

Intraspecific functional trait variation in weeds: A strategy in response to competition with crop and weed plants

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Funding information

Ministère de l'Éducation Nationale, de
l'Enseignement Supérieur et de la Recherche

Subject Editor: Guillaume Fried, ANSES,
Maisons-Alfort, France

Abstract

Weeds are a key component of agroecosystems and compete with crop plants. Crop-weed competition has been widely investigated over the past decades, although how functional traits mediate these competitive interactions has rarely been explored. In this study, we measured functional traits in 4400 individual plants belonging to 32 weed species, growing among four crops differing in functional traits. We assessed the intraspecific variation in weed functional traits in response to competition with crops but also with the other weeds. We found that the most abundant weeds have a lower intraspecific trait variability than other weed species for leaf dry matter content (LDMC), but this pattern was not observed for canopy height (CH) nor for specific leaf area (SLA). We found that most of the weed species tended to grow taller and have higher LDMC values when crop CH and LDMC increased. We propose that these species display a 'crop matching' strategy, tending to match crop functional trait values in response to competition. We also found that weed-weed competition affected weed functional traits, sometimes more strongly than crop-weed competition. This study highlights that intraspecific trait variation is important to consider when investigating the processes underlying weed species community assembly, especially resource competition. Further studies are required to identify the source of intraspecific trait variation in weeds and the consequences for weed fitness.

KEYWORDS

barley, canopy height, leaf dry matter content, oilseed rape, pea, specific leaf area, weed-weed competition, wheat

1 | INTRODUCTION

Weeds are a key component of agroecosystems. Although recognised as pests because of the yield loss caused by competition with crop plants for light and soil nutrients, weeds, defined here as any spontaneous plant present in a cropped field (Bourgeois et al., 2019), also support animal diversity and enhance multifunctionality in agroecosystems (Gaba et al., 2020). Managing weed diversity in agroecosystems is therefore an ongoing challenge. Several studies have been conducted to determine the drivers of weed assembly in arable fields (Fried et al., 2008; Gaba et al., 2018). At the field scale, weed species

are filtered, according to their traits, by both abiotic factors (e.g., soil conditions, Fried et al., 2008) and biotic interactions such as competition with crops (Gaba et al., 2018). Competition has been mostly studied to evaluate the deleterious effects of weeds on crop yield. However, few studies have been conducted in arable fields to understand the effect of crop-weed competition on weed species community assembly (but see the exception Gaba et al., 2018).

In contrast, the outcome of competition on plant species assembly has been widely studied in natural ecosystems, especially with functional diversity approaches (e.g., Mason et al., 2011). Several conceptual frameworks have been proposed. For instance, the limiting

similarity hypothesis postulates that two species can only coexist if they occupy different niches and thus exploit different resources (MacArthur & Levins, 1967). If two species occupy the same niche, the species with the higher competitive ability will outcompete and ultimately exclude the other one. Assuming that species sharing similar functional traits have similar ecological requirements, niche differentiation leads to a pattern of functional divergence between species (Bennett et al., 2016; MacArthur & Levins, 1967; Mason et al., 2007).

However, an alternative hypothesis could apply in cases of 'asymmetric competition'. In such cases, larger individuals obtain a larger proportion of resources. For example, competition for light may select only the tallest competitors (Freckleton & Watkinson, 2001). Thus, only a small set of trait values is related to species success, which results in a pattern of functional convergence at the community level (Mayfield & Levine, 2010).

In arable fields, competitive asymmetry is expected to occur after canopy closure, because light is likely more limiting than soil nutrients which are provided by fertilisation (Holt, 1995). Two strategies associated with different trait syndromes can be observed in response to competition for light between crop plants and weed species. Some successful weed species show a shade avoidance response when light is limited, which is characterised by the elongation of the stem (Munier-Jolain et al., 2014) and a lower specific leaf area (SLA) (Storkey, 2005) as the concentration of far red light increases in the shade (Ruberti et al., 2012). Therefore, weed species with shade avoidance responses show a trait syndrome similar to that of the crop, despite their biomass might be negatively affected, if etiolation occurs. Shade-tolerant weeds, with higher SLA and creeping growth (low CH), can also capture light (Bourgeois et al., 2019). Conversely, shade-tolerant weed species are thus functionally dissimilar from the crop.

To date, most studies on competition have focused on interspecific trait variation (e.g., Singh & Singh, 2012). However, intraspecific variability may contribute to more than 30% of the variability in community trait values worldwide (Siefert et al., 2015) and can affect species coexistence (Crawford et al., 2019; Siefert et al., 2015). The role of intraspecific variability in response to resource competition is however poorly known. Nevertheless, intraspecific variability can be a path for plant species with a lower competitive ability to cope with competition (Crawford et al., 2019), especially when species diversity is low because more niche spaces are available. Moreover, phenotypic plasticity in resource acquisition can be a successful strategy to survive in heterogeneous environmental conditions (Ashton et al., 2010). Weed species present a particularly high intraspecific variation in their trait values, especially for traits related to shade avoidance and tolerance, such as CH and SLA (Munier-Jolain et al., 2014; Perronne et al., 2014). Intraspecific trait variation can therefore be a way for weeds to face the competition with crop plants in arable fields.

In this study, we investigated the influence of crop-weed competition on weed intraspecific functional diversity. We focused on three functional traits with high intraspecific variability (Siefert et al., 2015), that is, canopy height (CH), specific leaf area (SLA) and leaf dry matter

content (LDMC). We measured these traits over a period of 3 years on 4400 weed individuals belonging to 32 species found in four crop types that differed in their phenological and aerial vegetative traits: spring pea (*Pisum sativum* L.), winter oilseed rape (*Brassica napus* L.), winter barley (*Hordeum vulgare* L.) and spring and winter common wheat (*Triticum aestivum* L.). We first analysed whether intraspecific trait variation was related to species abundance because abundance is generally a good proxy of plant success. We expected that, despite potentially higher intraspecific trait variation across the distribution area (Laughlin & Messier, 2015), the most abundant species would show a lower ITV at the plot scale compared to other species, due to an ability to finely adapt to local conditions. We also expected that in comparison to the less abundant species, the most successful (i.e., most abundant) weed species would have trait values positively correlated with those of crops. Then, because weed-weed competition can also arise at both interspecific and intraspecific levels, we analysed how the relationship between weed and crop functional traits vary with the abundance of other weed plants, from the same or different species. Following Adler et al. (2018), we expected intraspecific competition to have a higher impact than interspecific competition on the traits of the most abundant species, as they are expected to have a higher competitive ability. In contrast, intraspecific weed-weed competition should have a rather low effect compared to competition with the crop and others weed species on the traits of the less abundant species.

2 | MATERIALS AND METHODS

2.1 | Experimental site description

The experiment took place in two fields (A and B) of the Bouzule experimental farm (Champenoux, France, 48°44'N, 6°21'E). The area has a temperate oceanic climate (Köppen classification), with an average annual rainfall of 775 mm and an annual average temperature of 10°C. Monthly temperature and rainfall over the study period are reported in Table S1. The soils are a Vertic Cambisol (62% clay, 35% silt and 3% sand and a pH (water) of 7.1) and a Hypereutric Cambisol (36% clay, 53% silt and 7% sand and a pH (water) of 6.6) (World Reference Base classification), in fields A and B, respectively. Prior to the experiment, field A was cropped with the sequence 'maize-maize-spring barley'. In 2008, it was divided into three blocks (100 × 72 m²). Each block was divided into eight plots of 50 × 18 m² (Figure 1). The plots were cultivated in 3- or 5-year rotations in a randomised 'phase differences' design (Yates, 1954), allowing each crop of each rotation to be present each year in each block. The three-year rotation was: winter oilseed rape, winter wheat and winter barley and the five-year rotation was: winter oilseed rape, winter wheat, winter barley, spring pea and winter wheat. Wheat crops were replicated three times per block per year, rape and barley were replicated twice and pea was replicated once. The winter wheat sown in 2011 was destroyed by intense frost and replaced by spring wheat, sown in March 2012.

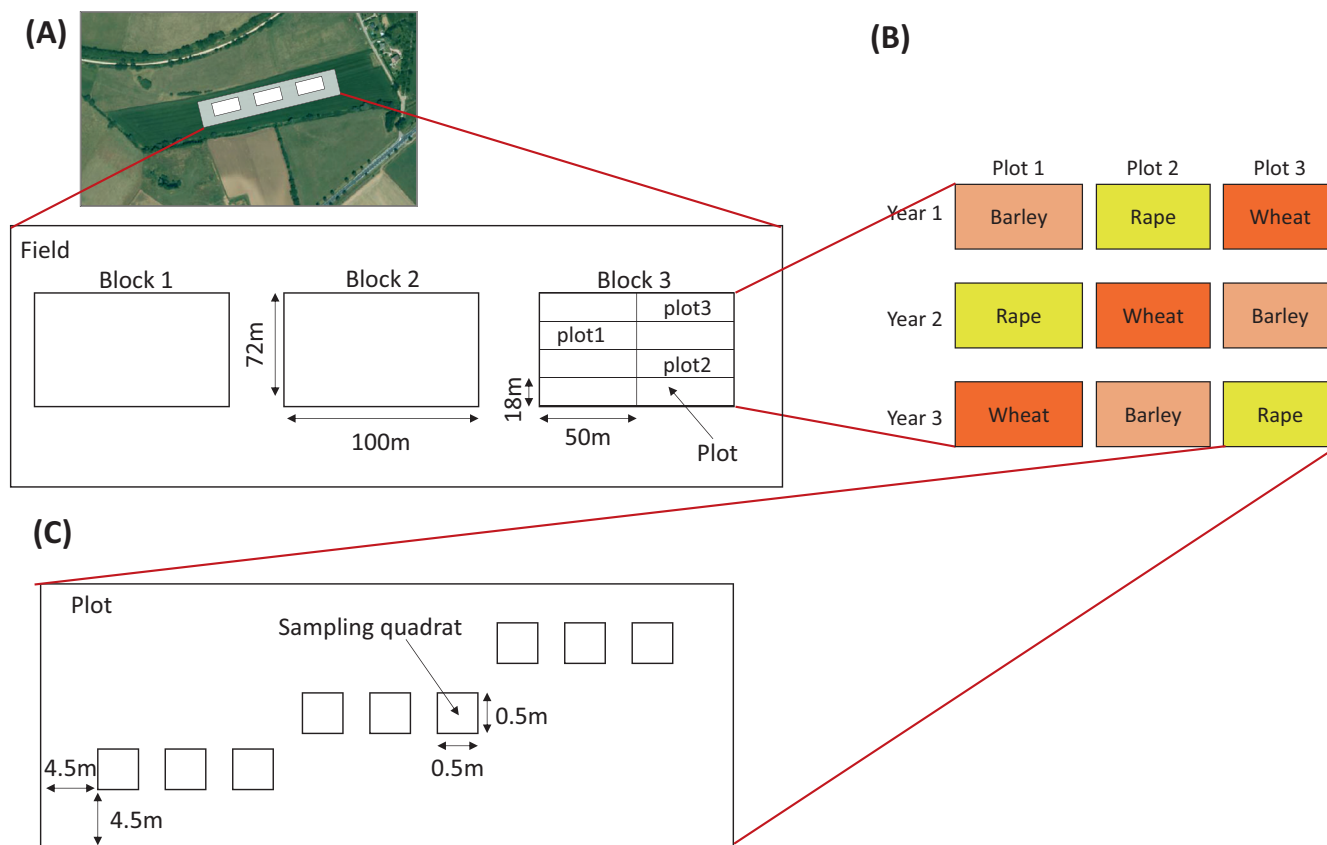


FIGURE 1 (A) The field position on the farm and the field experimental set-up, composed of a field divided in three blocks, themselves divided in eight plots. (B) Phases differences design of the crop rotation within a block. Sequences were randomised as illustrated for a 3-year rotation (oilseed rape, wheat, barley). Plot numbers refer to plots in Figure 1A. (C) Weeds sampling design at the plot level.

Prior to the experiment, field B was cropped with a maize monoculture. In August 2011, it was divided into two plots of $24 \times 250 \text{ m}^2$. The first plot was sown with spring pea in 2011–2012 and winter wheat the following year. The second plot was sown with winter wheat in 2011–2012 and spring pea the following year. Therefore, temporal crop sequences in field B were simplified (i.e., two-year rotation) compared to those in field A.

Cropping practices differed between crop types but were similar between the two fields. The plots were deep-tilled once a year with a mouldboard plough. Each year, winter wheat and winter barley were sown in October, and winter oilseed rape and spring pea were sown in September and March, respectively. All plots were fertilised with $95 \text{ kg P-Ca(H}_2\text{PO}_4)_2$ and $63 \text{ kg K-KCl ha}^{-1}$ in March 2011. Nitrogen (N) and sulphur (S) fertilisation was carried out with ammonium nitrate, urea, or ammonium sulfonitrate. Annual fertilisation was on average 174 kg N ha^{-1} and 60 kg S ha^{-1} for oilseed rape and 167 kg N ha^{-1} for wheat and barley. Pea was not fertilised with N or S. To ensure weed survival, the level of herbicides used was reduced by 50% compared to the regional treatment frequency index (TFI; Champeaux, 2006), varying from 0 to 1.56 according to the crop type and the year (mean TFI over all crops = 0.85). Sampling plots were covered by plastic sheets during the herbicide applications. A summary of cropping practices per crop type is given in Table S2.

2.2 | Sampling of weed and crop plants

Weed and crop plants were sampled in May 2011 in field A, and in June 2012 and June 2013 in fields A and B. Oilseed rape, pea and winter wheat were sampled in 2011, 2012 and 2013, and pea, spring wheat and barley were sampled in 2012.

Weeds were sampled in nine quadrats ($0.5 \times 0.5 \text{ m}^2$) per plot (Figure 1). Quadrats were located at least 4.5 m apart from the edges of the plot to avoid edge effects. In each quadrat, all weed plants were identified to the species level and the number of individuals of each species was recorded. In each quadrat, we measured the functional traits (see below for details on traits) of a maximum of 20 individuals per weed species as well as of 20 crop plants randomly selected.

2.3 | Measurement of functional traits

We focused on three traits related to plant functional responses to resource availability (Gaba et al., 2017): Canopy Height (CH), Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC). CH and SLA (ratio of leaf area to leaf dry mass) are proxies of plant competitive abilities for light. SLA and LDMC (ratio of leaf dry mass to leaf fresh mass) are functional markers of plant resource acquisition strategies.

LDMC is positively related to the outcome of competitive interactions and to the ability to conserve acquired resources (Singh & Singh, 2012). Although usually negatively correlated with SLA, LDMC captures different aspects of competitive ability, such as the acquisition of N and the ability to conserve resources, and is less plastic and less prone to measurement errors than SLA (Albert et al., 2011; Hodgson et al., 2011; Pérez-Harguindeguy et al., 2013).

We performed functional trait measurements following the recommendations of Pérez-Harguindeguy et al. (2013). For the SLA measurement, the most recently unfolded leaf was collected, stored in deionised water and brought back to the laboratory for measurement. When the most recently unfolded leaf was damaged or senescent, SLA was not measured. The leaf surface was determined using a planimeter LI 3050 (LI-COR Biosciences, Lincoln, USA). Leaf fresh weight was determined after 24 h of rehydration in deionised water in the dark. Leaf dry weight was measured after 72 h of drying at 60°C.

We retrieved data on the timing of emergence for each weed species from the Infloweb website (www.infloweb.fr) and, for missing species, from Bärberi et al. (2018). Annual species with a germination period starting in September–October and ending before May were considered autumn-germinating species; species with a germination period starting in February–April and ending before September were considered spring-germinating species; others were grouped as year-round germinating species. Perennial species were grouped together independently of the emergence period.

2.4 | Soil and meteorological data

Soil organic matter was determined at the plot level in November 2012. Analysis was carried out by AGRO-Systèmes (La Membrolle sur Choixille, France), following the Anne method (Anne, 1945), based on the determination of organic carbon content by colorimetry after oxidation of organic matter with potassium dichromate. Organic carbon content was converted into organic matter content using the correction factor 1.72 (in accordance with technical standard NF X31-109).

Differences in climatic conditions between years were taken into account using the annual precipitation, calculated as the sum of rainfall from crop sowing to the weed sampling day, and the annual temperature, calculated as the sum of degree days (base temperature of 0°C), computed from crop sowing to the weed sampling day for each year of the experiment. Daily rainfall (mm) and average temperature (°C) were obtained from a meteorological station located 1.5 km away from the experimental farm (Champenois 48°44'34"N, 06°20'57"E).

3 | DATA ANALYSIS

3.1 | Determination of weed species groups

Because intermediate and abundant species can respond differently to crop competition (Gaba et al., 2018), we defined weed species groups (i.e., 'abundant', 'intermediately common' and 'uncommon'),

based on the relative abundances of the weed species (Figure S1). The relative abundances of the selected species varied between 3% and 20% of the whole dataset. Abundant weed species were defined as those with a relative abundance greater than or equal to 5%, based on the shape of the rank-abundance distribution. Together, abundant weed species represented 67% of the dataset. To conduct data analyses on several years and crop species, we additionally selected among the abundant species those for which more than 10 individuals were sampled each year, in at least two different crops per year. Five species fitted these criteria: *Alopecurus myosuroides* Huds. (blackgrass), *Chenopodium album* L. (common lambs quarter), *Echinochloa crus-galli* (L.) P. Beauv. (barnyard grass), *Sonchus arvensis* L. (perennial sow thistle) and *Sonchus asper* (L.) Hill (prickly sow thistle). *A. myosuroides* is an autumn germinating annual weed, *C. album* and *E. crus-galli* are spring germinating annual weeds, *S. asper* is a year-round germinating annual weed and *S. arvensis* is a perennial whose shoots emerge in spring.

Abundant species that were excluded as they did not fit the criteria included the perennial *Elytrigia repens* (L.) Desv. Ex Nevski (couch grass) and the spring germinating annuals *Atriplex patula* L. (spear salt-bush) and *Solanum nigrum* L. (European black nightshade). They were analysed for comparison only.

We classified other weed species into 'intermediately common species' and 'uncommon species', corresponding to the species with relative abundances between 1% and 5% and those with relative abundances lower than 1%, respectively (Figure S1). Species represented by fewer than five individuals were excluded from all the analyses to avoid a sampling effect and therefore an unrepresentative intraspecific diversity value. We then performed a sensitivity analysis for varying threshold values (relative abundance) between abundant, intermediately common and uncommon weed species grouping which showed minor impacts on the analysis results (Figure S2).

Data analysis was conducted independently on each of the five abundant species, and on the groups of 'intermediately species' and 'uncommon species'. The number of functional trait measurements per species is given in Table S3.

3.2 | Calculation of the mean trait values and intraspecific functional diversity

The mean functional trait values of the crop species, abundant weed species and intermediately common and uncommon weed groups were calculated as the average of the individual trait values measured in each plot, for CH, SLA and LDMC.

Intraspecific functional diversity at the within-field scale was estimated independently for each functional trait using the coefficient of variation (CV; standard error divided by mean) (Albert et al., 2011). As we intend to measure the within-environment intraspecific diversity, the CV was calculated independently for each 'weed species—experimental plot—year' combination for species presenting a minimum of five individuals per plot in at least three plots. CV were then averaged at the species scale. The total CV of the retained species were also calculated for comparison.

3.3 | Relationship between crop and weed functional traits

We investigated the relationship between weed functional traits (at the individual scale) and biotic and abiotic factors related to competition and environmental conditions using linear regression models (LMs). The models included as covariates the three crop functional traits (CH, SLA and LDMC) averaged at the plot scale for a specific crop species, annual weather conditions (annual temperature and annual precipitation, both calculated from crop sowing day to weed sampling day, independently for each sampling plot) and soil organic matter content, here considered an integrative indicator of soil fertility. Annual weather conditions were included as covariates in the linear model to take into account the impact of climate on weeds development. We also included the number of individuals belonging to other weed species in the quadrat and their mean CH as proxies of interspecific competition (hereafter interspecific competition) and the number of plants of the same weed species in the quadrat as a proxy of intraspecific competition (hereafter intraspecific competition). For intermediately common and uncommon weed species groups, the species name and the timing of emergence were also included to take into account the potential effect of phenology. Interaction terms were included in the model between the different types of competition (interaction between crop competition and weed intraspecific competition, interaction between crop competition and weed interspecific competition, interaction between weed intraspecific and interspecific competition), using crop CH as a proxy of the competition exerted by the crop on weeds (Mason et al., 2007). The models were run independently for each weed functional trait and for each of the five abundant weed species, the intermediately common species and the uncommon species. When necessary, traits values were log-transformed to satisfy normality and homoscedasticity assumptions. Square-root transformation was used when log transformation gave unsatisfactory results. Log transformation was applied to the CH of *C. album*, *E. crus-galli*, *S. asper* and minor species while square-root transformation was applied to the CH of *S. arvensis* and intermediate species. SLA was log-transformed for all species and groups. LDMC was log-transformed for all species except *S. asper* and intermediate and uncommon weeds. Analyses were performed on standardised variables centred at 0 and scaled at 1.

We used an Akaike information criterion multimodel selection framework to select the best model using the `'dredge()'` function of the *MuMIn* library of R software (Barton, 2019). We successively used the sum of squares of each explanatory variable given by Analysis of Variance (ANOVA) to evaluate the contribution of each retained variable (Ginot et al., 2006). We tested for multicollinearity by calculating the variance inflation factor (VIF). The VIF was always less than 10, considered the threshold for negligible collinearity (O'Brien, 2007). All analyses were conducted in R software 3.5.1 (R Core Team, 2018).

4 | RESULTS

Crop and weed functional traits varied among species and years (Table S4). The highest crop CH and SLA were measured on oilseed rape in 2011 and the lowest on pea in 2013. The lowest crop LDMC was measured on oilseed rape in 2013 and the highest on wheat in 2011. Functional traits varied among weed species and weed species groups, by a factor of 5 for CH, 1.8 for SLA and 2 for LDMC (Table S4).

4.1 | Relationship between weed species abundance and intraspecific functional diversity

The intraspecific variation in CH, measured at the experimental plot scale by the coefficient of variation (CV), ranged from 0.16 ± 0.03 (mean \pm standard error) (*Bromus hordeaceus*) to 0.71 ± 0.08 (*Lipandra polysperma*). CH intraspecific diversity of weed species was not significantly correlated with their species abundance (Figure 2A). In particular, *A. myosuroides*, the most abundant species, had a relatively low intraspecific diversity for CH (CV = 0.20 ± 0.03). In contrast to CH, few differences in CV for SLA were observed between weed species (Figure 2B). SLA intraspecific diversity ranged from a CV of 0.21 ± 0.06 (volunteer *H. vulgare*) to a CV of 0.41 ± 0.06 (*Convolvulus arvensis*). LDMC intraspecific diversity ranged from a CV of 0.16 ± 0.01 (*C. album*) to a CV of 0.36 ± 0.09 (*Persicaria lapathifolia*). In contrast to other traits, the LDMC intraspecific diversity was negatively correlated with species abundance (Figure 2C). For all three traits, the total intraspecific diversity, calculated incorporating all species individuals, was not significantly correlated to the species abundance (data not shown).

4.2 | Response of weed species to biotic interactions and abiotic factors

We used linear models to assess the proportion of variance in weeds functional traits explained by crop competition (assessed by crop functional traits), intraspecific competition (assessed by the abundance of weeds of the same species), interspecific competition (assessed by the abundance and mean CH of weeds of other species) and their interactions, to weed functional traits. The analysis was limited to abundant weed species present in a wide array of crops and years (i.e., *A. myosuroides*, *C. album*, *E. crus-galli*, *S. arvensis* and *S. asper*) while other species were pooled as intermediately common and uncommon species. However, the response of abundant species excluded from the analysis due to a more restricted distribution (i.e., *A. patula*, *E. repens* and *S. nigrum*) will be mentioned for comparison.

The explanatory power of the models after the model selection procedure varied with the species and the trait under consideration. In general, higher explanatory power was observed for CH, with

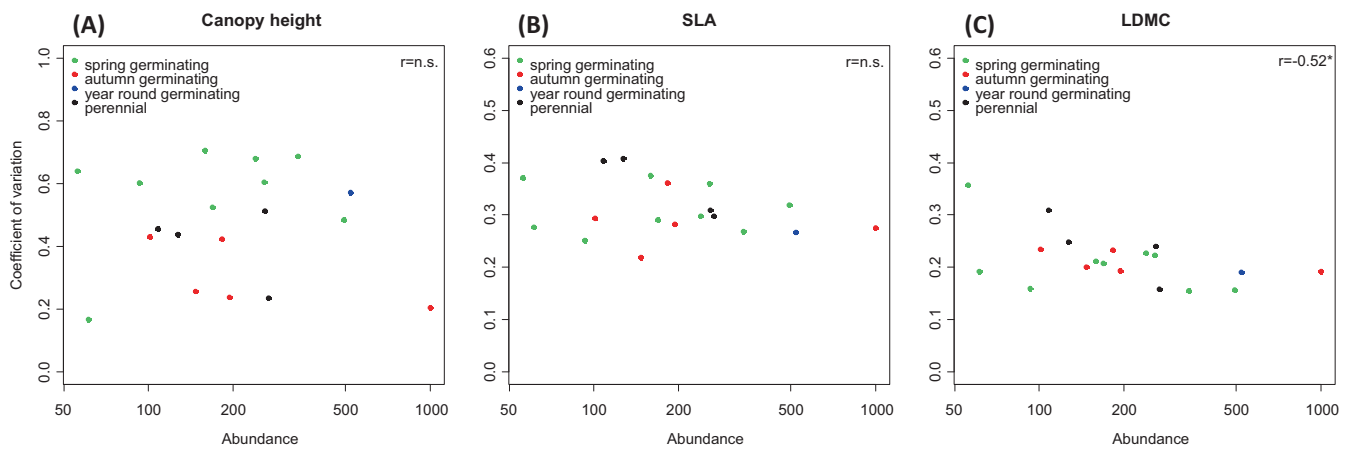


FIGURE 2 Relationship between intraspecific functional diversity at the within-environment scale and species abundance for weeds CH (A), SLA (B) and LDMC (C). Intraspecific functional diversity is the mean of the coefficients of variation calculated at the experimental plot scale. Abundance is expressed as the number of individuals sampled over the study. Note that abundance is represented on a logarithmic scale. r is the Spearman coefficient of correlation between the coefficient of variation and the base 10 logarithm of abundance. n.s., non-significant; $*p < 0.05$. The figure with species names is reproduced in Figure S3.

21%–61% of the variation explained (Figure 3A, Table 1), and for LDMC, with 23%–83% of the variation explained (Figure 3C, Table 2), while only 15%–49% of the SLA variation was explained (Figure 3B, Table 3). *Echinochloa crus-galli* was the species whose trait variations were on average the best explained by the models, while trait variations in *C. album* and *S. arvensis* were poorly explained.

Differing amounts of variation in weed traits were explained by crop functional traits, weed-weed competition and environmental conditions (i.e., climate and soil). Crop functional traits strongly explained the CH of *A. myosuroides*, for which more than 50% of the variance was explained by crop CH (Figures 3A and S4). The CH of *S. arvensis* and of the two groups of lesser common weeds also significantly increased with crop CH (Table 1; Figure S4). Crop functional traits explained significantly the variance of weeds SLA (Figure 3B) and LDMC (Figure 3C), particularly for *E. crus-galli*, *S. arvensis* (both foliar traits) and for the LDMC of *C. album*, *S. asper* and the uncommon species. It also strongly affected the SLA and LDMC of *S. nigrum*, an abundant weed present almost only in pea crops (Figure S5, Table S6). Crop CH significantly affected the values of SLA and LDMC of all the weed species except *S. asper* (Tables 2 and 3). This effect was either positive (on the SLA of *A. myosuroides*, *C. album*, *E. crus-galli* and *S. nigrum* and the LDMC of *A. myosuroides* and *S. arvensis*) or negative (on the SLA of *S. arvensis* and *S. asper* and the LDMC of *C. album*, *E. crus-galli*, *S. asper* and *S. nigrum*) depending on the species. By contrast, the crop LDMC was positively correlated to the LDMC of three abundant weed species and of the intermediately common species (Table 2). This was also observed for *E. repens* and *S. nigrum* (Table S6).

Our results also revealed a significant effect of weed-weed competition on weed species traits with higher responses observed for CH and SLA than for LDMC (Figure 3A,B). The canopy heights of *A. myosuroides* and *S. asper* were negatively impacted by both intra- and interspecific weed-weed competition, explaining 7.9% and 17%

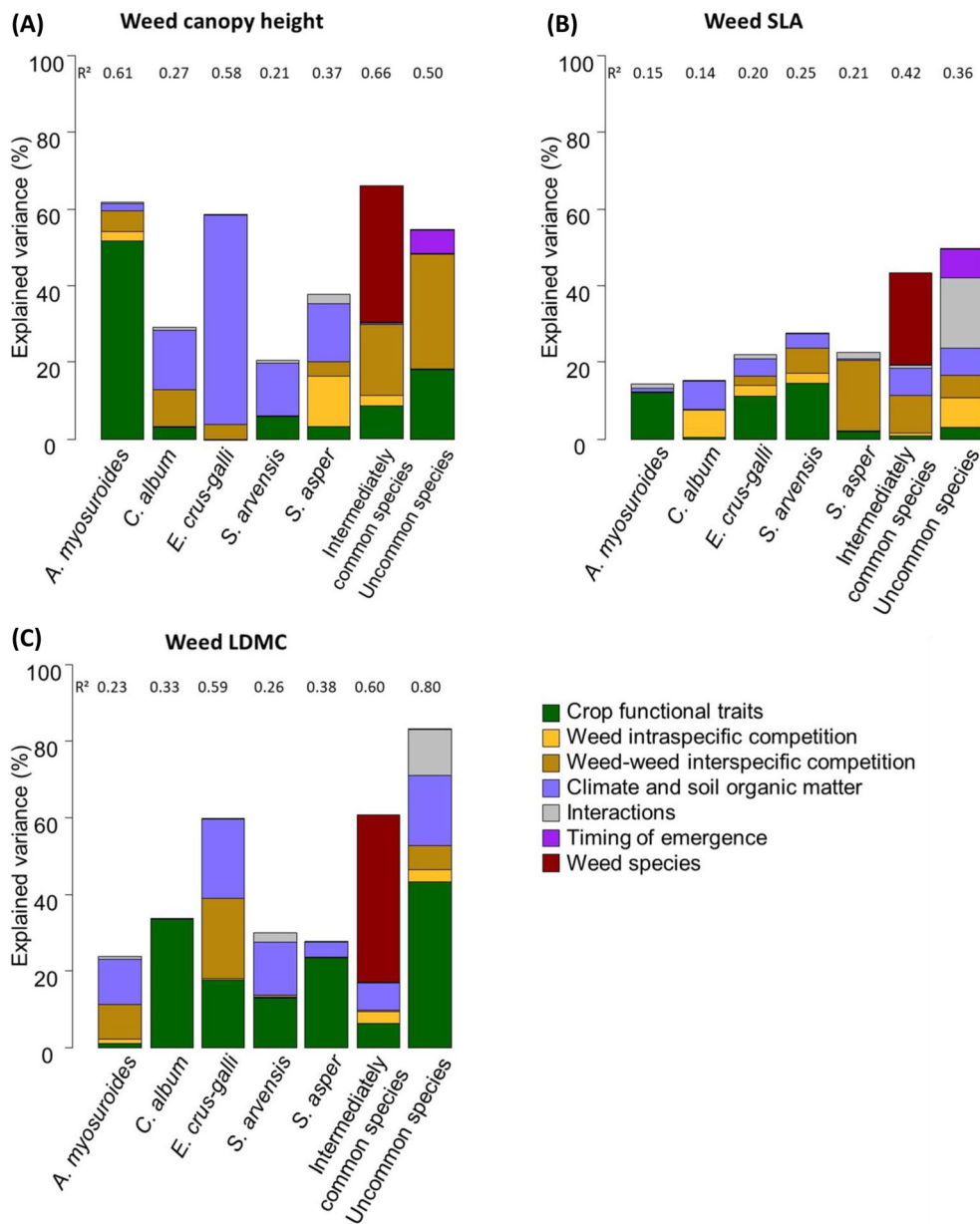
of the variance, respectively, for each species. However, intraspecific competition was stronger than interspecific competition for *A. myosuroides*, while the reverse was true for *S. asper*. On the opposite, a positive relationship was observed between the canopy heights of *E. repens* and of the neighbouring weeds from other species (Figure S5, Table S6). We also found a significant effect of intraspecific weed-weed competition on SLA values for three of the most abundant species (*C. album*, *E. crus-galli* and *S. arvensis*) as well as for intermediately common species and uncommon species. However, the response pattern varied. The uncommon species and *C. album* showed a higher SLA value when intraspecific competition was high, while other species had smaller SLA values.

Finally, several species strongly responded to environmental conditions, in particular *E. crus-galli*, for which more than 50% of the CH variance depended on temperature, precipitations and soil organic matter content (Figure 3A, Table 1).

5 | DISCUSSION

We measured functional traits on 4400 individual weed plants belonging to 32 species to assess how weed species respond to competition with the crop, the other weed species and the plants of the same species found in the same plot. We found functional trait values consistent with those found for crops and arable weeds in Europe (Bàrberi et al., 2018; Fried et al., 2009; Gunton et al., 2011). Overall, our results showed that at the plot scale the most abundant weed species had the lowest intraspecific variability for LDMC compared to the less abundant ones. All weed species, whatever their abundance, had values of CH, LDMC or both strongly related with either crop CH, LDMC or both. Such pattern was not observed for SLA. We found that crop competition, intraspecific competition and interspecific weed-weed competition significantly affected the intraspecific

FIGURE 3 Percentage of variance of functional traits of weed species explained by crop functional traits, weed-weed competition, yearly climate, soil organic matter and their interactions. Weeds functional traits are CH (A), SLA (B) and LDMC (C). Crop functional traits included crop CH, SLA and LDMC. Weed intraspecific competition included the abundance of weeds of the same species; weed interspecific competition included the abundance of weeds of other species and the mean CH of the weeds of other species. Climate and soil included the sum of degree days and the sum of precipitations since sowing and the soil organic matter content. Interactions included crop CH \times abundance of the species, crop CH \times abundance of other species, abundance of the species \times abundance of other species. For the groups of intermediately common and uncommon species, the weed species and the timing of emergence were also included. R^2 is the adjusted R^2 of the linear model.



variation in weed traits, with a magnitude strongly dependent on the traits and weed species considered.

5.1 | Abundant weeds show a lower intraspecific variability in LDMC but not in CH

We found a negative relationship between LDMC intraspecific variability and species abundance for weed species at plot scale. This suggests that finely adapting LDMC values to local environmental conditions (i.e., soil properties, crop density and growth), might be beneficial for weeds and that some LDMC values might be more successful than others. This might be particularly the case for *A. myosuroides* which has notably high LDMC values. However, as LDMC vary with plant development (Palacio et al., 2008), reduced

intraspecific variability might also indicate that in successful species all individuals emerged in a short time period.

In line with previous studies (e.g., Siefert et al., 2015), intraspecific CH variability was here much higher than that of SLA and LDMC. However, we did not observe any significant relationship between CH intraspecific diversity and weed species abundance. CH is a trait involved in shade avoidance and in the competitive effect for light, that is, the ability to pre-empt light from competitors (Navas & Fayolle, 2012). This absence of a relationship between CH intraspecific diversity and species abundance might be linked to the coexistence of shade-tolerance and shade-avoidance strategies among weeds, assuming that competition for light is the dominant competitive process (Perronne et al., 2014). This absence of relationship can also result from the coexistence of individuals with different ages in the same field (i.e., ontogenic variation). Recently emerged plants of

TABLE 1 Linear model outputs (estimated coefficients \pm SE) for weeds CH.

Response variable transformation	<i>A. myosuroides</i>	<i>C. album</i>	<i>E. crus-galli</i>	<i>S. arvensis</i>	<i>S. asper</i>	Intermediately common species	Uncommon species
		Log base 10	Log base 10	Square root	Log base 10	Log base 10	Log base 10
Crop functional traits							
CH	0.64 \pm 0.037***	0.05 \pm 0.135n.s.	-	0.55 \pm 0.19**	-0.07 \pm 0.116n.s.	0.20 \pm 0.026***	0.75 \pm 0.167***
SLA	-	0.28 \pm 0.10*	-	-0.17 \pm 0.12n.s.	0.44 \pm 0.086***	-	-
LDMC	-	-	-	-	-	-	-
Weed-weed competition							
Abundance of the species	-0.13 \pm 0.022***	-	-	0.096 \pm 0.12n.s.	-0.19 \pm 0.102n.s.	0.12 \pm 0.038**	-
Abundance of other species	-0.092 \pm 0.038*	-0.07 \pm 0.074n.s.	-	-0.093 \pm 0.077n.s.	-0.15 \pm 0.042***	-	-
Mean CH of other species	-	0.19 \pm 0.052***	0.29 \pm 0.041***	-	0.10 \pm 0.047*	0.16 \pm 0.022***	0.40 \pm 0.107***
Climate and soil							
Annual temperature	0.12 \pm 0.037**	0.69 \pm 0.235***	0.16 \pm 0.047***	-	-	0.21 \pm 0.034***	-0.21 \pm 0.12n.s.
Annual precipitations	-	-0.77 \pm 0.153***	-0.80 \pm 0.039***	-0.39 \pm 0.10***	-	-0.16 \pm 0.027***	-
Organic matter	-0.070 \pm 0.024**	-0.17 \pm 0.058**	0.17 \pm 0.042***	-0.22 \pm 0.14n.s.	-0.32 \pm 0.054***	-	-
Interactions							
Crop CH \times abundance of the species	-	-	-	0.42 \pm 0.14**	-0.55 \pm 0.125***	0.06 \pm 0.026**	-
Crop CH \times abundance of other species	-0.097 \pm 0.029***	0.011 \pm 0.060n.s.	-	0.19 \pm 0.082*	-	-	-
Abundance of the species \times abundance of other species	-	-	-	-	-	-	-
Weed species characteristics (only for intermediate and uncommon weeds)							
Weed species	na	na	na	na	na	+(see Table S5)	-
Timing of emergence							
Year round	na	na	na	na	na	-	0.18 \pm 0.224
Autumn	na	na	na	na	na	-	-0.42 \pm 0.159*
Spring	na	na	na	na	na	-	0.04 \pm 0.202

TABLE 1 (Continued)

Response variable transformation	<i>A. myosuroides</i>		<i>C. album</i>		<i>E. crus-galli</i>		<i>S. arvensis</i>		<i>S. asper</i>		Intermediately common species		Uncommon species	
	-	178	Log base 10	16	Log base 10	154	Square root	7	Log base 10	43	Log base 10	Log base 10	Log base 10	Log base 10
F value	0.61****		0.27****		0.58****		0.21****		0.37****		0.66****		0.50****	
r ²														

Note: Covariates in the linear models were crop functional traits (CH, SLA, LDMC), weeds abundance and CH, yearly weather, and soil. In the case of intermediately common and uncommon groups, weed species and timing of emergence were also included in the model. All explanatory variables were scaled and the response variable was transformed when necessary. na, not applicable; -- not retained in the model; + retained in the model (for weed species only, see Table S5 for estimated coefficients).

Abbreviation: n.s., non-significant.

*0.01 ≤ *p* < 0.05; **0.01 ≤ *p* < 0.001; ****p* ≤ 0.001.

small size can coexist with large plants that have emerged for several weeks (Perronne et al., 2014). Such pattern might be predominant for species with extended germination periods.

5.2 | Weed species tend to match crop canopy height and LDMC in response to competition

We observed positive relationships between the functional traits of crops and weeds for the five most abundant weed species considered in this study, confirming our hypothesis that abundant weed species have trait values positively correlated with those of crop species. Two species (*A. myosuroides* and *S. arvensis*) had CH values positively correlated to the CH of the crop they were growing in, while three species presented a positive correlation with the crop for LDMC (*C. album*, *E. crus-galli*, *S. asper*). It is worth noting that this relationship was observed in weeds with contrasted timings of emergence (including spring, autumn and year-round emerging weeds), growing in both winter and spring crops, pointing to a general behaviour.

We propose that these species display a ‘crop matching’ strategy. We use ‘crop matching’ as distinct from ‘crop mimicry’. Crop mimicry, sensu Vavilov (McElroy, 2014), is used to describe evolutionary processes by which weed species become phenotypically more similar to the crop. Instead, we use crop matching to describe processes of phenotypic similarity, originating either from phenotypic plasticity or from intraspecific genetic diversity. The ability to match a crop CH would allow these weed species to maintain access to or to pre-empt light in the context of asymmetric competition. This is a widely observed phenomenon in plant species (Munier-Jolain et al., 2014; Nagashima & Hikosaka, 2012; Vermeulen et al., 2008). Furthermore, it is detrimental for plants to be excessively higher than neighbours, due to the amount of resources required to build and maintain support tissues, and due to exposure to wind lodging (Nagashima & Hikosaka, 2011). The conjunction of the two phenomena results in CH convergence between competitors (Nagashima & Hikosaka, 2012; Vermeulen et al., 2008). Notably, the strongest relationship between weed and crop CH was observed for the most abundant species, *A. myosuroides*, which was also the only species able to truly match the crop CH, with *S. asper* remaining smaller. This result suggests that crop matching might be strongly advantageous for some weed species.

The reason some weed species would tend to match crop LDMC is less obvious. According to the literature, the LDMC is negatively correlated with the nutrient availability and positively correlated with the ability of plants to conserve acquired resources (Hodgson et al., 2011). Weeds and crop plants might increase their LDMC together when competition for nutrients increases. However, the correlation might also be an indirect consequence of phenological coordination between weeds and crop plants, as highlighted in Section 5.1. Weed SLA, however, was not correlated with crop SLA but was positively impacted by crop CH for three annual weed species. This result is consistent with the plastic response of SLA (Liu et al., 2016; Nagashima & Hikosaka, 2011), which increases in response to a decreasing light availability caused by crop competition, while CH is a

TABLE 2 Linear model outputs (estimated coefficients \pm SE) for weeds LDMC.

Response variable transformation	A. myosuroides	C. album	E. crus-galli	S. arvensis	S. asper	Intermediately common species	Uncommon species
	Log base 10	Log base 10	Log base 10	Log base 10	-	Square root	-
Crop functional traits							
CH	0.19 \pm 0.059**	-0.23 \pm 0.096*	-0.68 \pm 0.070***	1.02 \pm 0.159***	-0.04 \pm 0.11n.s.	-0.42 \pm 0.039***	0.86 \pm 0.150***
SLA	-0.27 \pm 0.044***	-0.31 \pm 0.11**	-	-	-	-0.13 \pm 0.038***	-
LDMC	-	0.49 \pm 0.080***	0.47 \pm 0.073***	-	0.42 \pm 0.055***	0.20 \pm 0.030***	-
Weed-weed competition							
Abundance of the species	-0.18 \pm 0.065***	-	0.17 \pm 0.050***	0.12 \pm 0.116n.s.	-	0.09 \pm 0.025***	0.38 \pm 0.088*
Abundance of other species	0.23 \pm 0.056**	-	-0.17 \pm 0.043***	-0.22 \pm 0.178n.s.	0.46 \pm 0.125***	-0.11 \pm 0.025***	0.19 \pm 0.097***
Mean CH of other species	-0.19 \pm 0.039***	-	-0.20 \pm 0.086*	-	-	-	-
Climate and soil							
Annual temperature	0.11 \pm 0.071n.s.	-	0.65 \pm 0.064***	-	0.52 \pm 0.103***	0.64 \pm 0.045***	-
Annual precipitations	-0.64 \pm 0.069***	0.088 \pm 0.057n.s.	-0.51 \pm 0.068***	-0.18 \pm 0.113n.s.	-	-0.25 \pm 0.033***	0.32 \pm 0.089***
Organic matter	-	-	0.32 \pm 0.040***	0.42 \pm 0.090***	0.26 \pm 0.049***	0.10 \pm 0.024***	0.24 \pm 0.104*
Interactions							
Crop CH \times abundance of the species	-	-	-0.019 \pm 0.042n.s.	0.33 \pm 0.176n.s.	-	0.04 \pm 0.019*	0.47 \pm 0.137**
Crop CH \times abundance of other species	0.13 \pm 0.059*	-	-	-	0.61 \pm 0.143***	-	-0.26 \pm 0.089***
Abundance of the species \times abundance of other species	-0.18 \pm 0.096n.s.	-	-	-0.38 \pm 0.018*	-	-	-
Weed species characteristics (only for intermediate and uncommon weeds)							
Weed species	na	na	na	na	na	na	na
Timing of emergence	na	na	na	na	na	na	na
Year round	na	na	na	na	na	na	na
Autumn	na	na	na	na	na	na	na
Spring	na	na	na	na	na	na	na
F value	23	35	75	8	40	79	24
r ²	0.23***	0.33***	0.59***	0.26***	0.36***	0.60***	0.80***

Note: Covariates in the linear models were crop functional traits (CH, SLA, LDMC), weeds abundance and CH, yearly weather, and soil. In the case of intermediately common and uncommon groups, weed species and timing of emergence were also included in the model. All explanatory variables were scaled and the response variable was transformed when necessary. na not applicable; -- not retained in the model; + retained in the model (for weed species only, see Table S5 for estimated coefficients).

Abbreviation: n.s., non-significant.

*0.01 \leq p < 0.05; **0.01 \leq p < 0.001; *** p \leq 0.001.

TABLE 3 Linear model outputs (estimated coefficients ± SE) for weeds SLA.

Response variable transformation	<i>A. myosuroides</i> Log base 10	<i>C. album</i> Log base 10	<i>E. crus-galli</i> Log base 10	<i>S. arvensis</i> Log base 10	<i>S. asper</i> Log base 10	Intermediately common species Log base 10	Uncommon species Log base 10
Crop functional traits							
CH	0.32 ± 0.066***	0.27 ± 0.11*	0.61 ± 0.094***	-0.66 ± 0.12***	-0.21 ± 0.101*	0.32 ± 0.038***	-0.66 ± 0.305*
SLA	-	-	-	-	-	-	-
LDMC	-0.15 ± 0.043***	-0.16 ± 0.075*	-0.29 ± 0.10**	-	0.12 ± 0.068n.s.	-	-
Weed-weed competition							
Abundance of the species	0.082 ± 0.055n.s.	0.30 ± 0.066***	-0.14 ± 0.062*	-0.22 ± 0.12***	-	-0.17 ± 0.038***	0.34 ± 0.162*
Abundance of other species	-0.036 ± 0.038n.s.	-0.13 ± 0.072n.s.	0.15 ± 0.052***	-	-0.11 ± 0.14n.s.	0.12 ± 0.029***	-0.20 ± 0.163n.s.
Mean CH of other species	-	-	-	0.40 ± 0.086***	0.19 ± 0.049***	-0.06 ± 0.031*	-0.27 ± 0.140n.s.
Climate and soil							
Annual temperature	-	-0.31 ± 0.10**	-	-	-0.31 ± 0.107**	-0.46 ± 0.052***	-
Annual precipitations	0.15 ± 0.053**	-	0.065 ± 0.053n.s.	0.17 ± 0.12n.s.	-	0.08 ± 0.040*	-0.49 ± 0.175**
Organic matter	-	0.16 ± 0.062*	-0.27 ± 0.055***	0.21 ± 0.089*	-	-0.09 ± 0.026***	-
Interactions							
Crop CH × abundance of the species	-0.20 ± 0.065**	-	-	-	-	-0.05 ± 0.023*	-
Crop CH × abundance of other species	-	-	-	-	-0.49 ± 0.163**	-	0.66 ± 0.191**
Abundance of the species × abundance of other species	-0.20 ± 0.087*	-	-0.28 ± 0.12*	-	-	0.07 ± 0.029*	-
Weed species characteristics (only for intermediate and uncommon weeds)							
Weed species	na	na	na	na	na	+	(see Table S5)
Timing of emergence							
Year round	na	na	na	na	na	-	-
Autumn	na	na	na	na	na	-	-0.23 ± 0.285n.s.
Spring	na	na	na	na	na	-	-0.19 ± 0.279n.s.
F value	21	8	19	11	23	39	4
r ²	0.15***	0.14***	0.20***	0.25***	0.21***	0.42***	0.36***

Note: Covariates in the linear models were crop functional traits (CH, SLA, LDMC), weeds abundance and CH, yearly weather, and soil. In the case of intermediately common and uncommon groups, weed species and timing of emergence were also included in the model. All explanatory variables were scaled and the response variable was transformed when necessary. na not applicable; - not retained in the model; + retained in the model (for weed species only, see Table S5 for estimated coefficients).

Abbreviation: n.s., non-significant.

*0.01 ≤ p < 0.05; **0.01 ≤ p < 0.001; ***p ≤ 0.001.

good proxy for light depletion (Navas & Fayolle, 2012). *S. arvensis* and *S. asper* behaved in a different way, as their SLA values decreased when crop CH increased. However, their SLA increased with the CH of the other weeds, which could have impacted them more than the crop.

Finally, in contrast to our initial hypothesis, intermediate and uncommon species also tended to display crop matching for CH and LDMC. Although interspecific variability added to intraspecific variability, this scenario stresses the necessity of access to light for most weed species, even for non-abundant species, as light is probably the main limiting resource for weeds (Holt, 1995).

5.3 | Weed-weed competition impact weed functional traits

Crop traits explained an important share of weed functional trait variance. Crop species are selected for traits that favour their competitive ability, such as a high height (Mason et al., 2007), and cropping practices create environmental conditions that maximise their biomass production. This scenario makes the crop the main competitor in the field (Gaba et al., 2018; Perronne et al., 2014). However, in this study, we also explored weed-weed competition, a process that has rarely been explored compared to crop-weed competition (Blaix et al., 2018). We found that this process can significantly affect weed traits, explaining up to 30% of the trait's variance. In some cases, weed-weed competition had a higher impact than crop-weed competition on weed traits (i.e., CH of *S. asper*, SLA of *C. album* and LDMC of *E. crus-galli*). Interestingly, we found that the CH of *A. myosuroides*, which displays a crop matching strategy for CH, was negatively affected by weed-weed competition. *E. crus-galli* decreased its SLA and increased its LDMC in response to intraspecific competition but increased its SLA and decreased its LDMC in response to interspecific competition. This result could be interpreted as a shift to a more stress-tolerant strategy in response to intraspecific competition and a more competitive strategy in response to interspecific competition. Such shifts were observed by Bennett et al. (2016) and interpreted as competition avoidance in the presence of conspecifics. Alternatively, these results could be interpreted as reduced competition and better growth conditions in situations of high *E. crus-galli* density, such as spots of failed crop emergence. Identical situations could also explain the positive correlation between the CHs of *E. repens* and other weed species. Unfortunately, the number of crop individuals was not measured, impeding to test this hypothesis. In contrast to *E. crus-galli*, *A. myosuroides* decreased its LDMC in the presence of intraspecific competitors and increased its LDMC in the presence of interspecific competitors. This scenario is difficult to explain, but the fact that different weed species display contrasting phenotypic responses to competition has already been reported (Munier-Jolain et al., 2014), and further generalisation would require more studies. Overall, mechanisms of weed-weed competition have been underexplored compared to crop-weed competition (Blaix et al., 2018), but these results highlight the potential of weed-weed competition to regulate weeds.

6 | CONCLUSION

This study highlights the importance of taking into account intraspecific trait variation when investigating the processes underlying weed species assembly, especially their response to competition. Our results revealed that weed species display different functional strategies in response to competition. All abundant species tended to match crop canopy height or LDMC values. These strategies were also observed in the uncommon and intermediately common species, revealing that intraspecific trait variation alone is not sufficient to ensure successful development. Interestingly, and to our knowledge for the first time, we revealed that weed-weed competition affects weed functional response in a way that could be used for a natural weed control through maintaining in-field weed diversity, as suggested by Storkey and Neve (2018). However, to make this approach operational, further studies are required for a better understanding of weed responses to different sources of competition (crop, weed and intra- and interspecific competition) and of the impact of weed-weed competition on the crop matching abilities. It is also important to accumulate knowledge on the way the species we want to control and those we want to preserve respond to competition, as they can behave differently.

This study was limited to aerial functional traits involved in competition for light. Root functional traits should be considered to deepen our understanding, particularly in organic or dry-climate cropping systems, where competition for nutrients and water might be of importance. Traits of interest might include root length density and specific root length, which are known to respond to competition for soil nutrients, as well as root diameter and biomass allocation to deep soil, which are related to water uptake (Fort et al., 2014, 2017). All root traits are known to be highly plastic. However, a main difficulty is the taxonomic identification of roots in field soil samples (see Cabal et al., 2021, for a review of available technics). Further studies are also required to identify the source of intraspecific trait variation in weeds (either phenotypic plasticity or genetic diversity) and the consequences for weed fitness.

ACKNOWLEDGEMENTS

This study was funded by the French Minister of Higher Education and Research. This article is dedicated to the memory of our colleague Bernard Amiaud (1969–2018), professor at the Université de Lorraine, who participated to the design of the experiment and is at the origin of the weed functional traits database used in this work. Joffrey Perrot and Caroline Kohler helped with weed sampling and functional traits measurements.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/wre.12592>.

DATA AVAILABILITY STATEMENT

All functional traits data supporting the analysis are available in the TRY Plant Trait Database File Archive (<https://try-db.org/TryWeb/Data.php>), in file 537_Weed and Crop traits (NE France).zip.

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Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Romillac, N., Piutti, S., Slezack-Deschaumes, S. & Gaba, S. (2023) Intraspecific functional trait variation in weeds: A strategy in response to competition with crop and weed plants. *Weed Research*, 1–14. Available from: <https://doi.org/10.1111/wre.12592>