INTRODUCTION

Weeds not only impact food security, but also biodiversity and ecosystem services (Neve et al., 2018). They are considered among the greatest threats to agriculture, causing huge crop losses each year worldwide (Vigueira et al., 2013). Some native weed species may build up large populations, especially when provided with available habitats by anthropogenic disturbance in arable fields or ruderal sites (Neve et al., 2018). Adaptation of weed species to such habitats may occur through genetic differentiation or phenotypic plasticity (Leiss and Müller-Shärer, 2001). Knowledge of the genetic variability of weed populations from molecular markers or from quantitative genetic traits
can provide useful information for management decisions. In particular, the level of genetic differentiation between weeds found in arable fields compared with conspecifics in adjacent semi-natural and natural habitats provides clues to the pathways of weed dispersal.

In crop fields, weeds have become adapted to disturbance, such as through increased plasticity and modified emergence patterns (Bommarco et al., 2010). Therefore, besides genetic drift, phenotypic traits of crop weeds are under selection by anthropogenic disturbance, biotic and abiotic conditions (Steinger et al., 2002), herbicides and climatic gradients (Neve et al., 2018), eventually leading to local adaptation. The resulting ‘agricultural weed syndrome’ includes rapid growth, high nutrient use efficiency, seed dormancy, efficient seed dispersal, crop mimicry and herbicide resistance (Vigueira et al., 2013).

Population differentiation caused by divergent selection on phenotypic traits can be analysed by a quantitative genetic approach (Steinger et al., 2002) that allows genetic effects to be disentangled from environmental effects on the phenotypes (Durka et al., 2017). There is evidence for genetic divergence within weed species occupying different types of habitats in the same landscape (Bommarco et al., 2010), since evolutionary variation among populations can occur over short distances and within the same region (Durka et al., 2017). This finding indicates that divergent directional selection plays an important role in the phenotypic differentiation of populations for these traits. For example, when grown under controlled environmental conditions, Senecio vulgaris L. from agricultural habitats had larger leaves, a greater number of capitula and greater reproductive biomass compared with plants from ruderal habitats, for pairs of populations separated by 3–86 km (Leiss and Müller-Shärer, 2001).

Herbicides represent a strong source of selection on weed populations. Chemical weed control began over a century ago and since 2000, acetolactate synthase (ALS) inhibitors provide satisfactory solutions for farmers. They act by inhibiting branched-chain amino acid synthesis, especially valine and isoleucine, and thus stopping cell division (Kraehmer et al., 2014). Amidosulfuron + iodosulfuron-methyl-sodium are two sulfonylureas that inhibit ALS, with a predominant foliar activity and a mode of transport in both the descending and ascending systems. However, many cases of resistance to ALS-inhibitor herbicides have been reported (Hatami et al., 2016), mainly through mutations of the ALS target site. Mixtures of ALS-inhibiting herbicides with auxin-type herbicides, such as florasulam + 2,4-D, are currently used to counteract the development of resistance (Ntoanidou et al., 2017). Florasulam acts by inhibition of ALS, blocking the synthesis of amino acids responsible for cell division in meristems, whereas the auxin-type herbicide 2,4-D acts by abnormally increasing cell wall plasticity, protein biosynthesis and ethylene production in plant tissues. Often, herbicide resistance comes with fitness costs that arise from the allocation of limiting resources away from present and future growth and reproduction or are directly caused by the mutation of the target site of the herbicide (Bingham et al., 2017). For instance, fitness costs are observed in pollen production and overall plant development of Brassica rapa atrazine-resistant versus atrazine-susceptible populations (Bingham et al., 2017), and resistant biotypes of S. arvensis to some auxinic herbicides showed significant reduction in plant height, leaf area and root length compared to susceptible biotypes (Hall and Romano, 1995).

In the present study, we assessed population differentiation on quantitative traits and herbicide resistance in the weedy annual plant Sinapis arvensis (wild mustard; Brassicaceae) in Algeria. Sinapis arvensis is an herbaceous cruciferous plant native to the Mediterranean Basin that now occurs throughout most temperate regions worldwide (Warwick et al., 2000). As a weed, S. arvensis has strong environmental adaptability to various biotic and abiotic stresses, occurring in crops and other disturbed habitats, such as roadsides, meadows and ruderal sites (Berrows and Tyril, 2013). In Algeria, S. arvensis is the most prominent competitive weed in cereal crops and their margins. The weed is reported to reduce grain yield and final biomass of wheat by 44% and 51% respectively (Dezfooli, 2000). Amidosulfuron + iodosulfuron-methyl-sodium and florasulam + 2,4-D are the most widely used herbicides for weed management in cereal crops in Algeria, since 2014 and 2011, respectively, and can be used without particular governmental recommendations. Thus, repeated applications per year and continued use of the same herbicides in a given field in subsequent years are widespread (Institut Technique des Grandes Cultures, Algeria, personal communication; Table S1), so that resistance of S. arvensis to these two ALS inhibitors might be expected. In a greenhouse study, we assessed (a) population differentiation in phenology and phenotypic traits by adopting a quantitative genetic approach and (b) herbicide resistance to amidosulfuron + iodosulfuron-methyl-sodium and florasulam + 2,4-D from sampling paired populations collected in crop and adjacent non-crop habitats in eight regions across Northern Algeria.

2 | MATERIALS AND METHODS

2.1 | Seed collection

Seeds of S. arvensis were collected in eight regions along a longitudinal gradient in Northern Algeria in June 2018 (Figure 1; Table S1). In each region, two populations were selected: a crop (wheat) field and an adjacent non-crop field, separated from each other by 1 to 2 km. The climatic characteristics of the 16 populations are summarised in Table S1 and illustrated in a principal component analysis (PCA) in Figure 1 (cf. Note S1 for details). In each of the 16 populations, 60 seeds of each 10 plants were collected along a W-shaped transect with a distance of ≥5 m between plants. In total, 9,600 seeds from 160 plants were sampled.

2.2 | Seed size and germination test

We recorded the size (projected surface area) of 10 seeds per mother plant and then germinated these with 20 other seeds (in total 30 seeds per mother plant) in small Petri dishes of 4.5 cm in diameter to assess
the germination rate. To break dormancy, seeds were placed on filter paper soaked with gibberellic acid 3 at a concentration of 250 mg/L (Luzuriaga et al., 2006). Seeds were then placed in a growth chamber (temperature 25±2°C; relative humidity 57%; photoperiod 12:12 hr; light intensity 6 klx) for at least 6 days. After germination, nine seedlings from each mother plant were planted in seedling trays for 1 week, then transplanted into 1 L pots filled with a mixture of soil (including vermiculite) and sand (2:1). Plants were kept in the greenhouse of the University of Fribourg under controlled conditions [temperature 27±2°C; relative humidity 72±2%; photoperiod 16:8 hr achieved with natural and artificial lights (400 W, Osram Powerstar, Slovakia); light intensity 16 klx]. From the nine seedlings transplanted per mother plant, three were used for the phenotyping study to assess quantitative genetic differentiation within and among populations by adopting a quantitative genetic approach. These three seedlings also served as control for the herbicide resistance experiment. The remaining six seedlings were used for the herbicide resistance experiment, with three seedlings per herbicide treatment. Both studies started when the seedlings reached the 4–6 leaf stage.

2.3 | Phenotyping study

Three seedlings per mother plant were randomly positioned on benches of the greenhouse of the University of Fribourg under controlled conditions [temperature 27±2°C; relative humidity 72±2%; photoperiod 16:8 hr achieved with natural and artificial lights (400 W, Osram Powerstar, Slovakia); light intensity 16 klx]. We recorded the number of leaves 5 days after transplanting into 1 L pots and the relative growth rate (RGR), calculated as, with $W_2$ and $W_1$ corresponding to plant height on day 20 ($t_2$) and day 10 ($t_1$) after transplanting (Hoffmann and Poorter, 2002). In addition, the phenological stage was recorded on day 10 after transplanting as 1: vegetative, 2: flower buds, 3: flowering, 4: fruit formation. At the end of flowering (i.e. 80 days after transplanting), we recorded the final height and dry weight of each plant after drying at 70°C for 48 hr.

2.4 | Herbicide resistance experiment

We used the two anti-dicotyledonous post-emergence herbicides described in the introduction: florasulam + 2,4-D (Mustang® 360 SE, florasulam 6.25 g a.i. L$^{-1}$, 2,4-D 300 g a.i. L$^{-1}$, SE, PROFERT ALGERIA) and amidosulfuron + iodosulfuron-methyl-sodium (Sekator® OD, amidosulfuron 25 g a.i. L$^{-1}$, iodosulfuron-methyl-sodium 100 g a.i. L$^{-1}$, safener 250 g a.i. L$^{-1}$, OD, CROP SCIENCE BAYER ALGERIA). To assess the resistance of plants collected from the 16 crop and non-crop populations, we allocated three seedlings per mother plant to each of the two herbicides and to the control treatment, resulting in 480 plants for each of the three treatments.

The herbicide resistance experiment was carried out in the greenhouse of the University of Fribourg under controlled
conditions, identical to the phenotyping study. The manufacturers’ recommended doses are 0.6 and 0.15 L/ha for florasulam + 2,4-D and amidosulfuron + iodosulfuron-methyl-sodium respectively. To ensure phytotoxicity on susceptible plants and since resistant biotypes are reported to also tolerate higher concentrations with no effect on biomass (Christoffers et al., 2006), we sprayed double the recommended dosage on the seedlings at the 4–6 leaf stage. The control treatment was sprayed with a similar volume of water. After spraying, plants were watered 2–3 times per week. The level of phytotoxicity was assessed 2, 4 and 6 weeks after spraying, using a modified European Weed Research Society (EWRS) scale for visual rating of phytotoxicity (Table S2) with eight classes ranging from 1 for healthy plants to 8 for dead plants. The presence of regrowth from treated plants was also recorded throughout the experiment. At the end of the experiment, that is 6 weeks after spraying, the dry weight of all herbicide-treated plants was measured after drying at 70°C for 48 hr. Plants of the control treatment and habitat type were included as fixed factors, while region nested within habitat type and mother plant nested within region, nested in turn within habitat type, were considered as random. The control treatment, displaying only healthy plants, was removed from the statistical analyses to avoid an overrepresentation of one category.

Normality of the residuals of models and heteroscedasticity of the data on all fixed factors were tested using QQ-plots and Levene’s tests respectively. Data were square-root or log10 transformed when necessary to meet the assumptions of LMMs.

$Q_{ST}$ is a standardised metric used to evaluate the degree of genetic differentiation among populations in quantitative traits (Lynch and Walsh, 1998). In this study, differentiation in quantitative traits between habitat types (Hab—Q$_{ST}$) and among regions within habitat type (Reg—Q$_{ST}$) were calculated as Hab—Q$_{ST}$ = $\sigma^2_H + 4\sigma^2_{MP}$ and, Reg—Q$_{ST}$ = $\sigma^2_H + 4\sigma^2_{MP}$ where $\sigma^2_H$ is the additive genetic variance explained by habitat type, $\sigma^2_R$ the additive genetic variance explained by region within habitat type, and $\sigma^2_{MP}$ the additive genetic variance among mother plants within regions. As seeds collected from one mother plant are considered as half-sibs, was estimated as four times the observed variance among mother plants. The LMM/GLMM models used to obtain variance components to calculate and included habitat type, regions nested within habitat type, and mother plants nested within regions nested in turn within habitat type as random factors. For LMMs, the additive genetic variance components were calculated using restricted maximum likelihood (REML) from the lme4 R package. For GLMMs, we used the QGglm R package to compute quantitative genetic parameters (de Villemereuil et al., 2016). We used the results of these statistical models to evaluate the significance of values.

In addition to $Q_{ST}$ metrics, the narrow-sense heritability ($h^2$), corresponding to the within-population variation, was calculated for each population and each quantitative trait as $h^2 = \sigma^2_{MP}/\sigma^2_{MP} + \sigma^2_{res}$, where $\sigma^2_{MP}$ is the additive genetic variance among mother plants and $\sigma^2_{res}$ the residual variance corresponding to the variation within mother plants. We tested for equality of the variance and mean of $h^2$ values between crop and non-crop populations for each quantitative trait and for the average, using F and Mann–Whitney tests for variance and mean comparisons respectively. Note that $h^2$ values were not calculated for the germination rate as this variable is composed of binomial data.

### 3 | RESULTS

#### 3.1 | Phenotyping study

##### 3.1.1 | Differentiation between habitat types

The LMM/GLMM models computed on phenotypic traits and on phenology showed no significant differences between plants from the two habitat types, with the exception of dry weight (Table S3), for which crop populations were heavier than non-crop populations (Figure 2). This trend was confirmed by the Hab—Q$_{ST}$ estimates.
(Table 1), which yielded a value of 0.154 for dry weight, while all other quantitative traits showed values of 0.

### 3.1.2 Variation among regions

LMM/GLMM models revealed a highly significant regional effect within habitat type for four out of seven traits and for five out of seven when disregarding the habitat type factor (Table S3), that is germination rate, seed size, final size, RGR and phenological stage. For these variables, estimates of Reg−QST were relatively low, ranging from 0.066 for seed size to 0.261 for the phenological stage. Among the five traits showing a significant regional effect, four were significantly correlated with PC1 of the climate analysis (Figure 3; Table S4a), which separated more western sites with higher precipitation and lower temperatures (e.g. REL and CHN, described as ‘temperate populations’ in the comparison below) from more eastern sites with higher temperatures and lower precipitation (e.g. ADE and BOI, described as ‘arid populations’; Figure 1; Note S1). For instance, seeds were smaller in temperate populations compared to arid ones, and plants from temperate populations matured earlier compared to arid ones (Figure 3). However, for some traits, these trends differed between the habitat types. For instance, the germination rate of non-crop populations was higher for arid populations compared to temperate populations, while no trend was observed for the crop populations, and an opposite was observed for the RGR (Figure 3). The second axis (PC2) of the climate analysis differentiates the two sites (SET) with the highest annual temperature range and the lowest precipitation seasonality, most likely related to the higher elevation of the SET sites (Table S1). However, none of the studied plant traits were correlated with PC2 (Table S4b).

### 3.1.3 Variation within populations

The narrow-sense heritability ($h^2$) of trait averages ranged from 0.28 ± 0.08 (SD) to 0.71 ± 0.19 for crop populations and from 0.40 ± 0.15 to 0.63 ± 0.22 for non-crop populations (Figure 4; Table S5a), and showed no significant differences between both habitat types (Figure 4; Table S5b). Furthermore, the F test of variance equality showed no significant difference between crop and non-crop populations, overall and for each phenotypic and phenological traits tested separately (Table S5).

### 3.1.4 Herbicide resistance

The herbicide resistance study revealed no resistant plants, that is 100% of plants had died 6 weeks after herbicide treatment (Figure 5a). For the phytotoxicity assessments after 2 and 4 weeks, dry weight and presence of regrowth, we found no significant effect of habitat type (Figure 5a; Table S6). However, the effect of the two herbicides differed significantly (Table S6): 2 weeks after spraying, the phytotoxicity symptoms of the florasulam + 2,4-D herbicide were more advanced compared to amidosulfuron + iodosulfuron-methyl-sodium. Consequently, florasulam + 2,4-D resulted in faster plant mortality already within 4 weeks after spraying. In line with this, plants treated with florasulam + 2,4-D showed significantly lower dry weight (Figure 5b) and fewer plants with regrowth compared to plants treated with amidosulfuron + iodosulfuron-methyl-sodium, that is among the 480 plants observed, 19% and 33% of them showed regrowth for florasulam + 2,4-D and amidosulfuron + iodosulfuron-methyl-sodium treatments respectively.

### 4 DISCUSSION

#### 4.1 Absence of differentiation between habitat types

The common garden study revealed no differentiation for most of the quantitative traits between S. arvensis populations collected in crop and non-crop fields. This absence of habitat differentiation suggests high gene flow between the two habitat types due to the proximity (≤2 km) of crop and non-crop populations (Vigueira et al., 2013). This allows natural dispersal of seeds and pollen between habitat types, as well as human-induced dispersal of seeds following harvesting activities, prominent in the cereal regions in Algeria. Transport of straw balls from wheat fields to livestock farming and plant residues after harvest can disperse weed seeds into adjacent...
non-crop fields (Glasner et al., 2019). Furthermore, free pasture of ruminants in crop fields after harvest results in the transportation of weed seeds to non-cultivated areas within the farm territory (Petit et al., 2012). Contrary to our expectations, we found no significant difference in within-population variation between the two habitat types, underlying as well a high gene flow between the two habitat types.

The fact that the phenology of *Ambrosia artemisiifolia* L. was found to not differ between ruderal and agricultural habitats when grown in a common garden has been suggested to indicate that phenological sensitivity is altered by environmental conditions, such as temperature, rather than by management interventions in agricultural habitats (Leiblein-Wild and Tackenberg, 2014). This finding is in line with the climatic trend in phenology observed in our greenhouse study (Figure 3, cf. 4.2 below). We also found no effect of habitat type on germination rate, which is congruent with results for *Senecio vernalis* Waldst. & Kit. populations from various habitat types, such as roadsides and semi-dry grasslands (Hantsch et al., 2013). Furthermore, our $Q_{ST}$ values revealed very low genetic divergence between the two habitat types. Similarly, Dodet (2009) found low among-population variation in *Cyperus esculentus* L., suggesting high dispersal and numerous new infestations.

Only dry weight differed between habitats, with higher biomass in plants from crop populations. This could be explained by increased nitrogen availability in the crop populations resulting in maternal environment effects (Leiblein-Wild and Tackenberg, 2014; Leiss and Müller-Shärer, 2001; Neve et al., 2018).

While a phenotyping study followed by quantitative genetic analysis is an effective approach to assess among- and within-population variation and population differentiation (Steinger et al., 2002), it does not directly assess evolutionary processes such as natural selection or phenotypic plasticity that may be at the origin (or lack) of phenotypic variation. Coupling our $Q_{ST}$ approach with a neutral molecular marker study ($F_{ST}$) would help distinguish between these evolutionary processes (Leinonen et al., 2013) and thus provide a better understanding of the lack of genetic differentiation in this species. Furthermore, phenotypic trait measurements should also be extended in future studies, for example by including reproductive traits.

### 4.2 Regional differentiation along temperature and precipitation gradients

Overall differences among regions were found for several traits, including germination rate, seed size, final size, RGR and phenological stage. Except for final size, the variation found between regions followed a climatic gradient from east to west. Plants collected in temperate populations displayed a more advanced reproduction and faster growth rates, smaller seed size and faster germination rates compared to arid populations. Both crop and non-crop populations were concerned, excepted for the RGR in non-crop populations and the germination rate in crop populations for which no significant climatic effects were found (Figure 3). Adaptation to such climatic gradients has commonly been found. For instance, larger seed size coincides with increasing local aridity for several species of *Glycine* in Australia (Murray et al., 2003), and larger seeds are found in environments with constantly low precipitation, while under highly fluctuating precipitation, either small or large seeds can be optimal (Volis and Bohrer, 2013). These findings are thus in line with the larger seed size of *S. arvensis* populations in arid populations (Table S1). Similarly, the faster germination and growth and more advanced reproduction observed in temperate populations might also be selected under the wetter conditions. Warmer temperatures generally have been found to accelerate the phenology of organisms around the world (e.g. Park et al., 2018 for 7,000 herbarium specimens representing 30 plant species in eastern United States), whereas our results show more advanced phenology in temperate regions than arid ones, which might be due to other environmental parameters in these regions. Smaller seeds are often reported to have a higher RGR (Turnbull et al., 2012), which is in line with our results, but a faster RGR in wetter conditions was only found for non-crop populations. Thus, the crop populations did not differ in RGR along the climatic gradient, which may be because plants from crop habitats are also affected by agricultural practices (Neve et al., 2009) that favour a high RGR throughout the region and explaining the observed higher biomass of the crop populations. The lack of significance for the difference in RGR between the habitat types might be due to the small sampling size.

### Table 1: Estimates of variation in quantitative genetic traits between crop and non-crop habitat types (Hab—$Q_{ST}$), and among regions within habitat types (Reg—$Q_{ST}$) for each phenotypic and phenological trait. Variance components of hierarchical models are given: $V_t$ (total variation observed), $V_{Hab}$ (variance between habitat types), $V_{Reg}$ (variance among regions within habitat types), $V_{MP}$ (four times the variance among mother plants within regions within habitat types), $V_{Res}$ (residual variance). Significant $Q_{ST}$ values ($p$-value < .001) are shown in bold (see Table S3 for results of the models).

<table>
<thead>
<tr>
<th>Trait</th>
<th>$V_t$</th>
<th>$V_{Hab}$</th>
<th>$V_{Reg}$</th>
<th>$V_{Res}$</th>
<th>$Q_{ST}$ Hab</th>
<th>$Q_{ST}$ Reg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Germination rate</td>
<td>0.1803</td>
<td>0.0000</td>
<td>0.0138</td>
<td>0.1437</td>
<td>0.1306</td>
<td>0.0000</td>
</tr>
<tr>
<td>Seed size</td>
<td>0.0463</td>
<td>0.0000</td>
<td>0.0083</td>
<td>0.1169</td>
<td>0.0088</td>
<td>0.0000</td>
</tr>
<tr>
<td>Leaf number</td>
<td>0.1850</td>
<td>0.0000</td>
<td>0.0232</td>
<td>0.2116</td>
<td>0.1089</td>
<td>0.0000</td>
</tr>
<tr>
<td>Final size</td>
<td>0.0168</td>
<td>0.0000</td>
<td>0.0012</td>
<td>0.0117</td>
<td>0.0127</td>
<td>0.0000</td>
</tr>
<tr>
<td>Dry weight</td>
<td>0.0558</td>
<td>0.0074</td>
<td>0.0013</td>
<td>0.0392</td>
<td>0.0373</td>
<td>0.1549</td>
</tr>
<tr>
<td>RGR</td>
<td>0.9895</td>
<td>0.0000</td>
<td>0.1593</td>
<td>1.2038</td>
<td>0.5293</td>
<td>0.0000</td>
</tr>
<tr>
<td>Phenological stage</td>
<td>0.3749</td>
<td>0.0000</td>
<td>0.1634</td>
<td>0.4617</td>
<td>0.0961</td>
<td>0.0000</td>
</tr>
</tbody>
</table>

Note: RGR, relative growth rate.
Resistance of weed populations to the two herbicides tested has been reported in Mediterranean countries. For instance, Galium spurium L. seedlings from three out of eight populations in Northern Greece showed a high level of resistance to florasulam + 2,4-D even at eight times the recommended dose (Papapanagiotou et al., 2019). Moreover, four out of 68 populations of Bifora radians M. Bieb. in Central Turkey were found to be resistant to amidosulfuron + iodosulfuron-methyl-sodium according to visual rating and molecular analyses (Altop et al., 2017). In the light of these recent findings and little regulation concerning the application of these herbicides in Algeria, resistance of crop weeds to the two herbicides tested could be expected.

In our preliminary analysis, however, we found no signs of resistance to the two herbicides tested. This could simply be explained by the low number of mother plants tested from each population (10 mother plants per population), resulting in a detection level of only 10%. Thus, resistance could well exist at a lower level, as the herbicide has only been applied in wheat crops in Algeria over the last 8 years and only once per season, but repeatedly at the same site due to the absence of crop rotation (Institut Technique des Grandes Cultures, Algeria, personal communication). Another reason for the absence of herbicide resistance in our study plants could be the fact that plants grown in the greenhouse are more sensitive to herbicides compared to open field conditions (Dalton and Boutin, 2010). Thus, the double dose used in our study may have killed even resistant biotypes. To provide a more sensitive test for herbicide resistance, a dose–response study in comparison with known susceptible and resistant populations is needed. Furthermore, seeds of S. arvensis can remain viable in the soil for 60 years (Warwick et al., 2000). Germinating seeds from the long-lived seed bank may therefore originate from plants never exposed to the herbicide (Moodie et al., 1997). Indeed, following continuous applications, resistant biotypes of some weedy species were reported only after 18, 9, 10, 25 and 10 years for 2,4-D, Dalapon, Atrazine, Picloram and Trifluralin.
herbicides respectively (LeBaron, 1991). Chemical control of weeds in Algeria starts during the winter season at the 2–6 leaf stage of most cereal weeds, thus re-emergence of *Sinapis arvensis* after spraying herbicide is very likely due to its short life cycle of around 100 days (Warwick et al., 2000), allowing it to still reach seed set before harvest. No resistant biotypes were detected for either amidosulfuron + iodosulfuron-methyl-sodium or florasulam + 2,4-D, but the latter showed earlier phytotoxicity symptoms, earlier mortality and thus reduced biomass of the plants compared to the former. We attribute this to the fact that florasulam + 2,4-D is a combination of ALS-inhibitor and auxin herbicide. As described by the manufacturers, florasulam + 2,4-D and amidosulfuron + iodosulfuron-methyl-sodium stop the growth of weeds 1 and 7 days after their application, with complete weed control after 2–4 and 4–5 weeks respectively. In line with this, the more frequent regrowth after amidosulfuron + iodosulfuron-methyl-sodium treatment suggests a lower efficiency compared to florasulam + 2,4-D.

### 4.4 | Implications for management

The studied *Sinapis arvensis* populations showed genetic differentiation in quantitative traits across regions, but strong similarity between crop and non-crop habitat types within the same region. This suggests significant gene flow through pollen or seeds between adjacent habitat types, but not across crop fields at a larger scale, as would be expected by contamination of crop seeds from common sources, or movement of agricultural machinery. This allows formulation of management advice in order to reduce *S. arvensis* densities in both habitats. Presently, *S. arvensis*, the most prominent competitive weed in cereal crops in Algeria, can be successfully controlled by herbicides, as also evidenced by our results. However, continual application of the same active ingredients in the same fields is expected to select for herbicide-resistant biotypes in the near future. Preventive measures to reduce *S. arvensis* densities in crop habitats are therefore needed. Firstly, spread of seeds from crop to adjacent habitats could be reduced by better protecting straw balls from losing weed seeds when they are transported from crop fields, and by restricting pasturing of ruminants in crop fields after harvest. Otherwise, once established in adjacent non-crop habitats, the same potentially resistant weed populations can re-infest crop fields by natural spread or human activities. Furthermore, more emphasis should be given to better management of high-density *S. arvensis* populations in the vicinity of crop fields, for example by overseeding more competitive and locally adapted native grass or leguminous species. Controlling weeds efficiently in crops without favouring herbicide resistance requires the integrated use of preventative, chemical and physical control measures, ideally under crop rotation schemes that allow for herbicides with different active ingredients and for different periods of management interventions (sowing, weed control, harvest and tillage).

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CONFLICT OF INTEREST
No conflict of interest.

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