: proportion of				
Summer annuals	0.2	0.57	0.15	<0.0001
Winter annuals	0.43	0.42		0.795
Indeterminate annuals	0.17	0	0.09	<0.0001
Perennials	0.19	0	0.1	<0.0001
Lifespan in annuals				
Minimum (months)	5.2	4.3	0.03	<0.0001
Maximum (months)	6.6	5.4	0.04	<0.0001
Seed traits				
Mass (mg)	75.46	5.86	0.17	<0.0001
Lipid content (g/g)	0.09	0.18	0.1	<0.0001
Epigeal preemergent growth (proportion)	0.406	0.788	0.15	<0.0001
Leaf traits				
Dry matter content (g/g)	167.3	174		0.0969
Nitrogen content (g/g)	44.6	27.5	0.35	<0.0001
Ecological habitat preferences				
Base temperature (°C)	2.78	4.36	0.07	<0.0001
Base water potential (MPa)	-1.51	-0.98	0.1	<0.0001
Ellenberg L	7.2	6.9	0.06	<0.0001
Ellenberg R	7.1	6.7	0.03	<0.0001
Ellenberg N in non-legumes	6.9	6.8		0.4284

w

Table 4

Explanatory traits and variables	Analysed parameters	
	Initial leaf area (cm ²) [§]	Relative growth rate (cm ² /cm ² /°Cdays)
Selection mode	backward	backward
<i>R</i> ²	<i>0.63</i>	<i>0.63</i>
<i>Number of species</i>	<i>49</i>	<i>49</i>
Intercept	-2.37	0.000892
Initial leaf area [§] (cm ²)		-0.00375
Weed (instead of crop)	-0.841	
Epigeal vs hypogeal species	0.756	
Seed weight [§] (mg/seed)	0.445	0.00348
Base temperature (°C)	0.0641	0.00249

[§] log_n-transformed

Table 5

Species traits	In unshaded conditions	Shading response
	LBR0 (g/g) [§]	LBR_mu
[1] Weed vs crop species		0.384
Plant growth form and <i>plant stage</i> (BBCH)		
[2] Prostrate	0.12 - 0.752 · stage	-0.0321 · stage
[3] Rosette	1.81 - 0.953 · stage	-0.0245 · stage
[4] Erect	1.07 - 0.843 · stage	-0.0219 · stage
[5] Climbing or twining	0 - 0.558 · stage	-0.0477 · stage
Potential plant dimensions		
[6] <i>Maximum plant height</i>		-0.000663
[7] <i>Maximum plant width</i>	-0.00651	
Morphology parameters		
[8] Leaf biomass ratio		-0.529
Life-cycle duration		
[9] Perennials	1.078	0.376
[10] Winter annuals	-0.002	-0.024
[11] Indeterminate annuals	0.722	0.174
[12] Summer annuals	0	0
Taxonomy, N2 fixation and photosynthetic pathway		
[13] Dicot vs Monocot	0.877	-0.145
[14] C4 vs C3 (in non-legume species)	-0.622	
[15] Legume vs non-legume (in C3 species)	-1.603	
Habitat requirements		
[16] <i>Ellenberg N</i> (nitrogen) if non-legume	-0.146	-0.0131
[17] <i>Ellenberg L</i> (light)		0.0741
[18] <i>Base water potential</i> (MPa)		-0.0539
Seed and leaf traits		
[19] <i>Seed mass</i> log10(mg)	-0.236	0.0632
[20] <i>Leaf dry matter content</i> (g/g)		-0.000726
[21] <i>Leaf nitrogen content</i> (g/g)		0.00223

[§] LBR was transformed to 10^{LBR} before analysis

Table 6a

























Parameters	Contrasted morphologies	Species types				
		Crop or weed, plant stage, and life-cycle duration	Plant growth form ^{&} , maximum plant dimensions, morphology	Taxonomy, N2 fixation and photosynthetic pathway	Habitat preference ^s	Seed and leaf traits ^s
Specific leaf area (SLA0)		Young plant, annuals,	Prostrate, tall and narrow	Dicots, non-legume, C3	N-poor, acid, warm	
		Old plant, perennial,	Climbing or twining, short and wide	Monocots, legume, C4	N-rich [#] , Basic, cool	
Leaf biomass ratio (LBR0)		Young plants, perennial	Climbing or twining, narrow	Dicots, non-legume, C3	N-poor	Small seeds
		Old plants, summer or winter annual	Prostrate, wide	Monocots, legume, C4	N-rich	Heavy seeds
Specific plant height (HM0)		Young plant	Erect or rosette, tall, stemmy		N-poor for non-legumes, shaded, warm	Lipid-poor seeds
		Old plant	Prostrate, climbing or twining, short, leafy		N-rich for non-legumes, sunny, cool	Lipid-rich seeds
Impact of plant biomass on plant height (b_HM)		Young plant, summer annual	Rosette or erect, tall per unit biomass	Dicots	Sunny, basic	Lipid-poor seeds
		Old plant, indeterminate annual	Climbing or twining, short per unit biomass	Monocots	Shaded, acid	Lipid-rich seeds
Specific plant width (WM0)			Tall	Non-legume, C4	Shaded, acid	N-rich leaves
			Short	Legume, C3	Sunny, basic	N-poor leaves
Impact of plant biomass on plant width (b_WM)		Weed	Wide, wide per unit biomass			
		Crop	Narrow, narrow per unit biomass			
Median leaf area height (RLH0)t		Weed, old plant, perennial			N-poor, basic, cool, moist	Small seeds, hypogeal growth, non-dense leaves
		Crop, young plant, summer annuals			N-rich, acid, warm, dry	Heavy seeds, epigeal growth, dense leaves

Table 6b

Parameters	Contrasting changes	Species types				
		Crops or weeds, plant stage, and life-cycle duration	Plant growth form ^{&} , maximum plant height and width, morphology	Taxonomy, N ₂ fixation and photosynthetic pathway	Habitat preference [§]	Seed and leaf traits [§]
Change in specific leaf area when shaded (mu_SL _A)		Old plants, summer annuals			N-rich, shaded	Lipid-rich seeds, N-rich leaves
		Young plants, indeterminate annuals			N-poor, sunny	Lipid-poor seeds, N-poor leaves
Change in Leaf biomass ratio when shaded (mu_LBR)		Weeds, young plants, perennials	Tall, stemmy	Monocots	N-poor, sunny, dry	Heavy seeds, non-dense or N-rich leaves
		Crops, old plants, summer or winter annuals	Short, leafy	Dicots	N-rich, shaded, moist	Light seeds, dense or N-poor leaves
Change in Specific plant height when shaded (mu_HM)		Old plants, summer annuals	Rosette or prostrate, tall and narrow, short per unit biomass	Legume, C ₃	Shaded, acid	Light seeds, hypogeal, dense leaves
		Young plants, perennials	Erect, climbing or twining, short and wide, tall per unit biomass	Non-legume, C ₄	Sunny, basic	Heavy seeds, epigeal, non-dense leaves
Change in Specific plant width when shaded (mu_WM)		Old plants	Narrow		Acid	
		Young plants	Wide		Basic	
Change in Median leaf area height when shaded (mu_RLH)		Old plants, perennials or winter annuals	Rosette, bottom-heavy	Dicots	Shaded	Lipid-poor or light seeds, non-dense leaves
		Young plants, summer or indeterminate annuals	Prostrate, top-heavy	Monocots	Sunny	Lipid-rich or heavy seeds, dense leaves

[§] Ellenberg N (nitrogen), L (light), R (pH), base temperature and water potential

[§] Seed mass and lipid-content, leaf dry matter content, leaf nitrogen content, epigeal or hypogeal growth

[&] Erect, prostrate, rosette, climbing or twining

[#] Only for non-legumes

Table 7

Parameters	Model type				
	All species	Weeds only	Crops	Monocotyledonous species only	Dicotyledonous species only
Number of species	61	25	36	15	46
Potential morphology (in unshaded conditions)					
Specific Leaf Area SLA0	0.42	0.30	0.55	0.49	0.55
Leaf biomass ratio LBR0	0.86	0.83	0.88	0.89	0.86
Specific plant height HM0	0.26	0.25	0.68	0.3	0.32
Sensitivity of plant height to biomass b_HM	0.59	0.63	0.85	0.79	0.59
Specific plant width WM0	0.22	0.26	0.45	0.24	0.40
Sensitivity of plant width to biomass b_WM	0.29	0.32	0.48	0.96	0.20
Median relative leaf area height RLH0	0.35	0.37	0.65	0.67	0.28
Shape of leaf area distribution b_RLH	0.62	0.45	0.71	0.93	0.68
Shading response of					
Specific Leaf Area SLA_mu	0.45	0.48	0.75	0.44	0.53
Leaf biomass ratio LBR_mu	0.41	0.51	0.54	0.54	0.44
Specific plant height HM_mu	0.42	0.53	0.58	0.61	0.41
Specific plant width WM_mu	0.09	0.21	0.23	0.46	0.1
Median relative leaf area height RLH_mu	0.39	0.56	0.58	0.48	0.41