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Abstract

In arable farming, weeds provide important floral and seed resources that have the potential to support the provision of ecosystem services such as pollination or pest control. Estimating the production of these weed resources in the landscape is however not trivial as large-scale surveys of weed communities are usually conducted once in the season with a timing that may not coincide with the flowering and fruiting stages of all weed species. More, intraspecific variation in the mortality and phenology of individual weed species may arise from differences in the quality of the growing environment of each plant. In this study, we monitored the phenology of 30 common weed species in the field core and the field edge of 64 commercial fields grown with 6 crop types. Our hypothesis was that the production of resources by an individual plant would be modulated by its within-field location and by the crop type where it grows. We quantified floral (proportion, starting date and duration of flowering, dry biomass at flowering as a proxy for the amount of flowers) and seed resource production (proportion and starting date of fruiting). For most species, flowering and fruiting success were higher in field edges than in field cores and were lower in cereal crops than in other crops. Weeds flowered and fruited earlier and the flowering period was longer in field edges, except those of cereal crops. Dry biomass at flowering varied with field location either way, depending on the weed species, but tended to be lower in cereal crops than in other crops. This important intraspecific phenological variability in the production of seed and/or flower or resources should be considered when evaluating the contribution of weed communities to ecosystem services. It also suggests that within an agricultural landscape, the amount, timing and duration of provision of services by weeds could be enhanced by maintaining sufficient lengths of field edges and by growing a diversity of crop types.

Key-words: phenology, field edge, farming management, flowering success, pollination, pest control

1. Introduction

There is growing evidence that arable weeds provide habitat and resources that are of key value for the maintenance of biodiversity and the delivery of ecosystem services in agroecosystems (Blaix et al., 2018). Weeds are an important source of floral and seed resources for various insects, birds and mammals (Wilson et al., 1999; Petit et al., 2011). Their role as providers of a continuous supply of pollen and nectar is of key importance for the maintenance of pollinators and the provision of the pollination service (Requier et al., 2015; Bretagnolle and Gaba, 2015). Weeds also supply trophic resources for many natural enemies (parasitoids, predators) and are thus contributing to the provision of pest control services (Tylianakis et al., 2004; DiTommaso et al., 2016). Some authors suggest that the decline of many insects and farmland birds is associated with changes in farming practices that adversely affect weeds (Marshall et al., 2003). Weed richness and abundance in arable farming has indeed drastically declined over the last decades as documented in Europe (Andreasen et al., 1996; Baessler and Klotz, 2006). In Northern France, Fried et al. (2009) estimated that weed richness and abundance within arable fields decreased respectively by 44 and 66% over the last 30 years. These authors also showed that this decline was dependent on the within-field location of weeds, with a much less pronounced decline in crop edges, i.e. the area between the field margin and first row of crop, because this habitat can act as refugia for many weed species (Solé-Senan et al. 2014).

Evaluating the capacity of agroecosystems to provide key resources and how this capacity is affected by farming management is of prime importance to enhance the ecological functioning of agricultural systems. Yet, there are few examples of such assessment at large spatial scales. Evans et al. (2011) evaluated the biomass and energy provided by berries and seeds at a farm scale in relation to the trophic value of such resources for farmland birds. Similarly, Vialatte et al. (2017) estimated the pollen resource provision within an agricultural landscape for hoverflies through the aggregation of mean provision values estimated by plant surveys in different types of semi-natural and cultivated habitats. Many studies have documented weed communities in different agricultural or landscape settings, yet, to our knowledge, no assessment of weed floral and seed resources within an agricultural landscape is yet available. One reason is that most arable weed surveys conducted at large scale are designed to assess the effect farming management or environmental conditions on weed communities (for a review, see Hanzlik and Gerowitt, 2016). The timing of the weed sampling is therefore often driven by agronomic considerations such as the completion of weed management measures (e.g. Hawes et al., 2010) or crop phenology (e.g. Andreasen and Stryhn, 2008). Weeds are often described once in the season, at an earlier or unspecified phenological stage (Hanzlik and Gerowitt, 2016). Such methodology is thus not tailored to assess the production of weed resources within an agricultural landscape. Between earlier phenological stages and the flowering and fruiting stages that are key in the provision of resources to other taxa, weed plant survival and development is likely to be impacted by the environment where it grows. The competition for resources (nutrients, water, light) exerted by the crop on weeds can significantly affect weed survival and growth (Kaur et al., 2018), with an effect often considered as weaker in field edges than in field cores (Cordeau et al., 2012; Perronne et al., 2014) and variable according to the type of crop grown. In addition, even after the completion of weed management operations, farming practices such as nitrogen fertilization can affect weed development (Bàrberi et al., 1997; Kleijn and van der Voort, 1997). The timing, frequency and intensity of these farming practices vary across farming systems and crop types and their adverse effect on weed development likely to be less intense in the edges of the field (Marshall and Moonen, 2002). One can thus expect that the chance for a weed plant to reach the next phenological stages will vary much within the same agricultural landscape, depending on the local plant growing conditions. Assessing this intraspecific variability in weed phenology thus appears a necessary step for assessing the production of weed resources within an agricultural landscape.

In this paper, we assessed the intraspecific phenological variability of 30 weeds species commonly found in arable farming in response to their location in the field (hereafter 'within-field location', i.e. field core vs. field edge) and to the crop grown. We monitored the phenology of 685 weed seedling patches across 64 commercial fields and 6 crop types over 6 months. We developed survival curves and estimated indicators of floral resources production (flowering success, starting date and duration of flowering and dry biomass at flowering as a proxy for the amount of flowers) and seed resource production (fruiting success, starting date of fruiting). We tested for the effect of within-field location, crop type and their interaction on the phenological indicators. We expected higher success and higher resource production in the field edge as this within-field location is less affected by farming practices and by crop competition. We also expected weed phenology to respond to the crop grown as the crop tested differed in terms of competitive ability, morphological traits and response to farming management.

2. Materials and methods

2.1 Study area

The study was conducted in the monitoring study area of Fénay, a 1000 ha arable farming area located in a plain 10km south of Dijon in eastern France (47°13’N, 5°03’E). Climatic conditions are continental (mean annual temperature 10.7°C and precipitation 744 mm) and land use is dominated by arable cropping, i.e. mostly rapeseed/cereals-based rotations. Climatic and soil conditions are quite homogeneous across the area, and such a low variability in pedoclimatic conditions across sampled fields was deemed advantageous to conduct intraspecific comparisons in weed phenology. Weed communities and farming practices are monitored in the study area since 2008, in between 70 and 140 fields, depending on the year. Field size average 9.8 ha and range from 0.5ha to 43ha. Field management in the area is conventional although the farmers differ in their farming strategies, and notably in terms of the diversity of crop rotations and their reliance on tillage and herbicides (for a full description of farming strategies in the area, see Yvoz et al., 2020). The standard annual weed monitoring includes weed recording at seedling stage in the field core within a 2000 m² zone (50 m x 40 m) located 20 m away from the field margin and in the field edge (i.e. the area between the field margin and the first row of crop) facing the field core zone along a 50 m long line. The annual survey spans from March (winter crops) to June (summer crops). The management by farmers ensure that the weed flora is kept under control in the area (Quinio et al., 2017) and over the years, 147 weed species have been recorded, among which 46 were solely observed in the field edge.

From the existing weed records, we identified the top 30 weed species (in terms of occurrence and abundance over the period 2008-2018) that occurred both in the core of fields and in field edges (Supp. Mat. Table S1). This list included 2 monocotyledon (*Alopecurus myosuroides* and *Bromus sterilis*) and 28 dicotyledon species. The flowers of some species are known to be of particularly high value for pollinators such as bees, bumblebees and hoverflies, e.g. the poppy *Papaver rhoeas*, the cornflower *Cyanus segetum*, the field bindweed *Convolvus arvensis* or the common knotgrass *Polygonum aviculare*), whereas other species produce floral resources of limited use (e.g. for pollinators, see Marshall et al., 2003; Ricou et al., 2014). Seeds produced by the 30 species can be used by invertebrate and vertebrate seed-eaters, and some species are known to be much consumed by generalist invertebrate predators such as carabid beetles e.g. the field pansy *Viola sp*, the dandelion *Taraxacum officinale* or the creeping thistle *Cirsium arvense* (Petit et al., 2014).

2.2 Weed phenological survey

In spring 2019, we surveyed the distribution of the 30 targeted weed species, first at seedling stage, across the Fénay area during the standard annual weed monitoring of 76 fields (called early weed survey, Figure 1). This allowed selecting a subset of 64 fields that were grown with 6 different crop types, i.e. two winter cereals (wheat, barley), two winter Brassicacae (oilseed rape, mustard), one spring crop (spring barley) and one summer crop (soya bean). The number of field sampled per crop type is provided in Supp. Mat. Table S2. The light condition prevailing in the field core and in the field edge of each of the 64 fields was quantified by conducting five measures of the photosynthetically active radiation (PAR) on top of the canopy and on the ground using a Sunscan PAR sensor (AT Delta-T Devices Cambridge England). PAR was measured once, at the flowering of the crop, as the rationale was to gather comparative information on light conditions in different within-field locations and crop types.

Within the 64 fields, we georeferenced a total of 685 weed patches (Figure 1) distributed per within-field location and crop type as described in Supp. Mat. Table S2. In the weed patch selection process, we maximised the co-occurrence of a targeted weed species in field core patches and field edge patches of the same field. The phenological survey was based on a simplified BBCH scale (Hess et al., 1997) with 10 stages from the cotyledon stage until the senescence (Supp. Mat. Table S3). We added a stage "DEATH" to account for record units dying before reaching the flowering stage. Within a weed patch, we recorded individually the phenological stage of the targeted weed species present. Obviously, not all the 30 species were present in all patches. When plants germinated after the early weed survey, we included them in the following surveys. When very different phenological stages (different by more than 2 stages on the scale) of the same weed species co-occurred in the same patch, they were considered as different record units. As a consequence, we monitored a total of 3770 records (called record units hereafter) distributed across within-field locations and crop types as described in Supp. Mat. Table S2.

The record units were monitored during six or seven (for winter wheat) successive surveys, spanning from 5th April till 21th September 2019 (Supp. Mat. Table S4). The first survey S1 was the early weed survey described above, implemented after all weeding operations. Field cores of oilseed rape and mustards could not be surveyed at S5 (end of the crop flowering) because it was too difficult to enter in the field. The last survey S6 (or S7 for winter wheat) occurred just after crop harvest and before any tillage (Figure 2).

When a record unit reached stage D2 or more (flowering), we sampled between one and three individual plants to quantify their dry biomass. To avoid any impact of plant removal on the following surveys, we collected plants in the surrounding, within a radius of 10 meters centred on the patch, when less than three individuals were present in the patch. Individual plants were dried (48 hours at 80°C) and weighted. For a subset of collected plants, we counted the number of flowers produced. The linear relationship between dry biomass at flowering and the number of flowers produced and the adjusted R-square of linear models for the 30 weed species is presented in Supp. Mat. Figure S1.

2.3 Estimation of resource production

The production of floral and fruit resources was estimated for each record unit by using a set of six indicators. The six indicators were applied to the 30 weed species surveyed.

The flowering success (FLS) was calculated as the proportion of patches within which the record unit reached any of the flowering stages D1 to E2. The starting date of flowering or flowering onset (FLOn) was estimated per record unit as the date where stage D1 was reached and was expressed in growing degree days since January 1st (base temperature = 0°C). The duration of the flowering period (FLD) was calculated per record unit as the difference between the end of the flowering (stage E1 reached) and FLOn and was also expressed in growing degree days. Similarly, the production of seed resources was estimated by the fruiting success (FRS) calculated as the proportion of patches within which the record unit reached stage D3 or later stages and the fruiting onset (FROn) estimated per record unit as the date where stage D3 was reached and was also expressed in growing degree days. We did not consider a fruiting duration in this study as we considered that after seed shed, seeds on the soil surface were available to seed consumers for duration that could be highly variable, depending on seed characteristics and notably seed size (Westerman et al., 2009). The sixth indicator was the dry biomass of record units at flowering. Dry biomass at flowering is a measure indicative of the number of flowers produced in the 30 species (see Supp. Mat. Figure S1). It is also strongly related to the amount of seed produced, as documented for many weed species (Senseman & Oliver, 1993;

Wilson et al, 1995; Lutman, 2002; Grundy et al., 2004 ; Lutman et al., 2008 ; Lutman et al., 2011).

2.4 Data analysis

Data analysis were done with the R software (R Core Team, 2019). Differences in light reaching the soil between field edges and field cores and between crop types were tested with a mixed linear model (package lme4) including Field as a random factor to account for differences in soil properties and farming management between fields. Significance was tested using the package [car] and pair-wise comparisons were conducted with the packages [emmeans] and [multcomp].

Models were fit for each species and phenological stages to test for the effect of Within-field location and Crop type on weed phenological development. We hypothesised that some species will respond to interactive effects, i.e. that the response to Within-field location will depend on Crop type. This assumption is built on the fact that the ecological properties of a field edge (width, light availability, etc.) can depend on the identity of the adjacent crop and associated farming practices (de Snoo, 1997). Interaction could not be tested for success indicators (FLS and FRS) as models failed to converge. In all models, Field was included as a random factor.

We first conducted a time-to-event analysis using survival curves comparison. For each species, the survival curve represents the proportion of individuals having already reached a particular stage over time (McNair et al., 2012). Cox proportional hazards models linking the characteristics of the species survival curve to Within-field location and Crop type were then developed with the *coxme* function from the [coxme] package. The effects of Within-field location, Crop type and their interaction were tested by a type II ANOVA using the function *Anova* from the [car] package.

The effect of Within-field location and Crop type (and when possible their interaction) was then assessed for the six phenological indicators for each species with logistic (FLS, FRS) or linear regression models (*glmer* and *lmer* functions of the [lme4] package). The effects were tested by a type II ANOVA using the function *Anova* from the [car] package. Comparisons between Within-field location (two-level factor) and between crop types were tested using the function *emmeans* from the [emmeans] package (computes the estimates) and the function *cld* from the [multcomp] package (implements the multiple comparison needed for the effect of crop type (multiple levels).Because of variations in the occurrence of weed species across within-field locations and among crop types, data were lacking for some situations and not all full models could be run for the 30 weed species.

3. Results

The proportion of light reaching the soil surface was significantly higher in field edges than in field cores for all crop types but mustard and oilseed rape. It did not differ between crop types, whether in crop edges or in field cores (Supp. Mat. Figure S2).

3.1 Overall differences in weed species phenology

The time to event analysis revealed that overall, the phenological development of all targeted weed species except AMASS was affected either by Within-field location, Crop type or both (see survival curves of the 30 species per within-field location and crop type and tests associated Cox proportional hazards models in Supp. Mat. Appendix 1). Across species, the proportion of plants that died before reaching the flowering stage (stage DEATH) was lower in field edges (mean±s.d., 0.21±0.19) than in field cores (0.39±0.23). The probability of new emergence (stage A) after the first survey (S1) was similar in field edges (0.17±0.22) and in field cores (0.15±0.14). For most species, earlier phenological stages (from A to C1) were affected by Crop type, according to the timing of crop sowing (i.e. stages were reached earlier in early sown crops, see Supp. Mat. Table S2) whereas latter stages (from E1 to E2) were mostly impacted by Within-field location, species shedding seeds (stages E2) earlier in field edges compared to field cores.

3.2 Production of resources by weeds

3.2.1 Flowering success, date and duration

The flowering success (FLS) across species was on average 0.70±0.22 in the field edge and 0.51±0.25 in the field core and was highly variable among species (Table 1). For one species (AMASS) we could only test the effect of Within-field location. FLS of 16 species appeared unaffected by Within-field location and Crop type (p-values in Table 2). Six species responded solely to Within-field location (Table 2), with higher FLS in field edges (Table 1). Three species responded solely to Crop type, with lower FLS in cereal crops than in other crop types (Table 2, Supp. Mat. Table S5). Five species responded both to Within-field location and Crop type, with lower FLS in field cores than field edges and in cereal crops than in other crop types (Figure 3).

The flowering onset (FLOn) across species occurred on average 113 degree days earlier in the field edge (1547±663) than in the field core (1660±682). Full models (i.e. Within-field location, Crop type and their interaction) were run for 22 species and partial models for seven species. Ten species appeared unaffected by Within-field location and Crop type (Table 2). FLOn of eight species differed solely by Crop type following the gradient of crop sowing date, as previously described (Table 2, Supp. Mat. Table S5). We detected a sole effect of Within-field location for one species (BROST) and additive (4 species) or interactive (6 species) effects of Within-field location and Crop type. When interactive effects were detected, they indicated earlier flowering only in the field edges of some of the crops (Table 1; Supp. Mat. Figure S3).

The flowering duration (FLD) across species was on average 63 degree days shorter in the field edge (807±244) than in the field core (870±320). Full models were run for 17 species and partial models for 11 species. Eleven species did not respond to Within-field location or Crop type. Within-field location (3 species) or its interaction with Crop type (5 species) affected FLD. For these species, except for EPHHE, FLD was longer in field edge than in field core (+60 degree days in average). Crop type affected FLD for 10 species (Table 2). Record units in cereal crops had a shorter FLD than those located in other crop types (341 degree days less on average, Supp. Mat. Table S5). Interactive effects indicated longer FLD in the field edges of cereal crops but shorter FLD in the field edges of winter mustard and oilseed rape compared to field cores (Supp. Mat. Figure S4).

3.2.2 Fruiting success and date

The fruiting success (FRS) across species was higher in the field edge (0.59±0.30) than in the field core (0.43±0.25) and was below 0.36 in cereal crops against above 0.74 in the other crop types (Supp. Mat. Table S5). Additive models were applied for 27 species and only the Within-field location was tested for the 3 others. Crop type and Within-field location did not appear to affect FRS of 17 species. For the other species, Within-field location (eleven species) and Crop type (six species) affected FRS (Table 2). Except for SONAS, FRS was always higher (+29 %) in the field edge than in the field core (Table 1). Crop type effects opposed cereal crops (low FRS) to the other crop types (Supp. Mat. Figure S5).

The Fruiting onset (FROn) across species occurred on average 166 degree days earlier in the field edge (2125±778) than in the field core (2291±741). Full models could be run for 18 species and partial models for nine other species. Ten of them responded neither to Within-field location nor to Crop type (Table 2). Within-field location had a significant impact on FROn, as the sole impacting factor for two species, in addition to Crop type for two species and in interaction with Crop type for six species (Table 2). With the exception of ANGAR, FROn occurred later (337 degree days) in field cores than in field edges although this trend could be restricted to some specific crop types (Table 1). In addition to the interactive effect, Crop type impacted 9 species with later FROn in mustard, oilseed rape or in soya compared to other crop types (Supp. Mat. Figure S6).

3.2.3 Dry biomass

Dry biomass at flowering did not differ strongly between field cores and field edges but tended to be lower in cereal crops than in the other crop types (Supp. Mat. Table S5). Full models could be run for 21 weed species and partial models for 8 species. Among them, the dry biomass of 13 species were affected nor by Within-field location neither by Crop type. Within-field location effects and interactive effects with Crop type were detected for respectively four and six weed species, with higher biomasses in field edge or in field core, depending on the species and the crop type (Table 1; Table 2). The biomass of six species was solely affected by Crop type, with higher biomass in mustard and oilseed rape compared to other crop types (Supp. Mat. Figure S7).

4. Discussion

A first rationale for this phenological survey was to assess the proportion of plants recorded at seedling stage, and after the completion of weed management operations, that would reach a stage where they provide floral and seed resources. Our results indicate that on average, only 60% of plants flowered and 50% fruited; this was mostly due to weed mortality which highly varied among the 30 species. We also expected resource production of individual weed species to be modulated by their location in the field and by the crop type where they stand. Our results support this hypothesis. Although weed responses were quite specific, we show that for a given weed species, the probability of reaching flowering and fruiting stages, as well as the timing, duration and amount of resources produced, estimated here by the dry biomass at flowering, vary according to their location in the field and to the crop type.

4.1 Intraspecific weed responses to field location and crop type

Our results demonstrate that in field cores, mortality before reaching the flowering stage was higher than in field edges. In addition, most weed species flowered and fruited more and earlier in field edges than in field cores. This observed higher mortality and delays in phenological development could be related to differences in the intensity of competition for resources. In field cores, competition for light is higher than in the field edge and decreases in light quality and quantity can delay weed flowering and seed production onsets (McLachlan et al., 1995; Yasin et al., 2019). It is also possible that in some fields, herbicides that were applied prior to our first survey were still acting, causing mortality or slowing the development of weeds, with possibly a more marked effect in field cores than in field edges, although this could highly depend on the way the farmer conducted the spraying. We also often observed a longer flowering period in the field edge than in field core which could also be explained by higher amount of light (Benvenuti et al., 1994). Some studies have established that weed dry biomass can also decrease as competition for light increases (McLachlan et al., 1993). We detected no such effect here, i.e. our estimates of dry biomass at flowering for a given weed species were comparable in the two within-field locations. This result could be related to (i) a possibly higher plant density in field edges which restrained each individual to a limited biomass (Wilson et al., 1995), (ii) competition for soil resources with the plants growing in the adjacent grass boundaries (de Cauwer et al., 2006; Cordeau et al., 2010), and/or (iii) a lower amount of nitrogen sprayed by famers in field edges than in field cores. Competition for soil resources could also explain some of the observed differences in weed mortality and phenology detected here. In field cores, N supply is higher than in field edges so that crops produce high aboveground biomass and thus outcompete weeds for water and nutrients (Moreau et al., 2014). This could explain the higher weed mortality observed in field cores, but also the fact that surviving weeds may have had access to important resources (Bischoff and Mahn, 2000), so that their biomass was not inferior to that of plants growing in field edges.

We also detected that crop type modulated weed development, especially at earlier phenological stages. This is congruent with results indicating that the period of tillage and crop sowing affects the timing of weed germination but also the post-germination life history characters of weeds (Zhou et al., 2005), and particularly their flowering date (Gunton et al., 2011). Weed phenological responses to crop type may also be partly explained by differences in light interception. Crop types exert different levels of light competition on weeds, in relation to their sowing density, row spacing and morphological characteristics (Swanton et al., 2015). Cereals crops are generally highly competitive because of small row spacing and of their tillering ability, a key characteristic to outcompete weeds (Jha et al., 2017). Our findings indeed suggest that weed plants in the field core of cereal crops suffered high mortality before reaching the flowering stage and, if they survived, exhibited an earlier and shorter flowering and fruiting period and a lower dry biomass. The earlier and shorter weed flowering period observed in cereal crops could also be a direct consequence of the low Red:Far Red ratio of light typically found in cereals (Franklin and Whitelam, 2005). The effect of Brassicaceae crops on weed phenology was quite different from that of cereals crops in our study. A major characteristic of oilseed rape and mustard crops is their high nitrogen demand and their subsequent high aboveground biomass (Blackshaw et al., 2003). Weed mortality in Brassicaceae crops could thus be explained by a combination of competition for soil resources and light. The later flowering onset detected in some species could reflect that in conditions of limited light and high nitrogen availability, some nitrophilous weed species, such as *Chenopodium album,* increase allocation of resources to leaves rather than investing in flowering (Moreau et al., 2014). Besides, an opening of the canopy during oilseed rape and mustard senescence leads to a reduction of competition for light. Thus, weed plants with delayed flowering have higher flowering and fruiting success.

4.2 Implications for resource provision by weeds within a landscape

It is well established that the composition of weed communities results from the combination of environmental, farming management and landscape factors (Fried et al., 2008; Petit et al., 2016). These factors thus drive the probability of occurrence and the spatial distribution of a particular weed species within a landscape (Alignier et al., 2013), with important consequences on the provision of weed resources at that level. Our findings highlight an additional factor affecting the production of weed resources. We provide evidence that a weed plant will deliver different amounts of floral and fruit resources, and at different times, depending on the habitat (within-field location and crop type) it occupies within the agricultural landscape. Our quantification of this phenological variability gives some insights into the relative contribution of the field cores and field edges of different crops to the provision of flowers and seeds. It also enables to explore to what extent the complementarity between these habitats could be used to enhance the provision of weed resources over time in a given landscape.

For 28 out of the 30 weed species, the overall duration of flower production by a given weed species at a field scale (core + edge of the field) is longer than the duration that results from the contribution of only one of the field locations. In half of these cases, the production of flowers in field edges started earlier and ended later than in the core of the fields, and hence the presence of individuals in field edges significantly increased the duration of the provision of flower resources at the field scale. For six weed species, the core field supplied flower resources for a longer period, with individuals starting earlier and ending flowering later than in the edge. For five species, field edges and cores were truly complementary, with flowering first occurring in the edge and ending in the core, with an intermediate period during which both field locations provided floral resources. Similarly, the co-occurrence of different crop types in the landscape could buffer variations in the amount and the temporal provision of weed resources. For example, our findings show a relatively low production of resources by weed plants located in cereal crops, compared to other crop types. This result suggests that it is of particular importance to maintain the extent of field edges in cereal crops but also that the presence of other crop types in the vicinity could also be used to counteract the low amount of weed resources provided by cereal core fields, with potentially positive effects on the biodiversity of many taxa (Sirami et al., 2019). The impact of changes in the composition and configuration of agricultural landscapes on weed services could be further investigated through landscape scale modelling predicting the impact of landscape change scenario on weed distribution (Ricci et al. 2018).

5. Conclusion

This study provides field-based evidence that the production of trophic resources by 30 individual weed species that are commonly found in arable farming is not a constant. Rather, we evidenced important intraspecific variability in the success of reaching phenological stages that are key to resource provision as well as in the timing of the production of resources in response to within-field location and crop type. It is important to account for this intraspecific variability when evaluating the contribution of weed communities to ecosystem services. It also suggests that at a landscape scale, the amount, timing and duration of provision of services by weeds can be enhanced by maintaining sufficient lengths of crop edges and by growing a diversity of crop types.

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Declaration of interest

None

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Table 1: Indicators of resource provision (mean, [min-max] and (number of observed record units) of the 30 weed species named according to their EPPO codes (see Supp. Mat. Table S1, https://gd.eppo.int/) and per Within-field location (FE: Field edge; FC: Field core). FLS: flowering success (rate); FLOn: flowering onset (growing degree day (GDD) since Jan 1st, base temperature = 0°C); FLD: duration of the flowering period (GDD); FRS: fruiting success (rate); FROn: fruiting onset (GDD); Dry biomass at flowering (g of dry matter). FE/FC represents the difference in the mean value of the indicator between the field edge and the field core, estimated as (mean FE – mean FC) for FLS and FRS and as (100 (mean FE – mean FC / mean FC)) for the other four indicators, in bold when FE/FC > 0 (value of indicator is higher in the field edge). n/a indicates that no data could be collected to estimate the indicator.

Species	**FLS**			**FLOn**			**FLD**		
EPPO code	FE	FC	FE/FC	FE	FC	FE/FC	FE	FC	FE/FC
AETCY	0.30 (37)	0.02 (60)	**28**	2507 [2174 - 3273] (10)	n/a		710 [278 - 1377] (5)	n/a	
ALOMY	0.94 (141)	0.88 (76)	**6**	1034 [684 - 2174] (133)	1099 [684 - 3273] (67)	-6	957 [289 - 1490] (132)	861 [278 - 1810] (67)	**11**
AMASS	0.75 (8)	0.84 (25)	-9	2657 [1741 - 3273] (6)	3025 [2174 - 3551] (19)	-12	755 [278 - 1532] (6)	611 [278 - 1377] (15)	**24**
ANGAR	0.60 (95)	0.52 (63)	**8**	1831 [887 - 2939] (56)	2053 [1741 - 2939] (31)	-11	975 [405 - 1810] (35)	540 [370 - 1198] (13)	**81**
ANRCA	0.38 (13)	0.42 (12)	-4	1112 [887 - 1376] (7)	1054 [887 - 1087] (6)	**6**	660 [289 - 1287] (7)	455 [289 - 1287] (6)	**45**
BROST	0.96 (103)	0.92 (25)	**4**	1006 [684 - 1376] (98)	1241 [887 - 2174] (22)	-19	846 [289 - 1287] (98)	631 [393 - 882] (21)	**34**
CENCY	0.67 (21)	0.56 (18)	**11**	1412 [1087 - 1769] (14)	1386 [1087 - 1769] (10)	**2**	763 [405 - 1087] (14)	666 [393 - 1087] (10)	**15**
CHEAL	0.62 (63)	0.65 (71)	-3	2516 [1741 - 3273] (37)	2764 [2174 - 3551] (45)	-9	840 [278 - 1810] (34)	685 [278 - 1377] (38)	**23**
CIRAR	0.33 (69)	0.24 (63)	**9**	2251 [1376 - 3551] (21)	2545 [1769 - 3273] (14)	-12	1136 [370 - 1377] (13)	811 [278 - 1377] (10)	**40**
CONAR	0.74 (259)	0.37 (41)	**37**	2009 [1376 - 2939] (191)	2208 [1741 - 2939] (15)	-9	781 [393 - 1810] (93)	827 [334 - 1198] (11)	-6
EPHEX	0.56 (16)	0.69 (32)	-13	1719 [1376 - 2174] (9)	2007 [1741 - 2174] (22)	-14	799 [433 - 1532] (6)	564 [405 - 1198] (5)	**42**
EPHHE	0.89 (45)	0.74 (23)	**15**	997 [561 - 3551] (40)	1273 [561 - 2544] (16)	-22	623 [200 - 1613] (38)	1047 [403 - 1810] (15)	-40
FUMOF	0.73 (41)	0.41 (32)	**32**	850 [561 - 1376] (30)	945 [561 - 2174] (13)	-10	841 [200 - 1490] (30)	1265 [289 - 1613] (12)	-34
GALAP	0.78 (110)	0.53 (91)	**25**	1458 [887 - 2939] (85)	1708 [887 - 2174] (43)	-15	563 [289 - 1087] (79)	568 [200 - 1087] (29)	-1
GERDI	0.90 (193)	0.40 (53)	**50**	1309 [887 - 2939] (173)	1725 [1087 - 2174] (20)	-24	702 [289 - 1532] (160)	648 [393 - 1087] (12)	**8**
MATSS	0.79 (24)	0.00 (3)	**79**	1385 [887 - 2174] (19)	n/a	n/a	717 [200 - 1087] (16)	n/a	n/a
MERAN	0.87 (68)	0.79 (98)	**8**	1988 [684 - 2939] (45)	2091 [684 - 2939] (47)	-5	1241 [393 - 1810] (45)	1366 [612 - 1810] (47)	-9
PAPRH	0.86 (150)	0.13 (39)	**73**	1615 [1087 - 2544] (129)	1690 [1376 - 1769] (5)	-4	602 [370 - 1087] (107)	503 [405 - 798] (4)	**20**
POLAV	0.56 (61)	0.11 (18)	**45**	1733 [1376 - 2939] (33)	1958 [1741 - 2174] (2)	-11	930 [405 - 1810] (20)	1594 [1377 - 1810] (2)	-42
POLCO	0.42 (119)	0.28 (200)	**14**	2024 [1376 - 2939] (50)	2116 [1741 - 2939] (54)	-4	1187 [393 - 1810] (18)	1472 [612 - 1810] (17)	-19
POLPE	1.00 (3)	0.42 (26)	**58**	2153 [1741 - 2544] (3)	2393 [1741 - 2939] (10)	-10	970 [803 - 1099] (3)	1102 [612 - 1532] (10)	-12
SCAPV	0.76 (63)	0.44 (41)	**32**	996 [684 - 1769] (48)	991 [684 - 1769] (17)	**1**	583 [289 - 1287] (45)	1041 [289 - 1490] (17)	-44
SENVU	0.75 (56)	0.75 (44)	0	1152 [561 - 3273] (41)	1255 [561 - 3273] (32)	-8	719 [200 - 1613] (37)	723 [200 - 1613] (31)	-1
SOLNI	0.20 (5)	0.70 (23)	-50	3273 (1)	2546 [1741 - 3273] (16)	**29**	278 [278 - 278] (1)	988 [278 - 1810] (16)	-72
SONAS	0.40 (63)	0.58 (88)	-18	2046 [1087 - 3273] (22)	2231 [1087 - 3273] (49)	-8	666 [278 - 1087] (15)	718 [278 - 1087] (30)	-7
STEME	0.92 (12)	0.75 (8)	**17**	629 [561 - 887] (12)	623 [561 - 684] (6)	**1**	1152 [200 - 1613] (12)	1153 [815 - 1490] (6)	**0**
TAROF	0.54 (87)	0.33 (36)	**21**	878 [561 - 2939] (47)	646 [561 - 1087] (12)	**36**	293 [123 - 692] (33)	435 [203 - 1613] (11)	-33
VERHE	0.92 (62)	0.79 (28)	**13**	621 [561 - 1087] (57)	598 [561 - 887] (22)	**4**	648 [123 - 1208] (57)	758 [403 - 1613] (22)	-15
VERPE	0.93 (206)	0.57 (21)	**36**	861 [561 - 2939] (184)	1015 [684 - 1769] (12)	-15	924 [289 - 1810] (178)	1118 [405 - 1490] (11)	-17
VIOSS	0.87 (89)	0.60 (130)	**27**	1187 [561 - 3273] (76)	1293 [561 - 2174] (72)	-8	1158 [200 - 1810] (75)	1203 [393 - 1810] (63)	-4

Species EPPO code	FRS FE		FC		FE/FC	FROn FE			FC			FE/FC	Dry Biomass FE			FC			FE/FC
AETCY	0.14	(37)	0.00	(60)	**14**	3551	[3551 - 3551]	(4)					3.13	[0.32 - 10.04]	(11)	0.49	[0.13 - 0.84]	(4)	**539**
ALOMY	0.94	(141)	0.86	(76)	**8**	1831	[1376 - 2544]	(132)	1795	[1376 - 2544]	(65)	**2**	4.81	[0.79 - 16.93]	(43)	5.32	[0.38 - 18.24]	(53)	-10
AMASS	0.63	(8)	0.52	(25)	**11**	3093	[2544 - 3551]	(5)	3281	[2544 - 3551]	(13)	-6	23.99	[1.11 - 108.52]	(10)	10.88	[0.06 - 85.76]	(25)	**120**
ANGAR	0.31	(95)	0.14	(63)	**17**	2714	[2174 - 3551]	(27)	2507	[2174 - 3273]	(9)	**8**	0.45	[0.01 - 2.96]	(53)	0.21	[0.01 - 1.03]	(30)	**114**
ANRCA	0.38	(13)	0.42	(12)	-4	1376	[1376 - 1376]	(6)	1509	[1376 - 2174]	(6)	-9	3.62	[0.78 - 10.27]	(4)	5.31	[0.10 - 17.46]	(8)	-32
BROST	0.91	(103)	0.88	(25)	**3**	1649	[1087 - 2174]	(93)	1715	[1376 - 2174]	(21)	-4	4.09	[0.38 - 16.80]	(40)	3.85	[0.75 - 11.89]	(20)	**6**
CENCY	0.67	(21)	0.50	(18)	**17**	1943	[1769 - 2174]	(14)	1949	[1769 - 2174]	(9)	**0**	8.76	[2.16 - 28.85]	(13)	2.54	[0.57 - 9.90]	(12)	**245**
CHEAL	0.48	(63)	0.54	(71)	-6	3382	[2939 - 3551]	(30)	3390	[2939 - 3551]	(38)	**0**	10.36	[0.02 - 66.23]	(27)	5.86	[0.07 - 64.97]	(45)	**77**
CIRAR	0.26	(69)	0.22	(63)	**4**	2932	[2174 - 3551]	(15)	3031	[2174 - 3551]	(13)	-3	n/a			n/a			n/a
CONAR	0.19	(259)	0.22	(41)	-3	2895	[2544 - 3551]	(48)	3013	[2939 - 3273]	(9)	-4	1.51	[0.16 - 8.35]	(91)	3.63	[0.16 - 9.03]	(27)	-58
EPHEX	0.50	(16)	0.53	(32)	-3	2161	[1741 - 2939]	(8)	2174	[2174 - 2174]	(17)	-1	0.37	[0.02 - 1.46]	(14)	0.3	[0.01 - 1.95]	(23)	**23**
EPHHE	0.84	(45)	0.65	(23)	**19**	1235	[887 - 3551]	(38)	1749	[1087 - 2544]	(14)	-29	0.75	[0.07 - 4.15]	(51)	1.25	[0.02 - 13.40]	(22)	-40
FUMOF	0.73	(41)	0.41	(32)	**32**	1457	[1087 - 2174]	(30)	2113	[1376 - 2174]	(13)	-31	4.84	[0.42 - 23.59]	(12)	17.19	[1.06 - 43.93]	(10)	-72
GALAP	0.78	(110)	0.53	(91)	**25**	1825	[1376 - 2939]	(85)	2045	[1087 - 2174]	(43)	-11	2.08	[0.06 - 9.48]	(44)	1.57	[0.02 - 10.08]	(23)	**32**
GERDI	0.89	(193)	0.36	(53)	**53**	1647	[1376 - 3273]	(172)	2039	[1769 - 2174]	(18)	-19	3.62	[0.02 - 25.19]	(56)	2.05	[0.07 - 19.56]	(15)	**77**
MATSS	0.63	(24)	0.00	(3)	**63**	1859	[1087 - 2174]	(15)	n/a			n/a	2.47	[0.04 - 17.11]	(16)	n/a			n/a
MERAN	0.79	(68)	0.69	(98)	**10**	3089	[887 - 3551]	(42)	3104	[887 - 3551]	(46)	0	2.13	[0.03 - 10.04]	(43)	3.04	[0.04 - 57.35]	(52)	-30
PAPRH	0.81	(150)	0.10	(39)	**71**	2017	[1376 - 2544]	(122)	2073	[1769 - 2174]	(4)	-3	10.24	[0.45 - 100.88]	(45)	6.33	[0.54 - 17.32]	(4)	**62**
POLAV	0.08	(61)	0.06	(18)	**2**	3238	[2544 - 3551]	(5)	3551		(1)	-9	6.92	[0.14 - 51.41]	(21)	1.86		(1)	**272**
POLCO	0.11	(119)	0.08	(200)	**3**	3366	[3273 - 3551]	(12)	3329	[3273 - 3551]	(15)	**1**	2.68	[0.03 - 29.13]	(49)	4.77	[0.01 - 48.44]	(59)	-44
POLPE	1.00	(3)	0.35	(26)	**65**	3123	[2544 - 3551]	(3)	3427	[3273 - 3551]	(9)	-9	0.99		(1)	15.57	[0.05 - 107.16]	(14)	-94
SCAPV	0.76	(63)	0.17	(41)	**59**	1449	[1087 - 2174]	(48)	2002	[1376 - 2174]	(7)	-28	4.4	[0.82 - 11.07]	(31)	4.83	[0.07 - 8.64]	(7)	-9
SENVU	0.73	(56)	0.68	(44)	**5**	1419	[684 - 3273]	(40)	1595	[887 - 3273]	(30)	-11	3.06	[0.04 - 26.53]	(38)	3.93	[0.20 - 16.46]	(32)	-22
SOLNI	0.00	(5)	0.43	(23)	-43	n/a			3440	[3273 - 3551]	(10)	n/a	0.65	[0.18 - 1.11]	(2)	6.69	[0.04 - 49.61]	(25)	-90
SONAS	0.29	(63)	0.52	(88)	-23	2398	[2174 - 2939]	(17)	2557	[2174 - 3273]	(45)	-6	5.06	[0.24 - 22.05]	(32)	3.02	[0.36 - 12.49]	(27)	**68**
STEME	0.92	(12)	0.75	(8)	**17**	1355	[887 - 2174]	(12)	1631	[1087 - 2174]	(6)	-17	1.23	[0.09 - 5.39]	(19)	4.06	[0.19 - 16.58]	(13)	-70
TAROF	0.54	(87)	0.33	(36)	**21**	1023	[684 - 2939]	(47)	870	[684 - 1087]	(12)	**18**	9.18	[0.88 - 40.12]	(23)	10.62	[1.16 - 35.26]	(10)	-14
VERHE	0.92	(62)	0.75	(28)	**17**	1093	[684 - 1769]	(57)	1159	[887 - 1376]	(21)	-6	1.57	[0.12 - 10.01]	(49)	0.76	[0.06 - 2.64]	(22)	**107**
VERPE	0.91	(206)	0.57	(21)	**34**	1409	[684 - 3273]	(181)	1907	[1376 - 2174]	(12)	-26	2.04	[0.03 - 14.01]	(108)	1.64	[0.05 - 6.44]	(14)	**24**
VIOSS	0.71	(89)	0.53	(130)	**18**	2256	[1087 - 3551]	(62)	2354	[2174 - 3551]	(63)	-4	0.82	[0.05 - 4.62]	(60)	0.97	[0.02 - 4.85]	(72)	-15

Table 2: Effects of Crop type, Within-field location and their interaction on the six indicators of resource provision of the 30 weed species named according to their EPPO codes (see Supp. Mat.Table S1, https://gd.eppo.int/). FLS: flowering success (rate); FLOn: flowering onset (growing degree day (GDD) since Jan 1st, base temperature = 0°C); FLD: duration of the flowering period (GDD); FRS: fruiting success (rate); FROn: fruiting onset (GDD); Dry biomass at flowering (g of dry matter). Results are presented as the p-value of the regression model (ns = p > 0.1; - means the effect cannot be tested due to insufficient data).

Species	FLS		FLOn			FLD			FRS		FROn			Dry Biomass		
EPPO code	Crop	Location	Crop	Location	Interaction	Crop	Location	Interaction	Crop	Location	Crop	Location	Interaction	Crop	Location	Interaction
AETCY	ns	<0.1	<0.05	-	-	-	-	-	ns	ns	-	-	-	NS	ns	ns
ALOMY	ns	<0.05	<0.001	<0.05	<0.05	<0.001	<0.001	<0.05	ns	<0.05	<0.001	ns	ns	<0.001	ns	<0.001
AMASS	-	ns	-	ns	-	-	ns	-	-	ns	-	ns	-	-	<0.05	-
ANGAR	<0.001	ns	<0.05	<0.001	ns	<0.05	<0.1	ns	<0.05	ns	<0.001	<0.05	ns	<0.1	ns	ns
ANRCA	ns	ns	-	-	-	-	-	-	ns	ns	-	-	-	ns	ns	-
BROST	ns	ns	ns	<0.001	ns	<0.05	<0.001	ns	ns	ns	ns	ns	ns	<0.001	ns	ns
CENCY	ns	ns	-	ns	-	-	ns	-	ns	ns	-	ns	-	-	<0.05	-
CHEAL	<0.05	ns	<0.001	<0.05	ns	<0.1	<0.05	-	ns	ns	-	ns	-	ns	ns	ns
CIRAR	<0.05	<0.05	<0.05	ns	ns	-	ns	-	<0.05	<0.05	<0.001	ns	ns	-	-	-
CONAR	<0.001	<0.001	<0.001	ns	ns	<0.001	<0.1	ns	-	<0.05	-	<0.05	-	<0.001	<0.001	ns
EPHEX	ns	ns	<0.001	<0.001	<0.05	ns	ns	-	-	ns	ns	ns	ns	ns	ns	-
EPHHE	<0.1	ns	<0.001	<0.001	<0.001	ns	<0.001	ns	ns	ns	<0.001	<0.05	ns	<0.001	<0.001	<0.001
FUMOF	ns	ns	ns	ns	ns	ns	<0.05	<0.05	ns	ns	ns	<0.001	<0.05	ns	ns	ns
GALAP	ns	<0.001	<0.001	<0.001	<0.001	<0.001	ns	<0.001	ns	<0.001	ns	<0.001	ns	ns	ns	<0.001
GERDI	ns	<0.001	<0.001	<0.001	<0.001	<0.001	ns	ns	ns	<0.001	<0.001	<0.001	<0.001	<0.001	<0.1	ns
MATSS	ns	ns	ns	-	-	ns	-	-	ns	ns	ns	-	-	ns	-	-
MERAN	<0.05	<0.05	<0.001	ns	ns	<0.001	ns	ns	<0.05	<0.1	<0.001	<0.05	<0.05	<0.001	ns	<0.001
PAPRH	ns	<0.001	<0.05	<0.05	ns	<0.001	ns	-	<0.1	<0.001	<0.001	ns	-	ns	ns	ns
POLAV	ns	ns	ns	ns	-	<0.001	ns	-	ns	ns	-	ns	-	ns	-	-
POLCO	<0.001	<0.05	<0.05	ns	ns	<0.05	ns	-	ns	ns	-	ns	-	<0.001	ns	ns
POLPE	ns	ns	-	ns	-	-	ns	-	ns	ns	-	<0.1	-	ns	-	-
SCAPV	ns	ns	<0.1	ns	ns	ns	<0.001	<0.001	ns	<0.001	ns	<0.001	<0.05	ns	ns	ns
SENVU	ns	ns	<0.001	ns	ns	ns	ns	ns	ns	<0.1	<0.001	ns	ns	<0.05	ns	ns
SOLNI	ns	ns	-	ns	-	-	ns	-	ns	ns	-	-	-	-	ns	-
SONAS	<0.001	<0.1	<0.001	ns	ns	<0.001	ns	ns	<0.05	<0.05	<0.001	ns	ns	ns	<0.05	<0.05
STEME	ns	ns	ns	ns	ns	ns	ns	<0.05	ns	ns	ns	ns	ns	ns	<0.05	ns
TAROF	<0.05	<0.05	<0.001	ns	ns	ns	ns	ns	<0.05	<0.05	<0.001	ns	ns	ns	<0.1	ns
VERHE	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	<0.05	<0.05	<0.05	<0.05	<0.05
VERPE	ns	<0.05	<0.001	<0.001	ns	ns	ns	ns	ns	<0.05	<0.001	<0.001	<0.05	<0.05	ns	ns
VIOSS	ns	<0.001	<0.001	<0.001	<0.05	<0.001	<0.1	ns	<0.001	<0.001	<0.001	ns	ns	<0.001	ns	ns