



HAL
open science

Use of radiomics in the radiation oncology setting: Where do we stand and what do we need?

U. Schick, F. Lucia, V. Bourbonne, G. Dissaux, O. Pradier, V. Jaouen, F.
Tixier, D. Visvikis, M. Hatt

► To cite this version:

U. Schick, F. Lucia, V. Bourbonne, G. Dissaux, O. Pradier, et al.. Use of radiomics in the radiation oncology setting: Where do we stand and what do we need?. *Cancer/Radiothérapie*, 2020, 24 (6-7), pp.755 - 761. 10.1016/j.canrad.2020.07.005 . hal-03035725

HAL Id: hal-03035725

<https://hal.science/hal-03035725v1>

Submitted on 21 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

3

4 Nathalie Colbach^{1*}, Nicolas Munier-Jolain¹, François Dugué¹, Antoine Gardarin², Florence Strbik¹,
5 Delphine Moreau¹,

6 ¹Agroécologie, AgroSup Dijon, INRAE, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, F-
7 21000 Dijon

8 ²UMR Agronomie, INRAE, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon,

9 France

10

11 * Address for correspondence

12 Nathalie Colbach

13 INRAE

14 UMR1347 Agroécologie

15 BP 86510

16 17 rue Sully

17 21065 Dijon Cedex

18 France

19 Nathalie.Colbach@inrae.fr

20

21 **Highlights**

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

27 **Abstract**

28 To assess the competitive ability of plant species, ecologists describe many species from contrasting
29 habitats with traits that are proxies of ecophysiological functions whereas agronomists describe few
30 species from similar habitats with process-based parameters. Here, we combined both approaches and
31 compared many contrasting crop and weed species of temperate European arable crops in terms of
32 competition for light, to understand weed response to shading by crop canopies and to choose light-
33 competitive crop species and varieties. We (1) measured species parameters that drive light-
34 competition processes in 26 crop and 35 weed species of temperate European arable cropping systems,

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

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

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

145

146 **2.2 Plant material**

147 35 weed species and 26 crop species from temperate European arable cropping systems were
148 investigated in the present study (Appendix 1 and Appendix 2). Both crop and weed species were
149 chosen to be frequent but contrasting in terms of species features. Sixteen species were tested in two
150 different years, with several seasons per year for five of these (section [B.4](#) online). For wheat, pea and
151 faba bean, two or three varieties were investigated. Species were chosen to be contrasting in terms of
152 clade, emergence or sowing period, length of life cycle and plant structure. Crop species included both
153 cash crops and cover crops.

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

161

162 **2.3 Early growth**

163 **2.3.1 Experimental conditions**

164 The experiment was conducted in an unheated greenhouse at Dijon, Burgundy, France
165 (47°19'2.624"N, 5°4'26.883"E, 257m asl) without artificial light. Several series of experiments with 8
166 to 12 species were carried out, from 2009 to 2012, each lasting for three to four weeks. As far as
167 possible, species were tested during their usual emergence season, i.e. winter species in autumn, spring
168 species in spring and summer species in early summer. Temperature was recorded every 20 minutes
169 with PT100 (ARIA) sensors. Seeds were put onto filter paper inside watered Petri dishes inside growth
170 chambers at optimal temperature and light conditions (details in section [A.4](#) online). Once germinated,
171 seeds were planted 2 cm deep in pots (13 cm x 13 cm x 13 cm) filled with dry potting soil (NFU 44-
172 551 consisting of peat, wood fibers and clay, with 1.2 kg/m³ of 14-16-18 NPK fertilizer and pH 6.5)
173 over clay pebbles, with one plant per plot. For each species or variety, 20 pots were prepared. The
174 greenhouse was equipped with an automatic conveyor belt which moved the pots continuously to
175 provide the most similar thermal and light conditions to all plants.

176

177 **2.3.2 Measurements and statistics**

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

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

191 For the ten plants monitored throughout the experiment, a linear regression was fitted to the \log_n -
192 transformed leaf area LA_p (cm²) vs thermal time TT_p (°C days, with species-dependent base
193 temperatures) since plant emergence for each plant p using the `lm()` function of R (R Core Team,
194 2016). The slope of this regression is the relative growth rate RGR_p (cm² cm⁻² °C⁻¹ days⁻¹) and the
195 constant is the \log_n -transformed leaf area at emergence $LA0_p$ (cm²) (Storkey, 2004):

$$196 [1] \quad \log_n(LA_p) = RGR_p \cdot TT_p + \log_n(LA0_p)$$

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

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

209

210 **2.4 Potential plant morphology and response to shading**

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

214 **2.4.1 Experimental conditions**

215 The second series of experiments was carried out in garden plots at INRA Dijon from 2009 to 2016.
216 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.
217 The area was divided into four blocks. The soil was covered with a permeable opaque plastic sheet to
218 avoid emergence of plants other than those sown for the experiment. A 3-m-high metallic cage was
219 erected over half the area of all the blocks, and covered with a shading net to intercept at least 60% of
220 the incident photosynthetically active radiation (PAR). Outside, only the area unshaded by the cage
221 was used for the experiment. Temperature was measured with Testo sensors (175-T1) placed 1 m
222 above ground and protected from the sun, with two sensors inside and two outside the cage. Incident
223 PAR was measured every 10 minutes with quantum sensors (silicium sensors; Solems, Palaiseau,
224 France) at 60, 90 and 110 cm above soil surface inside and outside the shading cage. The shading
225 index inside the cage was calculated as 1 – the slope of a linear regression fitted to incident PAR
226 inside vs. outside the cage during the experiment (details in section [D.1.5](#) online). Shading index was
227 0.82 in the 2010 and 2012 experiments, 0.60-0.61 in the other experiments. Section 2.4.3 explains how
228 this index was used to estimate comparable shading response parameters.

229 For each species or variety, seeds were sown into 4 x 4 x 4 cm peat clods (Jiffy pastilles, Puteaux SA)
230 inside plastic seedling trays, preparing 100 clods with 2-3 seeds per clod. The clods were watered and
231 put into lightened growth chambers at 4°C for those species that needed to be vernalized, or directly
232 into an unheated greenhouse without artificial light. Plant stage was monitored on the BBCH scale, i.e.
233 a generic scale applying to both mono and dicotyledonous weed species to identify their growth stages
234 (Hess *et al.*, 1997). Once seedlings had reached the 2-leaf stage (stage 2 on the BBCH scale),
235 superfluous plants were eliminated to keep only one plant per clod, and clods were transplanted into
236 the garden plots. Half of the plants (at least 16, if possible 32) were placed inside the shaded cage, and
237 the remaining outside, in the unshaded area. Plants were placed inside holes in the plastic sheet, with
238 at least 50 cm between plants to avoid shading and root interference. In each experimental series, up to
239 10 species or varieties were tested simultaneously, with at least one plant in each block of each light
240 treatment. In case of climbing or twining species, a circular meshed trellis was set up for each plant.
241 The plots were regularly hand-weeded, and watered if necessary. To avoid N stress, 50 kg N/ha were
242 added at the end of winter during the years the experiments were conducted.

243

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.

253

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 (~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).

270

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 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} :

286 eq. 2. $HM = H / BM^{b_{HM}}$

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

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

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 $RCLA$ ($cm^2 \cdot cm^{-2}$) vs relative plant height rh ($cm \cdot cm^{-1}$) (Munier-Jolain *et al.*,
 296 2014):

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

298 RLH is the relative plant height ($cm \cdot cm^{-1}$) 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
316 parameter values were logical from a biological point of view. For instance, specific leaf area SLA
317 must be > 0 , leaf biomass ratio LBR must be in $[0, 1]$ etc. Predictions were also capped by minimum
318 and maximum measured values to avoid extremely small or large values in case of extrapolation for
319 late stages when only a few early stages were measured.

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

322

323 **2.5 Effects of species features on plant morphology and shading** 324 **response parameters**

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

344 For the analysis of the potential morphology and shading response parameters, further features (plant
345 growth form, distinguishing prostrate, erect, rosette and climbing or twining, section [A.2.1](#) online),
346 parameters (e.g. potential HM when analysing shading response HM_{μ}) as well as plant stage (in
347 BBCH scale, and distinguishing early, mid and late life) were added (Table 3). Interactions between
348 stage and plant growth form were also included. Features were chosen for their biological relevance to
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
351 preference index for temperature).
352 First, correlations among parameters were investigated with a Principal Component Analysis (PCA),
353 followed by a Ward ascendant hierarchy classification to cluster crop and weed species into functional
354 groups, using the PCA() and hclust() functions of the FactoMineR package of R. To identify which
355 species features were linked to parameters, the species features were projected onto the PCA axes.
356 Moreover, two-by-two correlations were analysed among parameters and features as well as between
357 parameters and features, using both Pearson correlation coefficients (cor() function of R) and linear
358 regressions (lm function of R).
359 Then, the effect of species features on parameters was analysed with linear models using PROC
360 GLMSELECT of SAS (version 9.4) which was developed to select from a very large number of
361 effects (Cohen, 2006) and has been successfully used in various disciplines (e.g., Van der Borghet *et*
362 *al.*, 2011). Features were removed sequentially (backward selection), by removing effects that at each
363 step produce the smallest value of the Schwarz Bayesian information criterion (SBC) statistic and
364 stopping when removing any effect increased the SBC statistic again. The final model was chosen
365 among the successive models as the one that yielded the lowest predicted residual sum of square with
366 cross validation. For potential plasticity and shading response, forward selection was used as
367 backward selection tended to produce over-fitted models. We moreover eliminated any feature whose
368 effect was not significant at $p=0.05$. Using a method including cross-validation leads to more robust
369 relationships and avoids fitting regressions that are based on a single extreme species behaviour. The
370 detailed results on all parameters can be found in supplementary material online (section [E.1](#)). Here,
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.

411

412 **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).

427

428 **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.

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

460

461 **3.4 Which features influenced initial growth?**

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

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

476

477 **3.5 Which features influenced potential morphology and shading** 478 **response?**

479 **3.5.1 Leaf biomass ratio as a case study**

480 **Plant stage and growth form.** In young plants, leaf biomass ratio in unshaded conditions (LBR0) was
481 the highest for rosette-shaped and erect plant species (regressor values of 1.81 and 1.07 in lines [3] and
482 [4] in Table 5) and the lowest for prostrate and climbing or twining plant species (values of 0.12 and 0
483 in lines [2] and [5]). LBR0 decreased with plant stage, i.e. young plants consisted mostly of leaf
484 biomass and old plants mostly of stem biomass (Figure 1.C). The decrease was the fastest for rosette-
485 shaped and erect plants (regressor values of -0.953 and -0.843 for *stage* in lines [3] and [4] in Table 5)
486 and the slowest for prostrate and climbing or twining species (values of -0.752 and -0.558 in lines [2]
487 and [5]). So, in old plants ($stage = 10$), rosette-shaped plants presented the lowest leaf biomass ratio
488 ($1.81 - 0.953 \cdot 10 = -7.72$) and climbing or twining species the highest leaf biomass ratio ($0 - 0.558 \cdot$
489 $10 = -5.58$).

490 Shading response generally increased with plant stage, i.e. parameter values became increasingly
491 positive or negative (Figure 1.D). Generally, older plants tended to attribute less biomass to leaves
492 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
494 response with many species increasing their leaf biomass ratio (approximately 50% of values above
495 zero at stages 8-10 in Figure 1.D).

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

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

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

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

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

530 **3.5.2 The other parameters**

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

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

550

551 **3.5.3 The importance of interactions**

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

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

564 **4 Discussion**

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

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

583

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

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

596 As we worked with original parameters, it was often difficult to find literature studies to compare to
597 our results. This was particularly true for shading response. The rare studies that investigated
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
600 compare results.

601 The best documented variable is specific leaf area SLA. The LEDA trait data base (Kleyer *et al.*,
602 2008) reported larger values for the species used here ($275 \pm 71 \text{ cm}^2/\text{g}$ over sources and species in the
603 data base compared to $179 \pm 70 \text{ cm}^2/\text{g}$ over stages and species in our study), without any correlation
604 between the two types of data ($p=0.6468$ for Spearman correlation, section **F.1.1** online). Indeed, we
605 measured SLA in unshaded conditions using all plant leaves and including petioles, whereas some
606 previous studies often only considered the top leaf limbs and did not specify shading conditions. But
607 SLA has been shown to vary along plant height, because of self-shading (Ishida *et al.*, 1999), and we
608 similarly showed that SLA usually increased with shading. When comparing our results to Storkey's
609 (2004) who also worked in unshaded conditions and calculated SLA over all plant leaves, our data
610 were correlated (Spearman $r = 0.63$, section **F.1.2** online). Our SLA values are still lower than
611 Storkey's, probably because he excluded petioles from his measurements (J. Storkey, pers. comm.
612 2018).

613 These methodological differences probably also explain why we did not observe the frequently
614 reported correlation between relative growth rate RGR and specific leaf area SLA (Poorter and
615 Remkes, 1990; Reich *et al.*, 1997; Poorter and Van Der Werf, 1998; Storkey, 2004), except very
616 slightly at vegetative stage. Another explanation could be that our RGR ($\text{cm}^2/\text{cm}^2/^\circ\text{Cday}$) was based
617 on plant leaf area growth and not on plant biomass growth as the literature RGR (g/g/days). The two
618 are only equivalent if temperature, leaf biomass ratio and specific leaf area are constant over time,
619 which is not the case (see section 3.5.1). But Storkey's (2004) who used the same approach as we did
620 (but also included radiation effects) found the same magnitude in terms of relative growth rate RGR
621 and initial leaf area LA0, and the species were ranked similarly (Pearson correlation coefficient = 0.31
622 and 0.82 for RGR and LA0, respectively). Storkey's RGR and LA0 were in average respectively 40%
623 and 50% larger than ours, because they included stem area in their calculation of RGR, and they
624 started leaf area measurements only a few days after emergence.

625 Most probably, we could not find a trade-off between RGR and SLA in the present study because we
626 focused on crops and weeds (which cohabit in the same type of habitat) whereas ecological studies
627 cover a larger range of habitats and species types (or $100\text{-}400 \text{ cm}^2/\text{g}$ in Poorter and Remkes, 1990; e.g.
628 SLA measured here at stage 5 ranged from approximately $75\text{-}300 \text{ cm}^2/\text{g}$ compared to $60\text{-}600 \text{ cm}^2$ in
629 Reich *et al.*, 1997). Storkey (2004) who worked with species similar to ours could only observe the
630 RGR-SLA correlation when discriminating monocots vs dicots and spring vs autumn growth seasons.
631 Other studies focusing on crops were also unable to identify an RGR-SLA trade-off and explained this
632 by their limited species pool as well as a domestication effect which could have distorted the
633 relationship (Tribouillois *et al.*, 2015).

634 These differences in methods and species pools probably also explain other discrepancies between our
635 results and previous reports from literature. For instance, we did not observe the expected negative
636 correlation between the leaf dry matter content LDMC and the specific leaf area SLA (Wilson *et al.*,
637 1999; Roche *et al.*, 2004; McIntyre, 2008; Tribouillois *et al.*, 2015) or the positive correlation between
638 RGR or SLA and Ellenberg N (Poorter and Remkes, 1990). Indeed, the latter was observed with
639 biomass-based RGR and single-leaf SLA on a species pool whose Ellenberg N indices varied from 1
640 to 8. Our species ranged from 5 to 9 and in that range Poorter & Remkes' data did not show any
641 notable correlation either (section [F.2](#) online). The same was true for many other correlations with
642 Ellenberg indicator values reported in literature (Table 2).

643 In conclusion, the identification of functional relationships depends on measurement conditions,
644 methods as well as on the investigated species pool. Our results clearly show the limits of transposing
645 results from comparative ecology, which focuses on a wide range of habitats, to agricultural fields.
646 The trade-offs among plant traits identified on large sets of wild species are not necessarily valid when
647 analysing plant strategies of species from a narrower range of habitats.

648

649 **4.2 Disentangling species differences from environmental effects**

650 The present study combined the method developed by Munier-Jolain *et al* (2014) to characterize plant
651 morphology in heterogeneous crop:weed canopies with the method developed by Gardarin *et al* (2010;
652 2011) to link difficult-to-measure species parameters to easily accessible species features. Munier-
653 Jolain's parameters were essential to separate the effect of radiation on biomass accumulation from
654 that of shading response. Indeed, shaded plants are usually smaller and lighter than unshaded plants,
655 but the shading-response parameters used here check whether plants change their rules for allocating
656 biomass and determining morphology.

657 These parameters are very expensive to measure in terms of time, space and labour. But their nature
658 makes their values largely independent of the experimental conditions (see e.g. section 2.3.2
659 explaining this for relative growth rate RGR) and thus makes it possible to compare species tested in
660 different years or outside growth chambers, albeit some methodological precautions. To minimize the
661 risk of confusing species and year effects, the experimental setup in the garden plots aimed to ensure
662 optimal water and nitrogen conditions, and the initial growth phase was studied in greenhouse where
663 plants were protected from frost damage. Working in garden plots has the disadvantage that the
664 amount of available light varies with the years (see section [E.6](#) online), but it has the major advantage
665 over climate chambers of having natural light (in terms of magnitude, quality and daily variation), and
666 allowing us to space plants sufficiently to avoid shading from neighbours. By sampling plants at key
667 stages (instead of fixed dates), we moreover accounted for differences in temperature not only between
668 shaded and unshaded conditions, but also among experimental years and seasons. Moreover, we
669 recently started to test our species in quite different conditions (University of Rostock, North-Eastern

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 to 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.

711

712 **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).

745

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).

768

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.

788

789 **6 Acknowledgements**

790 Over the years, this project was supported by INRA, the French project CoSAC (ANR-15-CE18-
791 0007), the European projects AMIGA (FP7-KBBE-2011-5-CP-CSA), the Casdar RAID project funded
792 by the French Ministry in charge of Agriculture and Food (Ministère de l'Agriculture et de
793 l'Alimentation, avec la contribution financière du compte d'affectation spéciale 'Développement
794 agricole et rural') and ReMIX (European Union's Horizon 2020 Research and innovation programme,
795 N. 727217). Numerous students participated in the experiments (Rémi Bonnot, Claire Compayre,
796 Jérôme Lecuyer, Fanny Marlangeon, Laureline Van Ryseghem) which also benefitted from the
797 technical assistance of the greenhouse staff. The study has further been supported by the TRY
798 initiative on plant traits (<http://www.try-db.org>). The TRY initiative and database is hosted, developed
799 and maintained by J. Kattge and G. Bönisch (Max Planck Institute for Biogeochemistry, Jena,
800 Germany). TRY is currently supported by DIVERSITAS/Future Earth and the German Centre for
801 Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.

802 **7 References**

803

804

- 805 Alghamdi, S. S., 2009. Chemical Composition of Faba Bean (*Vicia faba* L.) Genotypes under Various
806 Water Regimes. *Pakistan Journal of Nutrition* 8, 477-482.
- 807 Angus, J. F., Cunningham, R. B., Moncur, M. W., Mackenzie, D. H., 1981. Phasic development in
808 field crops. I. Thermal response in the seedling phase. *Field Crops Research* 3, 365-378.
- 809 Bartelheimer, M., Poschlod, P., Ejrnæs, R., 2014. The response of grassland species to nitrate versus
810 ammonium coincides with their pH optima. *Journal of Vegetation Science* 25, 760-770.
- 811 Bartelheimer, M., Poschlod, P., 2016. Functional characterizations of Ellenberg indicator values – a
812 review on ecophysiological determinants. *Functional Ecology* 30, 506-516.
- 813 Batlla, D., Verges, V., Benech-Arnold, R. L., 2003. A quantitative analysis of seed responses to cycle-
814 doses of fluctuating temperatures in relation to dormancy: development of a thermal time model
815 for *Polygonum aviculare* L. seeds. *Seed Science Research* 134, 197-207.
- 816 Benvenuti, S., Macchia, M., 1993. Calculation of threshold temperature for the development of
817 various weeds. *Agricoltura Mediterranea* 123, 252-256.

818 Bouaziz, A., Bruckler, L., 1989. Modeling wheat seedling growth and emergence. I. Seedling growth
819 affected by soil water potential. *Soil Sci. Soc. Am. J.* 53, 1832-1838.

820 Bretagnolle, F., Matejicek, A., Gregoire, S., Reboud, X., Gaba, S., 2016. Determination of fatty acids
821 content, global antioxidant activity and energy value of weed seeds from agricultural fields in
822 France. *Weed Research* 56, 78-95.

823 Brisson, N., Mary, B., Ripoche, D., Jeuffroy, M. H., Ruget, F., Nicoullaud, B., Gate, P., Devienne-
824 Barret, F., Antonioletti, R., Dürr, C., Richard, G., Beaudoin, N., Recous, S., Tayot, X., Plenet,
825 D., Cellier, P., Machet, J. M., Meynard, J. M., Delecolle, R., 1998. STICS: a generic model
826 for the simulation of crops and their water and nitrogen balances. I. Theory and
827 parameterization applied to wheat and corn. *Agronomie* 18, 311-346.

828 Bruckler, L., 1983a. Rôle des propriétés physiques du lit de semences sur l'imbibition et la
829 germination. II. Contrôle expérimental d'un modèle d'imbibition des semences et possibilités
830 d'applications. *Agronomie* 3, 223-232.

831 Bruckler, L., 1983b. Rôle des propriétés physiques du lit de semences sur l'imbibition et la
832 germination. I. Élaboration d'un modèle du système "terre-graine". *Agronomie* 3, 213-222.

833 Bürger, J., Colbach, N., 2018. Basistemperatur der Keimung und relative Wachstumsrate von 13
834 Unkrautarten im Vergleich der Samen aus zwei mitteleuropäischen Herkünften (Germination
835 base temperature and relative growth rate of 13 weed species - comparing populations from
836 two geographical origins). In: German Conference on Weed Biology and Weed Control,
837 Braunschweig, Germany, 27 Feb-01 Mar 2018,

838 Chauvel, B., 1996. Variabilité de la production de semences chez le vulpin (*Alopecurus myosuroides*
839 Huds.) en fonction de la culture. In: Xe Colloque international sur la biologie des mauvaises
840 herbes, Dijon, 43-50.

841 Cohen, R., 2006. Introducing the GLMSELECT PROCEDURE for Model Selection.
842 <http://www2.sas.com/proceedings/sugi31/207-31.pdf>

843 Colbach, N., Chauvel, B., Dürr, C., Richard, G., 2002a. Effect of environmental conditions on
844 *Alopecurus myosuroides* germination. I. Effect of temperature and light. *Weed Research* 42,
845 210-221.

846 Colbach, N., Dürr, C., Chauvel, B., Richard, G., 2002b. Effect of environmental conditions on
847 *Alopecurus myosuroides* germination. II. Effect of moisture conditions and storage length.
848 *Weed Research* 42, 222-230.

849 Colbach, N., Bertrand, M., Busset, H., Colas, F., Dugué, F., Farcy, P., Fried, G., Granger, S., Meunier,
850 D., Munier-Jolain, N. M., Noilhan, C., Strbik, F., Gardarin, A., 2016. Uncertainty analysis and
851 evaluation of a complex, multi-specific weed dynamics model with diverse and incomplete
852 data sets. *Environmental Modelling & Software* 86, 184-203.

853 Colbach, N., Gardarin, A., Moreau, D., 2019. The response of weed and crop species to shading:
854 which parameters explain weed impacts on crop production? *Field Crops Research* 238, 45-
855 55.

856 den Dobbelden, K. C., Verburg, R. W., 1996. Inherent allocation patterns and potential growth rates of
857 herbaceous climbing plants. *Plant and Soil* 184, 341-347.

858 Duke, S. O., 2020. Glyphosate: environmental fate and impact. *Weed Science* 68, 201-207.

859 Dürr, C., Dickieb, J. B., Yang, X.-Y., Pritchard, H. W., 2015. Ranges of critical temperature and water
860 potential values for the germination of species worldwide: Contribution to a seed trait
861 database. *Agricultural and Forest Meteorology* 200, 222-232.

862 Ellenberg, H., 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas Göttingen, Germany,
863 Ellenberg, H., Weber, H. E., Düll, R. R., Wirth, V., Werner, W., Paulißen, D., 1992. Zeigewerte von
864 Pflanzen in Mitteleuropa. 260 p.

865 Fayaud, B., Coste, F., Corre-Hellou, G., Gardarin, A., Dürr, C., 2012. Early growth in intercrops: an
866 experimental and simulation approach for a range of species under different sowing
867 conditions. In: ESA, Helsinki, Finland, 20-24 August 2012, 54-55.

868 Fayaud, B., Coste, F., Corre-Hellou, G., Gardarin, A., Durr, C., 2014. Modelling early growth under
869 different sowing conditions: A tool to predict variations in intercrop early stages. *European*
870 *Journal of Agronomy* 52, 180-190.

- 871 Fichtner, K., Schulze, E.-D., 1992. The effect of nitrogen nutrition on growth and biomass partitioning
872 of annual plants originating from habitats of different nitrogen availability. *Oecologia* 92, 236-
873 241.
- 874 Fournier, 1990. *Les quatres flores de France*. Lechevalier,
- 875 Gardarin, A., 2008. Modélisation des effets des systèmes de culture sur la levée des adventices à partir
876 de relations fonctionnelles utilisant les traits des espèces. Université de Bourgogne, Dijon,
877 France.
- 878 Gardarin, A., Dürr, C., Colbach, N., 2010. Effects of seed depth and soil structure on the emergence of
879 weeds with contrasted seed traits. *Weed Research* 50, 91-101.
- 880 Gardarin, A., Dürr, C., Colbach, N., 2011. Prediction of germination rates of weed species:
881 relationships between germination parameters and species traits. *Ecological Modelling* 222,
882 626-636.
- 883 Gardarin, A., Colbach, N., 2015. How much of seed dormancy in weeds can be explained by seed
884 traits? *Weed Research* 55, 14-25.
- 885 Gardarin, A., Coste, F., Wagner, M.-H., Dürr, C., 2016. How do seed and seedling traits influence
886 germination and emergence parameters in crop species? A comparative analysis. *Seed Science*
887 *Research* 26, 317-331.
- 888 Garnier, E., Navas, M. L., 2012. A trait-based approach to comparative functional plant ecology:
889 concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable*
890 *Development* 32, 365-399.
- 891 Granier, C., Massonnet, C., Turc, O., Muller, B., Chenu, K., Tardieu, F., 2002. Individual leaf
892 development in *Arabidopsis thaliana*: a stable thermal-time-based programme. *Annals of*
893 *Botany* 89, 595-604.
- 894 Grime, J. P., Hunt, R., 1975. Relative growth-rate - its range and adaptive significance in a local flora.
895 *Journal of Ecology* 63, 393-422.
- 896 Grundy, A. C., Phelps, K., Reader, R. J., Burston, S., 2000. Modelling the germination of *Stellaria*
897 *media* using the concept of hydrothermal time. *New Phytologist* 148, 433-444.
- 898 Guillemain, J.-P., Gardarin, A., Granger, S., Reibel, C., Colbach, N., 2013. Determination of base
899 temperatures and base water potentials for germination of weeds. *Weed Research* 53, 76-87.
- 900 Gummerson, R. J., 1986. The effect of constant temperatures and osmotic potentials on the
901 germination of sugar beet. *Journal of Experimental Botany* 37, 729-741.
- 902 Hess, M., Barralis, G., Bleiholder, H., Buhr, L., Eggers, T., Hack, H., Stauss, R., 1997. Use of the
903 extended BBCH scale—general for the descriptions of the growth stages of mono; and
904 dicotyledonous weed species. *Weed Research* 37, 433-441.
- 905 Hur, S. N., Nelson, C. J., 1985. Temperature Effects on Germination of Birdsfoot Trefoil and
906 Seombadi1. *Agronomy Journal* 77, 557-560.
- 907 Ishida, A., Uemura, A., Koike, N., Matsumoto, Y., Hoe, A. L., 1999. Interactive effects of leaf age and
908 self-shading on leaf structure, photosynthetic capacity and chlorophyll fluorescence in the rain
909 forest tree, *Dryobalanops aromatica*. *Tree physiology* 19, 741-747.
- 910 Jha, P., Kumar, V., Godara, R. K., Chauhan, B. S., 2017. Weed management using crop competition in
911 the United States: A review. *Crop Protection* 95, 31-37.
- 912 Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M.,
913 Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P.
914 M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin,
915 O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W.
916 J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin,
917 F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka,
918 W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., Fernández-Méndez, F., Fidelis,
919 A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R.
920 V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A.,
921 Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops,
922 J. M. H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens,
923 F., Lenz, T., Lewis, S. L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M. D., Manning,
924 P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., Müller, S. C., Nadrowski, K., Naem,
925 S., Niinemets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda,

926 Y., Ordoñez, J., Overbeck, G., Ozinga, W. A., Patiño, S., Paula, S., Pausas, J. G., Peñuelas, J.,
927 Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R.,
928 Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S.,
929 Shipley, B., Siefert, A., Sosinski, E., Soussana, J. F., Swaine, E., Swenson, N., Thompson, K.,
930 Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle,
931 S., Zanne, A. E., Wirth, C., 2011. TRY – a global database of plant traits. *Global Change*
932 *Biology* 17, 2905-2935.

933 Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod,
934 P., Groenendael, J. M. v., Klime, L., Klime, J., Klotz, o. S., Rusch, G. M., D, M. H.,
935 Boedeltje, A. G., Bossuyt, B., Dannemann, A., Endels, P., Gätzenberger, L., Hodgson, J. G.,
936 Jackel, A. K., Kühn, I., Kunzmann, D., Ozinga, W. A., Rämmermann, C., Stadler, M.,
937 Schlegelmilch, J., Steendam, H. J., Tackenberg, O., Wilmann, B., Cornelissen, J. H. C.,
938 Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: a database of life-history traits
939 of the Northwest European flora. *Journal of Ecology* 96, 1266-1274.

940 Larsen, K., 1977. Self-incompatibility in *Beta vulgaris* L. I. Four gametophytic, complementary S-loci
941 in sugar beet. *Hereditas* 85, 227-248.

942 Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem
943 functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16, 545-556.

944 Lüttge, U., 2013. Fat – carbohydrate – protein: Storage in plant seeds. *Lipid Technology* 25, 79-81.

945 Marshall, B., Squire, G. R., 1996. Non-linearity in rate-temperature relations of germination in oilseed
946 rape. *Journal of Experimental Botany* 47, 1369-1375.

947 Masin, R., Loddo, D., Benvenuti, S., Zuin, M. C., Macchia, M., Zanin, G., 2010. Temperature and
948 Water Potential as Parameters for Modeling Weed Emergence in Central-Northern Italy.
949 *Weed Science* 58, 216-222.

950 McGiffen, M., Spokas, K., Forcella, F., Archer, D., Poppe, S., Figueroa, R., 2008. Emergence
951 prediction of common groundsel (*Senecio vulgaris*). *Weed Science* 56, 56-65.

952 McIntyre, S., 2008. The role of plant leaf attributes in linking land use to ecosystem function in
953 temperate grassy vegetation. *Agriculture Ecosystems & Environment* 128, 251--258.

954 McKenzie-Gopsill, A. G., Amirsadeghi, S., Earl, H. J., Jones, A. M. P., Lukens, L., Lee, E., Swanton,
955 C. J., 2019. Early physiological and biochemical responses of soyabean to neighbouring
956 weeds under resource-independent competition. *Weed Research* 0,

957 Moreau, D., Busset, H., Matejicek, A., Munier-Jolain, N., 2014. The ecophysiological determinants of
958 nitrophily in annual weed species. *Weed Research* 54, 335-346.

959 Moreau, D., Abiven, F., Busset, H., Matejicek, A., Pagès, L., 2017. Effects of species and soil-
960 nitrogen availability on root system architecture traits. Study on a set of weed and crop
961 species. *Annals of Applied Biology* 171, 103–116.

962 Muneret, L., Mitchell, M., Seufert, V., Aviron, S., Djoudi, E. A., Pétilion, J., Plantegenest, M., Thiéry,
963 D., Rusch, A., 2018. Evidence that organic farming promotes pest control. *Nature*
964 *Sustainability* 1, 361-368.

965 Munier-Jolain, N. M., Savoie, V., Kubiak, P., Maillet-Mézeray, J., Jouy, L., Quéré, L., 2005a.
966 DECID'Herb, a decision support system on the WEB, designed for sustainable weed
967 management in cultivated fields. In: XIII European Weed Research Society Symposium,
968 Bari, Italy,

969 Munier-Jolain, N. M., Savoie, V., Kubiak, P., Maillet-Mézeray, J., Jouy, L., Quéré, L., 2005b.
970 DECID'Herb, a decision support system on the WEB, designed for sustainable weed
971 management in cultivated fields. In: 13th International EWRS Symposium, Bari, Italy, 19-23
972 June 2005,

973 Munier-Jolain, N. M., Guyot, S. H. M., Colbach, N., 2013. A 3D model for light interception in
974 heterogeneous crop:weed canopies. Model structure and evaluation. *Ecological Modelling*
975 250, 101-110.

976 Munier-Jolain, N. M., Collard, A., Busset, H., Guyot, S. H. M., Colbach, N., 2014. Investigating and
977 modelling the morphological plasticity of weeds in multi-specific canopies. *Field Crops*
978 *Research* 155, 90-98.

- 979 Nasab, A. D. M., 2011. Effects of water potential on germination and seedling growth of two varieties
980 of lentil (*Lens culinaris* Meidck). International Journal of Agriculture and Crop Sciences 3,
981 61-61.
- 982 Pakeman, R. J., Karley, A. J., Newton, A. C., Morcillo, L., Brooker, R. W., Schöb, C., 2015. A trait-
983 based approach to crop–weed interactions. European Journal of Agronomy 70, 22-32.
- 984 Palta, J. P., Li, P. H., 1979. Frost-Hardiness in Relation to Leaf Anatomy and Natural Distribution of
985 Several Solanum Species1. Crop Science 19, 665-671.
- 986 Perry, L. G., Neuhauser, C., Galatowitsch, S. M., 2003. Founder control and coexistence in a simple
987 model of asymmetric competition for light. Journal of Theoretical Biology 222, 425-436.
- 988 Poorter, H., Remkes, C., 1990. Leaf-area ratio and net assimilation rate of 24 wild-species differing in
989 relative growth-rate. Oecologia 83, 553-559.
- 990 Poorter, H., Van Der Werf, A., 1998. Is inherent variation in RGR determined by LAR at low
991 irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers, H.,
992 Poorter, H. and Vuuren, M. M. I. V. (Eds.) Inherent variation in plant growth. Physiological
993 mechanisms and ecological consequences, Backhuys Publishers, Leiden, The Netherlands
- 994 Poorter, H., Garnier, E., 2007. The ecological significance of variation in relative growth rate and its
995 components. In: Pugnaire, F. I. and Valladares, F. (Eds.) Functional Plant Ecology. 2nd edn. ,
996 CRC press, Boca Raton, USA
- 997 R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for
998 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- 999 Reich, P. B., Walters, M. B., Ellsworth, D. S., 1997. From tropics to tundra: Global convergence in
1000 plant functioning. Proc. Natl. Acad. Sci. U. S. A. 94, 13730-13734.
- 1001 Reich, P. B., 2014. The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. Journal
1002 of Ecology 102, 275-301.
- 1003 Roche, P., Diaz-Burlinson, N., Gachet, S., 2004. Congruency analysis of species ranking based on leaf
1004 traits: which traits are the more reliable? Plant Ecology 174, 37--48.
- 1005 Rolletschek, H., Fuchs, J., Friedel, S., Börner, A., Todt, H., Jakob, P. M., Borisjuk, L., 2015. A novel
1006 noninvasive procedure for high-throughput screening of major seed traits. Plant Biotechnology
1007 Journal 13, 188-199.
- 1008 Schambow, T. J., Adjesiwor, A. T., Lorent, L., Kniss, A. R., 2019. Shade avoidance cues reduce Beta
1009 vulgaris growth. Weed Science 67, 311-317.
- 1010 Scherner, A., Melander, B., Jensen, P. K., Kurds, P., Avila, L. A., 2017. Germination of winter
1011 annual grass weeds under a range of temperatures and water potentials. Weed Science
- 1012 Seibert, A. C., Pearce, R. B., 1993. Growth Analysis of Weed and Crop Species with Reference to
1013 Seed Weight. Weed Science 41, 52-56.
- 1014 Storkey, J., 2004. Modelling seedling growth rates of 18 temperate arable weed species as a function
1015 of the environment and plant traits. Annals of Botany 93, 681-689.
- 1016 Tardieu, F., 2003. Virtual plants : modelling as a tool for the genomics of tolerance to water deficit.
1017 Plant Science 8, 9-14.
- 1018 Tardieu, F., Tuberosa, R., 2010. Dissection and modelling of abiotic stress tolerance in plants. Current
1019 Opinion in Plant Biology 13, 206-212.
- 1020 Tribouillois, H., Fort, F., Cruz, P., Charles, R., Flores, O., Garnier, E., Justes, E., 2015. A Functional
1021 Characterisation of a Wide Range of Cover Crop Species: Growth and Nitrogen Acquisition
1022 Rates, Leaf Traits and Ecological Strategies. PLoS ONE 10, e0122156.
- 1023 Tribouillois, H., Dürr, C., Demilly, D., Wagner, M.-H., Justes, E., 2016. Determination of germination
1024 response to temperature and water potential for a wide range of cover crop species and related
1025 functional groups. PLOS one 11, e0161185.
- 1026 Trudgill, D. L., Honek, A., Li, D., Van Straalen, N. M., 2005. Thermal time - concepts and utility.
1027 Annals of Applied Biology 146, 1-14.
- 1028 Van der Borgh, K., Van Craenenbroeck, E., Lecocq, P., Van Houtte, M., Van Kerckhove, B.,
1029 Bacheler, L., Verbeke, G., van Vlijmen, H., 2011. Cross-validated stepwise regression for
1030 identification of novel non-nucleoside reverse transcriptase inhibitor resistance associated
1031 mutations. BMC Bioinformatics 12, 386.
- 1032 van der Meulen, A., Chauhan, B. S., 2017. A review of weed management in wheat using crop
1033 competition. Crop Protection 95, 38-44.

- 1034 Van Der Weide, R. Y., 1993. Population dynamics and population control of *Galium aparine* L.
1035 Wageningen Agricultural University, Wageningen.
- 1036 Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the
1037 concept of trait be functional! *Oikos* 116, 882-892.
- 1038 Waggoner, J., Henneberger, P., Kullman, G., Umbach, D., Kamel, F., Beane Freeman, L., Alavanja,
1039 M. R., Sandler, D., Hoppin, J., 2013. Pesticide use and fatal injury among farmers in the
1040 Agricultural Health Study. *International Archives of Occupational and Environmental Health*
1041 86, 177-187.
- 1042 Washitani, I., Takenaka, A., 1987. Gap-detecting mechanism in the seed germination of *Mallotus*
1043 *japonicus* (Thunb.) Muell. Arg., a common pioneer tree of secondary succession in temperate
1044 Japan. *Ecological Research* 2, 191-201.
- 1045 Wilson, P. J., Thompson, K., Hodgson, J. G., 1999. Specific leaf area and leaf dry matter content as
1046 alternative predictors of plant strategies. *New Phytologist* 143, 155-162.
- 1047 Wilson, S. D., Tilman, D., 1993. Plant competition and resource availability in response to disturbance
1048 and fertilization. *Ecology* 74, 599-611.
- 1049 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J.,
1050 Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J.,
1051 Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L.,
1052 Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet,
1053 C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J., Villar, R., 2004. The worldwide leaf
1054 economics spectrum. *Nature* 428, 821-827.
- 1055

1056 **8 Tables**

1057 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
1058 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

1059 [§] For B and C, over all stages.

1060 [&] standard-deviation/mean, except for shading response where standard-deviation because of negative values of mean close to zero

1061 [§] Biomass is always dry (leaf or plant) mass.