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Published on: 01 Feb 2019 - Weed Research (John Wiley & Sons, Ltd)

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Variability in seedling emergence for European and North American populations of *Abutilon theophrasti*

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Received 27 February 2018

Revised version accepted 24 October 2018

Subject Editor: Rob Freckleton, Sheffield, UK

Summary

Abutilon theophrasti is a weed that is spreading worldwide and that has had to adapt to different combinations of environmental conditions. Wide interpopulation variability has been reported regarding dormancy and germination. This variability, controlled by the interaction of genetic diversity and maternal effect, could hinder the adoption of Integrated Weed Management (IWM) tools. A collaborative project was conducted to compare emergence dynamics of 12 European and North American populations under diverse environmental conditions. The main aim was to assess interpopulation variability and explain this according to environmental conditions in the seed collection sites. Seeds were sown at six experimental sites, and seedling emergence was monitored. The *AlertInf* model was tested to evaluate its ability to predict emergence dynamics of the different populations. A wide

interpopulation variability was observed for emergence percentage and dynamics with consistent trends across sites and related to different seed dormancy levels. Populations from Catalonia, Iowa and Minnesota reached higher emergence percentage with earlier and concentrated emergence flushes probably due to low dormancy level, while populations from Croatia, Serbia and Hungary, given their low average emergence percentage, presented high dormancy levels. Good predictive accuracy of *AlertInf* model was obtained at the different sites, confirming the possibility of adopting it across a wide range of environmental conditions. Achieving a better knowledge of interpopulation variability can allow specific control strategies to be designed, facilitating the replacement of solely herbicide-based management with true IWM.

Keywords: velvetleaf, population variability, germination, emergence, emergence modelling.

LODDO D, BOZIC D, CALHA IM, DORADO J, IZQUIERDO J, ŠČEPANOVIĆ M, BARIĆ K, CARLESİ S, LESKOVSEK R, PETERSON D, VASILEIADIS VP, VERES A, VRBNIČANIN S, MASIN R (2018). Variability in seedling emergence for European and North American populations of *Abutilon theophrasti*. *Weed Research*. <https://doi.org/10.1111/wre.12343>.

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6 Introduction

Weeds can be considered pioneer species that colonise frequently disturbed habitats, such as cultivated fields, so they have to adapt their biological cycles to the specific environmental disturbances caused by farming operations. Since germination is a crucial moment in the life cycle of annual weeds, and germination timing strongly affects their survival probability, competitive ability and reproductive success (Berti *et al.*, 2008), local populations of globally widespread species have therefore adapted to germinate at the most favourable time to emerge according to different combinations of environmental and agronomic conditions. Consequently, weeds may present wide intra-specific variability regarding dormancy and germination ecology (Eslami, 2011; Loddo *et al.*, 2014). For example, populations growing in cold areas have been reported to have lower base temperature for germination and less dormant seeds (Loddo *et al.*, 2013; Tozzi *et al.*, 2014) than those in temperate areas. The variability is affected by the interaction of genetic diversity and maternal effect, that is the environmental conditions experienced during growth of mother plants and seed ripening (Andersson & Milberg, 1998; Karlsson *et al.*, 2008; Gesch *et al.*, 2016). This variability could hinder the broad adoption of Integrated Weed Management (IWM) strategies and tools, which were often developed for local weed populations growing under specific conditions.

Abutilon theophrasti Medik. is an important weed spreading worldwide in spring–summer crops with a relevant economic impact in many European countries (Recasens *et al.*, 2005). Several studies have been conducted on different aspects of *A. theophrasti* biology and ecology, such as germination (Dorado *et al.*, 2009a; Masin *et al.*, 2010a,b), seedling emergence (Dorado *et al.*, 2009b; Masin *et al.*, 2012, 2014), seed-bank dynamics (Liebman *et al.*, 2014) and competition (Vrbnicanin *et al.*, 2017). Contrasting information has been reported about the intra-specific variability of *A. theophrasti* germination and seedling emergence. Nurse and DiTommaso (2005) described variability of seed size, seed coat and dormancy due to different crop competition levels, and Dorado *et al.* (2009b) observed differences in field emergence patterns of populations in Portugal and Spain. In contrast, similar values of base temperature for germination were reported for European and Iranian populations (Loddo *et al.*, 2013, 2018). No exhaustive studies are available comparing germination and seedling emergence among several populations of *A. theophrasti*, and most of the existing information can only be considered representative of local situations.

A collaborative project was therefore conducted to compare the emergence dynamics of several European and North American populations across different sites under diverse environmental conditions. The main aim was to assess the intra-specific variability and to identify patterns explaining this variability according to environmental conditions in the seed collection sites. In addition, an existing emergence predictive model *AlertInf*, created in Veneto, north-eastern Italy (Masin *et al.*, 2010a,b), was tested to evaluate its ability to predict the emergence dynamics of the different populations of *A. theophrasti* across different sites. This information is intended to facilitate the development and adoption of tailored IWM strategies according to specific characteristics of local populations.

Materials and methods

Seed source

Seeds were collected during summer–autumn 2013 from spontaneous populations of *A. theophrasti* at 12 different sites in Europe and United States: two in Spain (pop. MAD-Madrid and CAT-Catalonia), Italy (pop. TUS-Tuscany and VEN-Veneto) and United States (pop. IOWA-Iowa and MIN-Minnesota) and one each in Croatia, Greece, Hungary, Portugal, Serbia and Slovenia (pop. CRO, GRE, HUN, POR, SER and SLO). Geographical and climatic information on the collection sites is presented in Table 1. The sites are characterised by different climates, ranging from the warmer conditions in Pisa (Italy), Golegã (Portugal) and Arganda del Rey (Spain) to the colder conditions in Monona and Morris (Iowa and Minnesota, USA). Seeds were collected from several plants to obtain a representative sample of the whole population. Seeds were cleaned and left to dry at room temperature (20°C) for some days and then stored in paper bags at room temperature for 4 weeks until the start of the experiment. Storage duration and conditions were the same for all 12 populations.

Preliminary tests

Seed dry weight (expressed as 1000 seeds weight) was measured by weighing four 1000 seed replicates per population after drying at 65°C for 48 h. Means and SE were calculated, and the Tukey HSD test ($P < 0.05$) was used to detect significant differences between means. Seed germinability of the different populations was assessed in a preliminary experiment. Physical dormancy was removed by soaking seeds in boiling water for 10 s (Nurse & DiTommaso, 2005)

Table 1 List of *Abutilon theophrasti* populations with geographical and climate information of their collection sites

Population code	Country	Site	Latitude	Longitude	Altitude	Climate*
MIN	USA	Morris	45°35'N	95°54'W	350	Dfb (Snow, fully humid with warm summer)
IOWA	USA	Monona	43°03'N	91°23'W	360	Dfa (Snow, fully humid with hot summer)
POR	Portugal	Golegã	39°24'N	8°29'W	20	Csa (Warm temperate with dry and hot summer)
MAD	Spain	Arganda del Rey	40°19'N	3°29'W	550	Csa (Warm temperate with dry and hot summer)
CAT	Spain	Lleida	41°37'N	0°38'E	150	Cfa (Warm temperate, fully humid with hot summer)
TUS	Italy	Pisa	43°40'N	10°20'E	2	Csa (Warm temperate with dry and hot summer)
VEN	Italy	Legnaro	45°20'N	11°58'E	15	Cfa (Warm temperate, fully humid with hot summer)
SLO	Slovenia	Murski Črnci	46°38'N	16°06'E	192	Cfb (Warm temperate, fully humid with warm summer)
CRO	Croatia	Čazma	45°45'N	16°37'E	120	Cfb (Warm temperate, fully humid with warm summer)
HUN	Hungary	Rackeve	47°09'N	18°54'E	100	Cfb (Warm temperate, fully humid with warm summer)
SER	Serbia	Rimski Sancevi	45°40'N	19°05'E	80	Cfb (Warm temperate, fully humid with warm summer)
GRE	Greece	Makrochori	40°32'N	22°14'E	60	Cfa (Warm temperate, fully humid with hot summer)

*Climate classification according to the updated Köppen–Geiger classification (Kottek *et al.*, 2006).

and then placing them in Petri dishes on filter paper moistened with 5 mL of deionised water. Petri dishes were then incubated at 20°C with 12-h light/12-h dark photoperiod. Three replicates of 50 seeds each were included per population. After one week of incubation, germination surpassed 75% for all populations (data not shown), so problems of germinability were excluded.

Field experiment for emergence monitoring

Seeds of the 12 populations were sown in November 2013 at six different experimental sites in Southern and Eastern Europe: (i) Oeiras, Lisbon (Portugal), (ii) Arganda del Rey, Madrid (Spain), (iii) Viladecans, Catalonia (Spain), (iv) Legnaro, Veneto (Italy), (v) Zagreb (Croatia), (vi) Belgrade (Serbia). Soil characteristics and climatic classification of the six experimental sites are reported in Table 2. All sites are characterised by a warm temperate climate with differences regarding the amounts of precipitation and summer temperatures. Soil texture ranged from sandy loam at Zagreb (Croatia) to silt loam at Belgrade (Serbia) and Legnaro (Italy). Seeds were mixed with local soil and distributed randomly in the top 2 cm soil layer. Four replicates were included for each population. Replicates were made up of 250 seeds for CAT, CRO, HUN, VEN, POR, SER, MAD, TUS, 150 seeds for

SLO and 100 for GRE, IOWA, MIN in accordance with the availability of seeds. Each replicate occupied a single 1-m² plot, and the experimental sites were set up in areas where no spontaneous population of *A. theophrasti* had been observed. Weather conditions (daily air and soil temperature and rainfall) were monitored throughout the experiment. Emerged seedlings were counted and removed weekly during the typical period of *A. theophrasti* emergence (normally from February to August).

Data analysis

Mean and SE were calculated for emergence percentage of each population at each experimental site, as well as for average emergence percentage of each population (considering the data of all replicates across the different experimental sites) and each experimental site (considering the data of all replicates of the different populations). Emergence percentage was analysed using a generalised mixed model with a binomial distribution, assuming the emergence percentage as the probability of a single seed germinating and emerging or not. Variance was weighted by the number of seeds in each replicate. The random part of the model consisted of a nested design; replicates were nested within population, which were nested within the experimental site. Models were created using lme4 (Bates *et al.*,

Table 2 List of experimental sites with geographical, climate and soil characteristics information

Site	Country	Latitude	Longitude	Altitude	Climate*	Soil characteristics					
						Sand %	Loam %	Clay %	Texture	OM %	pH
Oeiras	Portugal	38°41'N	9°18'W	20	Csa	55.7	18.9	25.4	Sandy clay loam	1.4	8.0
Arganda del Rey	Spain	40°19'N	3°29'W	550	Csa	35.9	44.3	19.8	Loam	1.3	7.8
Viladecans	Spain	41°18'N	2°0'E	20	Csa	38.0	37.6	24.4	Loam	1.4	8.4
Legnaro	Italy	45°20'N	11°58'E	15	Cfa	16.0	64.9	19.1	Silt loam	1.8	8.0
Zagreb	Croatia	45°49'N	16°01'E	130	Cfb	66.7	30.0	3.3	Sandy loam	1.6	7.9
Belgrade	Serbia	44°47'N	20°27'E	110	Cfb	8.0	66.6	25.4	Silt loam	1.3	8.0

*Climate classification according to the updated Köppen–Geiger classification (Kottek *et al.*, 2006).

2015), post hoc test using lsmean (Lenth, 2016), residual overdispersion was tested using DHARMA non-parametric overdispersion test, and homogeneity of residuals was tested using a Kolmogorov–Smirnov test on 1000 time resampled residuals, using DHARMA (Hartig, 2016) packages for R 3.3.2 (R core team, 2017). To evaluate the effect of climate on population emergence behaviour and germination–emergence conditions, climate classification of collection and experimental sites was tested in the mixed models as a fixed factor.

Emergence modelling

Emergence patterns of the different populations were compared within each experimental site and across the different experimental sites. Mean emergence patterns were identified at each site combining data from all populations. The version of *AlertInf* model adopted is based on the ‘hydrothermal time concept’ (Gummerson, 1986) and aims to simulate seedling emergence according to soil temperature and rainfall (Masin *et al.*, 2010b). The first step involves the calculation of hydrothermal time accumulation (HT):

$$HT_i = \sum n * \max(T_{smi} - T_b, 0) + HT_{i-1} \quad (1)$$

where T_{smi} (°C) is the average daily soil temperature of day i , and T_b (°C) is the base temperature for germination. To evaluate whether soil moisture content is limiting or not for germination, total rainfall in the preceding given number of days (x) is compared with P_{limit} (mm) that is the minimum total rainfall required to produce emergence. No HT accumulation ($n = 0$) is calculated if total rainfall in the past x days is lower than P_{limit} , while HT accumulation occurs ($n = 1$) if it is higher than P_{limit} . The values of T_b , x and P_{limit} for *A. theophrasti*, estimated in previous studies are reported in Table 3 and on the *AlertInf* webpage

(http://www.arpa.veneto.it/upload_teolo/agrometeo/fix/AlertInf%20scheda%20english.pdf).

When the accumulation of hydrothermal time (HT_{*i*}) has been calculated for a given day i , the corresponding cumulated total emergence percentage (CE_{*i*}) is determined by the following Gompertz equation:

$$CE_i = 100 * \exp[-a * \exp(-b * HT_i)] \quad (2)$$

where a represents an HT lag before seedling emergence starts and b represents the rate of increase of seedling emergence once it is initiated. The values of a and b are species-specific and were estimated in previous studies (unpubl. obs.), they are reported in Table 3.

The starting point of accumulation of hydrothermal time is normally set at crop sowing or seedbed preparation date in the case of modelling weed emergence in crop fields. However, this approach was not feasible for this study. The starting point of accumulation was therefore established for each experimental site considering the first date of observation of emerged seedlings and counting backwards for a number of days (usually 3–5) necessary to accumulate the amount of HT corresponding to the lag before seedling emergence (approximately 20 HT), as estimated in previous unpublished studies. The *AlertInf* model was run independently for each experimental site using the local data of soil temperatures and rainfall. The Portuguese site of Oeiras was not included, due to the lack of appropriate soil

Table 3 Values of parameters adopted for the accumulation of hydrothermal time (HT, Eqn 1) and the estimation of cumulated percentage of total emergence (CE, Eqn 2)

	T_b	P_{limit}	x	a	b
HT (Eqn 1)	3.9	4.5	12		
CE (Eqn 2)				5.486	0.0155

temperature records. A single curve representing emergence dynamics of *A. theophrasti* was obtained for each site, and this was compared with the curves of observed mean emergence of the different populations, assessing *AlertInf* performance by calculating an efficiency index (EF) with the following equation (Loague & Green, 1991):

$$EF = \frac{\sum_{i=1}^n (O_i - \bar{O})^2 - \sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (O_i - \bar{O})^2} \quad (3)$$

where P_i is the predicted value, O_i the observed value and \bar{O} the mean of observed values. EF ranges from 1 (exact predictions) to a negative value, while an EF = 0 indicates a model of poor fit. The mean bias error (MBE) was also calculated. The MBE is an indication of the average deviation of the predicted from the observed values and is related to magnitude of values (Willmott, 1982).

$$MBE = \frac{1}{N} \sum_{i=1}^N (P_i - O_i) \quad (4)$$

where N is the number of observations, P_i is the predicted value, and O_i is the observed value. A negative MBE value indicates that the model is, on average, underestimating the observed values and vice versa (Wallach, 2006).

Results

Seed weight

Significant differences were detected among seed weights of the different populations (Appendix S1), with the highest values for populations from Catalonia and Greece (10.4 ± 0.04 and 10.1 ± 0.09 g for 1000 seed weight, respectively) and lowest for the population from Hungary (8.4 ± 0.04 g for 1000 seed weight).

Weather conditions

The experimental sites were characterised by diverse weather conditions (Fig. 1). The Belgrade and Zagreb sites experienced prolonged cold periods, with average daily air temperature below 10°C and minimum daily air temperature frequently close or below 0°C from December to mid-March. Winter was also cold at Arganda del Rey and Legnaro with average daily air temperature below 10°C from December to the end of February, while the Viladecans and Oeiras sites had warmer winter conditions. Considering the main seedling emergence period (February–July), the Oeiras and Viladecans sites had the highest mean temperatures

(21.5 and 17.1°C, respectively) and the Zagreb and Belgrade sites the lowest (14.6 and 15.9°C respectively). Extreme differences were observed across the experimental sites regarding amounts of precipitation. From February to July, the three sites in the Iberian Peninsula (Oeiras, Arganda del Rey and Viladecans) received less than 200 mm of precipitation, while the other three (Legnaro, Belgrade and Zagreb) had more than 600 mm.

Emergence percentage

The generalised mixed model identified significant effects ($P < 0.001$) of the population ($\chi^2 = 583.25$, d.f. = 11; $P < 0.001$) and experimental site ($\chi^2 = 883.66$, d.f. = 5; $P < 0.001$) factors and their interaction ($\chi^2 = 200.25$, d.f. = 55; $P < 0.001$) on emergence percentage. Average emergence percentage varied notably, with significant differences among populations (Fig. 2). Populations from Minnesota, Catalonia and Iowa had the highest emergence percentage (30.2 ± 4.71 , 29.5 ± 3.77 and $28.4 \pm 4.07\%$, respectively, mean of all sites) while the lowest percentage was observed for the Serbian population ($4.5 \pm 0.53\%$, mean of all sites). Similarly, significant differences were detected regarding the average emergence percentage of all populations pooled at the experimental sites (Fig. 3), with the highest percentage being at Belgrade and the lowest at Oeiras (39.9 ± 2.69 and $6.8 \pm 1.02\%$ respectively). However, wide variability was observed among the emergence percentages obtained by each population across the diverse experimental sites (Fig. 4). For example, the population from Minnesota reached $73.0 \pm 3.02\%$ of emergence at Belgrade and only $9.1 \pm 2.00\%$ at Arganda del Rey and the population from Iowa obtained $65.8 \pm 3.27\%$ at Belgrade and $13.1 \pm 4.11\%$ at Oeiras. Nevertheless, the ranking of the different populations in terms of emergence percentage remained quite similar across the diverse experimental sites, with the populations from Catalonia, Iowa and Minnesota reaching the highest emergence percentage in most sites.

Climate classification of experimental sites resulted as a not significant parameter ($P = 0.164$) in affecting emergence probability. Conversely climate classification of seed collection sites of the different populations significantly affected emergence percentage ($\chi^2 = 132.825$, d.f. = 3; $P < 0.001$) with a significant interaction with experimental site ($\chi^2 = 40.115$, d.f. = 15, $P = 0.006$). When different populations were grouped according to the climate type of their seed collection sites, the general ranking of emergence percentage in all sites was Cfb, Csa, Cfa and Df in ascending order, except for

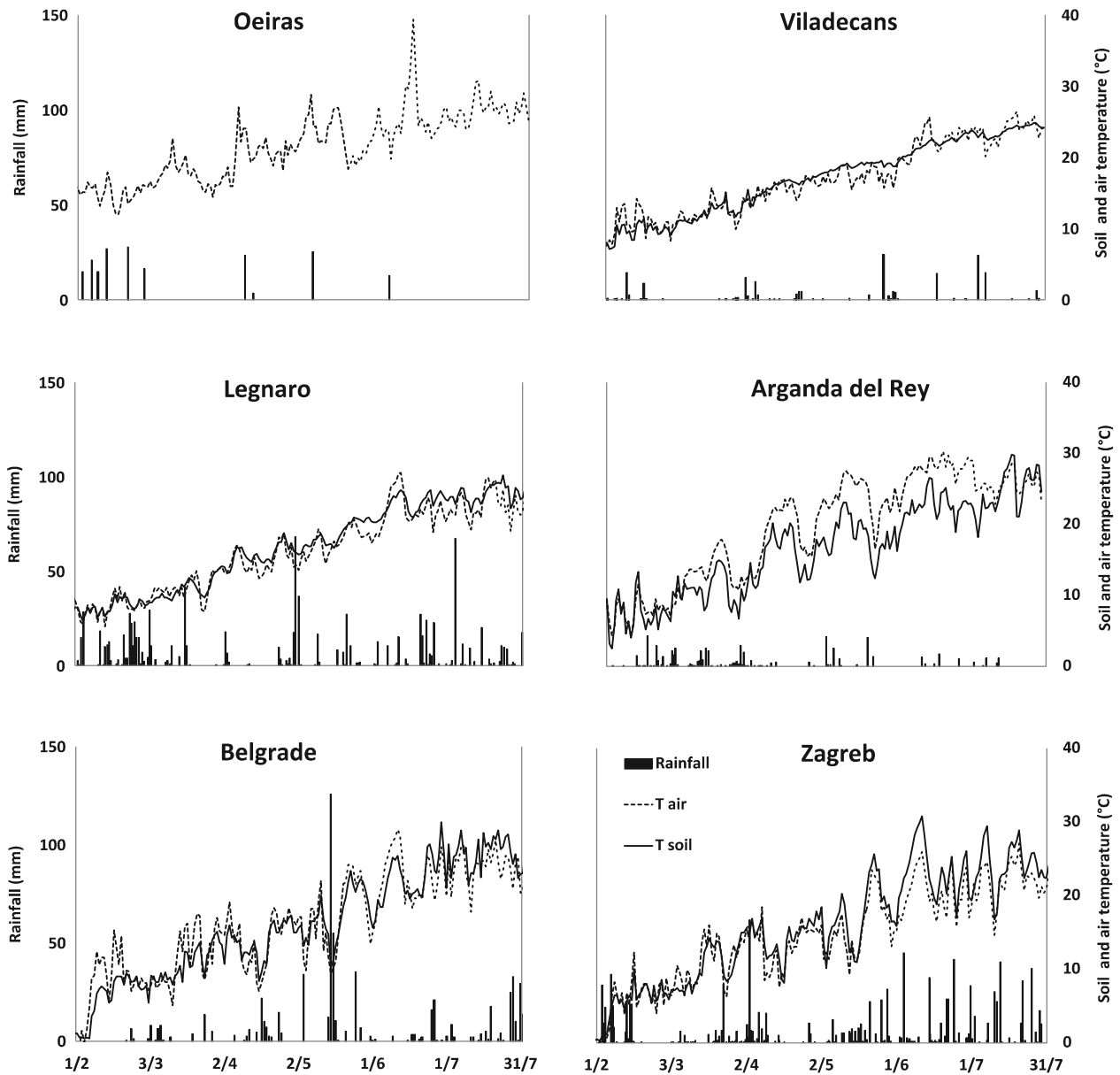


Fig. 1 Weather conditions at the experimental sites. Daily average soil and air temperature (continuous and dotted lines, respectively) and rainfall (bar) are reported.

Arganda del Rey where Cfa and Cfb showed a higher emergence percentage. The factor population explained emergence probability better than climate classification of the population seed collection site ($P < 0.001$).

Emergence dynamics

The first seedlings were observed around mid-February at Oeiras, Arganda del Rey, Viladecans and Legnaro, whereas only on 13 and 21 March at Belgrade and Zagreb (Fig. 5). Considering all populations at each experimental site, the main emergence period lasted approximately from 6 (Arganda del Rey and Belgrade) to 10 weeks (Legnaro). No seedlings

emerged at Arganda del Rey after the end of April, while almost 15% of total emerged seedlings at Legnaro were observed after the end of May. Although the single populations of *A. theophrasti* presented different emergence patterns across the six experimental sites, some tendencies were consistent. The populations from Iowa and Minnesota showed earlier emergence dynamics in comparison with the other populations at almost all sites, while the population from Portugal had later emergence dynamics (Fig. 5). The amplitude of these differences varied across the experimental sites, with a minimum level at Arganda del Rey where the emergence dynamics of the various populations were almost identical. The emergence

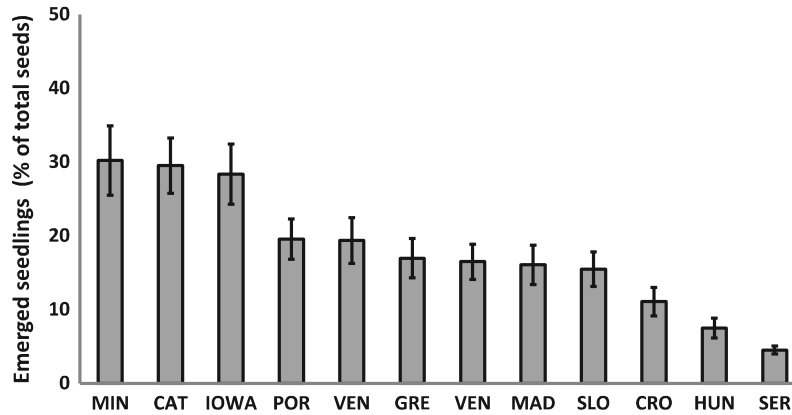


Fig. 2 Percentage of emerged seedlings on the total number of seeds for the different populations of *Abutilon theophrasti*. Values are means of each population across the six experimental sites ($n = 24$; d.f. = 288). Vertical bars represent SE.

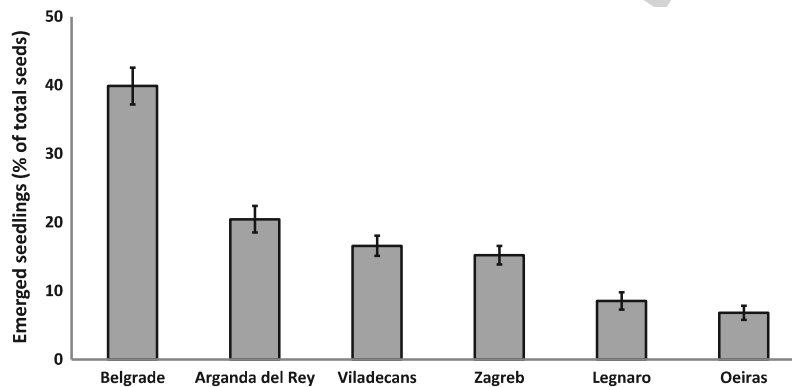


Fig. 3 Percentage of emerged seedlings on the total number of seeds at the experimental sites. Values are means of all populations at each experimental site ($n = 48$; d.f. = 288). Vertical bars represent SE.

dynamics of all populations at all experimental sites are reported in Appendix S2.

When the emergence dynamics observed at the different sites were compared according to accumulated hydrothermal time (HT) instead of calendar days, differences among sites decreased. Most seedling emergence occurred within 500 HT at all sites, even if it was prolonged after 1000 HT in the case of late-emerging populations at Legnaro and Zagreb (Fig. 6).

Accuracy of the *AlertInf* simulation varied across the different sites and populations. Good simulation accuracy was obtained in general at Arganda del Rey and Belgrade, with EF values above 0.85 for most populations. Contrasting results were instead observed between the simulation accuracy for the different populations at Legnaro, where *AlertInf* simulated the emergence curves of MIN and IOWA populations with high accuracy (EF = 0.97), while it notably overestimated the emergence curves of other populations such as CAT, GRE and SLO (EF < 0.2, MBE > 25). Intermediate situations were observed for *AlertInf* accuracy at Zagreb and Viladecans with a general slight overestimation,

identified by the positive MBE values of the predicted emergence curves in comparison with the observed data for the different populations. Considering the results for the different populations across all the sites, high and stable simulation accuracy was obtained for MIN and IOWA populations (EF values always above 0.87), while relevant variability was observed for CAT (EF ranging from 0.99 to 0.19), GRE (EF ranging from 0.95 to -0.42) and SLO (EF ranging from 0.99 to -0.03). The values of EF and MBE for all populations at all experimental sites are reported in Appendix S3.

Discussion

Variability across experimental sites

Weather conditions at the end of winter determined the start of emergence at the different experimental sites. The lower temperatures at Belgrade and Zagreb during January and February 2014 delayed seedling emergence by almost 1 month in comparison with the other sites (from mid-February to mid-March). Even a

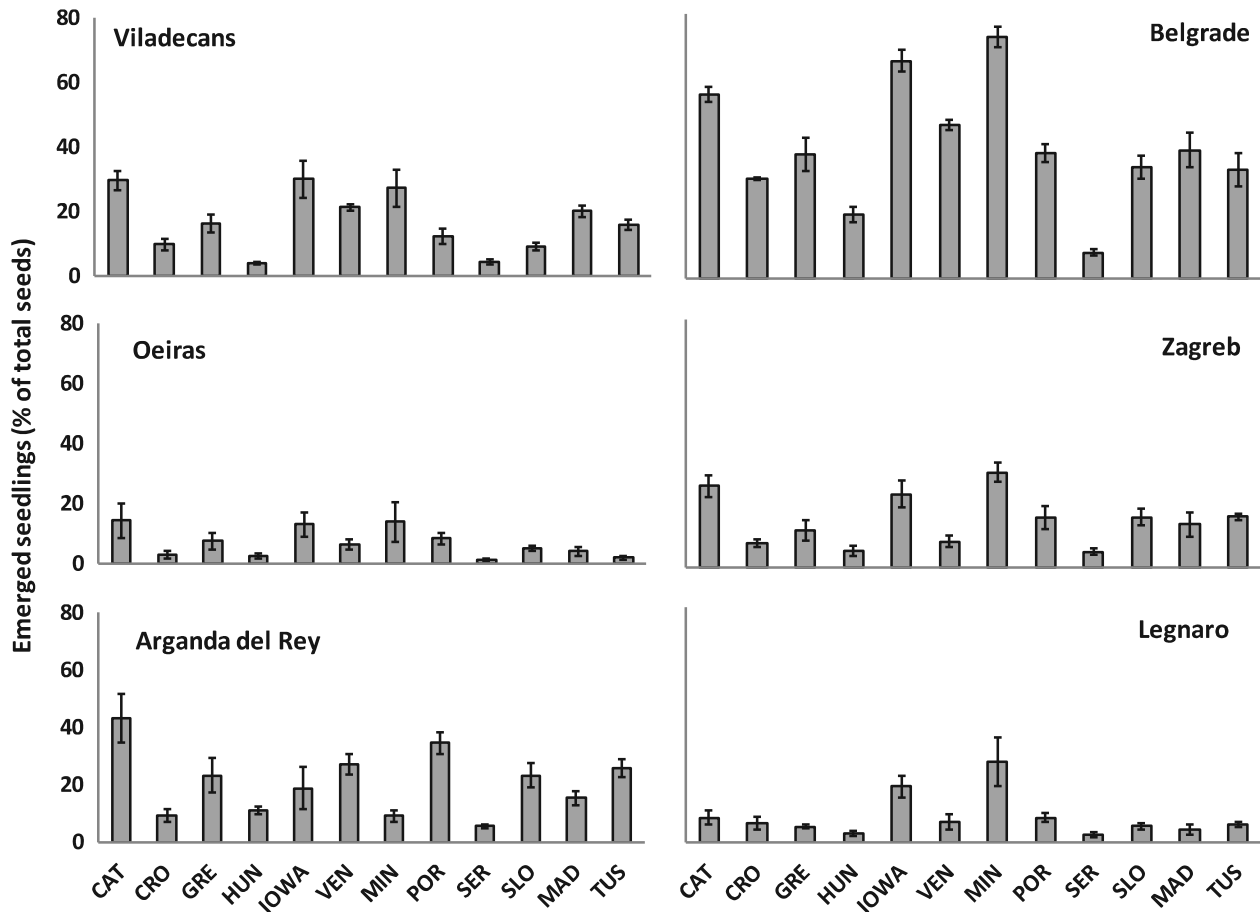


Fig. 4 Percentage of emerged seedlings on the total number of seeds for the different *Abutilon theophrasti* populations at the six experimental sites. Values are means of each population at each experimental site ($n = 4$; d.f. = 288). Vertical bars represent SE.

few degrees of difference in average temperatures can substantially modify the emergence dynamics, considering that in previous laboratory experiments the start and 50% of germination were observed after 5 and 7 days of incubation at 8°C, respectively, while only after 3 and 4 days at 10°C (Loddo, unpubl. obs.). Moreover, the minimum daily air temperature in that period remained close or below 0°C for weeks at the two sites, causing a relevant limitation for seed germination.

In contrast, winter temperatures were reported to not considerably affect physical dormancy of *A. theophrasti* seeds that usually declines rapidly during the first autumn after seed dispersal and then remains stable during the following winter and spring (Cardina & Sparrow, 1997). Environmental conditions during winter months were instead reported to influence seed decay; in particular, Schutte *et al.* (2008) suggested that prolonged exposure to wet soil conditions could increase inner osmotic pressure of *A. theophrasti* seeds and consequently soften and damage the seed coat, facilitating microbial attack. However, previous studies reported an extremely variable

range of overwinter seed decay, from 2% of initial seedbank (Gómez *et al.*, 2014) to 16% or even above 40% (Buhler & Hartzler, 2001; Davis *et al.*, 2006). Different levels of seed decay could therefore be supposed for the various populations at the six experimental sites, according to the interaction of local environmental conditions and seed coat characteristics of each population. However, measuring this process or estimating its impact on seedling emergence was beyond the aim of this study. Precipitation patterns notably influenced the emergence dynamics at the different experimental sites; in particular, the abundance or scarcity of rainfall during May and June determined the prolongation of emergence flushes till early summer. Considering the four sites (Oeiras, Arganda del Rey, Viladecans and Legnaro) where seedling emergence started simultaneously in mid-February, Legnaro had the highest amount of precipitation (approximately 160 mm) from May to June and 20% of total emergence occurred in this period. The Oeiras and Viladecans sites presented a medium-low amount of precipitation (40 and 60 mm, respectively) in the same period and only 10% of total seedlings emerged from

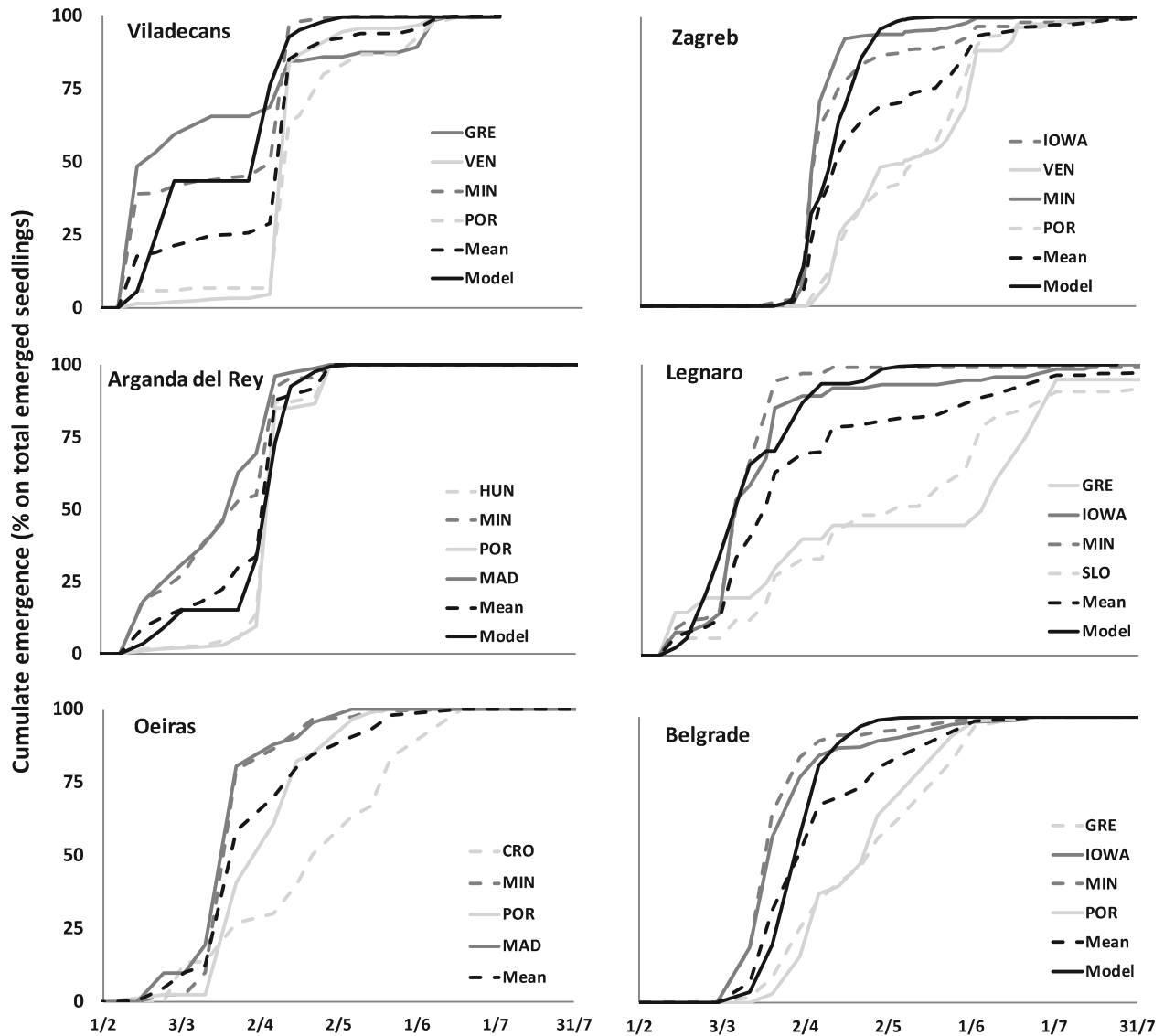


Fig. 5 Cumulative emergence of the different *Abutilon theophrasti* populations (expressed as % of total emerged seedlings for each population) during the main seedling emergence period (1 February–31 July 2014). The two earliest (dark grey lines) and latest emerging (light grey lines) populations for each experimental site are reported. Values are means of three replicates. Mean cumulative emergence dynamics (black dotted lines) estimated considering all the populations and the emergence curves predicted by *AlertInf* model (black continuous lines) are reported.

May to June. Lastly, precipitation was scarce at Arganda del Rey (25 mm in the 2 months), and consequently, no emergence was reported from May onwards. Variability in seedling emergence observed across the six experimental sites could therefore be considered a result of the interaction between local environmental conditions and seed characteristics (dormancy, germinability, seed coat thickness) of the different populations. This interaction could affect the various processes leading to seedling emergence, that is seed decay and persistence, dormancy release, germination and emergence. Comprehensive knowledge on the specific effect of the different environmental factors on seedbank dynamics has not yet been attained for

A. theophrasti. *AlertInf* and some other existing models (Archer *et al.*, 2006) are able to simulate the temporal dynamics of seedling emergence for *A. theophrasti* according to weather trends, while estimating emergence magnitude according to the environmental conditions is still extremely difficult.

Variability among the populations

Regardless of the variability observed across the experimental sites, different behaviours in the emergence patterns could be detected among populations. Since these differences remained consistent across the six sites, their origin could be related to interpopulation

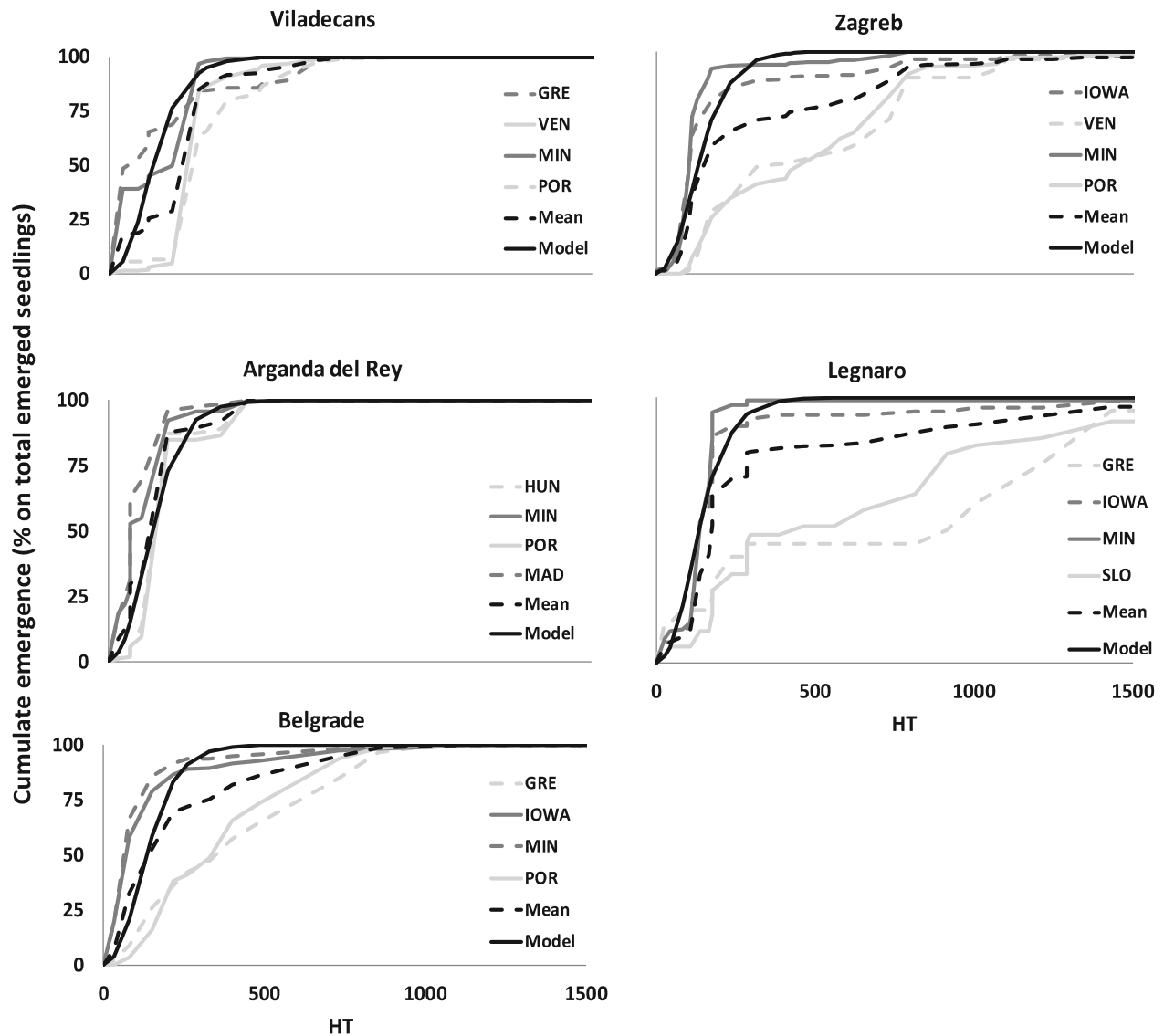


Fig. 6 Cumulative emergence of the different *Abutilon theophrasti* populations (as % of total emerged seedlings for each population) during the main seedling emergence period (1 February–31 July 2014) expressed on the basis of hydrothermal time accumulation (HT) estimated at each experimental site. The two earliest (dark grey lines) and latest emerging (light grey lines) populations for each experimental site are reported. Values are means of three replicates. Mean cumulative emergence dynamics (black dotted lines) estimated considering all the populations and the emergence curves predicted by *AlertInf* model (black continuous lines) are reported.

variability regarding seed dormancy level. Populations from Catalonia, Iowa and Minnesota, which reached higher emergence percentage and presented earlier and more concentrated emergence flushes, probably had a lower dormancy level. An intermediate condition could be supposed for populations coming from Greece, Veneto, Tuscany, Madrid, Portugal and Slovenia that obtained average emergence percentages with later and more prolonged emerge flushes. Lastly, populations from Croatia, Serbia and Hungary probably had a higher level of seed dormancy given their low average emergence percentage. Variability in seed dormancy level and base temperatures for germination among

local populations has already been reported for various weed species (Loddo *et al.*, 2013, 2014; Tozzi *et al.*, 2014). However, similar values of base temperature for germination were detected in several studies for *A. theophrasti* populations coming from different countries, after the removal of seed physical dormancy by chemical or mechanical scarification (Masin *et al.*, 2010a,b; Loddo *et al.*, 2013, 2018). As a consequence, the variability in seed physical dormancy, that is in seed coat characteristics, could be supposed to be responsible for the differences in emergence patterns for the various *A. theophrasti* populations. Differences in seed coat among populations could be related to

1 genetic interpopulation variability as a result of adap-
2 tation processes to local environmental conditions.
3 Populations from Iowa and Minnesota could have a
4 lower level of seed physical dormancy as an adaptation
5 to the local climatic conditions at Morris and Monona,
6 which are significantly colder than the other collection
7 sites, since being able to germinate as soon as soil con-
8 ditions are favourable is an important adaptation to
9 complete the annual life cycle in areas with a short
10 growing season. However, this could hardly be pro-
11 posed as the only explanation for germination beha-
12 viour of the population from Catalonia, since the
13 Lleida collection site climate is classified as warm tem-
14 perate, similarly to many other collection sites. Mater-
15 nal effect, that is environmental conditions during
16 mother plants' growth and seed ripening, is known to
17 strongly affect seed coat characteristics. For example,
18 Cardina and Sparrow (1997) observed that
19 *A. theophrasti* seeds produced by mother plants grown
20 in warmer, drier conditions had a thicker seed coat
21 and higher level of physical dormancy. Nevertheless,
22 this cannot be supposed as the main driving factor for
23 the dormancy variability observed in this study
24 because seeds were mainly collected in irrigated crop
25 fields and mother plants therefore probably did not
26 experience relevant water stress. Moreover, the popula-
27 tions with the highest dormancy levels (i.e. those from
28 Croatia, Serbia and Hungary) were collected in sites
29 with the lowest summer temperatures. The presence of
30 crop competition during mother plant growth was also
31 reported to influence seed coat weight (Nurse &
32 DiTommaso, 2005), but no information regarding this
33 was available for the different collection sites. The
34 interaction of genetic factors and maternal effect could
35 determine year-by-year differences in seed coat charac-
36 teristics, and consequently in seed dormancy level, even
37 for the same population and the same location, as
38 already observed by Schutte *et al.* (2008). It was not
39 possible to quantify with the present study the specific
40 contribution of genetic factors and environmental fac-
41 tors (i.e. the maternal effect) in determining the differ-
42 ent dormancy levels observed for the *A. theophrasti*
43 populations and further experiments are required to
44 adequately address this issue. For example, growing
45 the different populations at the same site, according
46 to the so-called 'common garden' experimental methodol-
47 ogy (Loddo *et al.*, 2014), would make the maternal
48 environment uniform, consequently the effect of
49 genetic factors on dormancy level of seeds produced
50 by the different populations could be adequately evalu-
51 ated. Improving our knowledge of these processes is
52 important within a control perspective. Populations
53 with early and concentrated flushes of seedling emer-
54 gence can generate strong competition with crops, but

at the same time several control tools can be effective,
such as false or stale seedbed, pre-emergence or post-
emergence herbicides. In contrast, populations with
late and prolonged emergence flushes would reason-
ably be less competitive against crops. However, some
of the late-emerging seedlings can escape control tools
that are applied before their emergence and go on to
produce significant seed rain. In similar situations,
postponing control operations and switching from pre-
emergence to post-emergence herbicide application
could be necessary. Moreover, populations with low
dormancy level can present large and problematic seed-
ling emergence in the first 1–2 years after dispersal but
their seedbank persistence is consequently limited. If
control strategies succeed in killing emerged seedlings
and avoiding further dissemination, seedbank depletion
will occur in a few years. Instead, populations with
dormant seeds do not have large seedling emergence in
the first years after dissemination, so competition with
crops will probably be lower but seedbank persistence
longer and its depletion difficult. Acquiring better
knowledge of the different aspects and effects of inter-
population variability could therefore allow more
specific and efficient control strategies to be designed,
facilitating the replacement of solely herbicide-based
management with true IWM strategies involving alter-
native and complementary tools and tactics. This is a
key component of the present evolution in weed man-
agement for addressing the societal challenge both to
increase food production and to reduce the environ-
mental impact of agriculture (Liebman *et al.*, 2016).

Finally, rather encouraging indications emerged
from the test of the *AlertInf* model. Good predictive
accuracy of the emergence dynamics of the different
populations was obtained at Arganda del Rey and Bel-
grade, where higher emergence percentage and more
concentrated emergence flushes were observed for all
populations. However, the *AlertInf* model was not able
to accurately simulate emergence dynamics of late-
emerging populations, especially in the case of low
emergence percentage, and this caused the contrasting
results obtained for the different populations at Leg-
naro, with very good accuracy for the early-emerging
IOWA and MIN and marked overestimation instead
of the two late-emerging GRE and SLO. This situation
could probably be due to the fact that *AlertInf* model
was developed, calibrated and validated under arable
field conditions, where soil tillage for seedbed prepara-
tion tends to stimulate *A. theophrasti* seed germination
producing concentrated seedling emergence flushes.
However, achieving good predictive accuracy is gener-
ally difficult in the case of populations with low emer-
gence percentage, such as GRE and SLO at Legnaro,
because their emergence curves are usually irregular

due to the limited number of observations of emerged seedlings. The possibility of adopting the *AlertInf* model across a quite wide range of environmental conditions and *A. theophrasti* populations can be therefore supposed. Nevertheless, further experiments are necessary to calibrate the parameters of its equations according to the intra-specific variability of seed dormancy.

Acknowledgements

This study was supported by Padova University Research Project CPDAI44499: 'Mitigazione della contaminazione da erbicidi delle acque superficiali in agricoltura conservativa con la combinazione di misure in-field e edge-of-field'. The authors are grateful to Alison Garside for revising the English text.

References

- ANDERSSON L & MILBERG P (1998) Variation in seed dormancy among mother plants, populations and years of seed collection. *Seed Science Research* **8**, 29–38.
- ARCHER DW, FORCELLA F, KORTH A, KUHN A, EKLUND J & SPOKAS K (2006) WeedCast version 4.0. Available at: <http://www.ars.usda.gov>
- BATES D, MAECHLER M, BOLKER B & WALKER S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- BERTI A, SATTIN M, BAALDONI G *et al.* (2008) Relationships between crop yield and weed time of emergence/removal: modelling and parameter stability across environments. *Weed Research* **48**, 378–388.
- BUHLER DD & HARTZLER RG (2001) Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. *Weed Science* **49**, 230–235.
- CARDINA J & SPARROW DH (1997) Temporal changes in velvetleaf (*Abutilon theophrasti*) seed dormancy. *Weed Science* **45**, 61–66.
- DAVIS AS, ANDERSON KI, HALLETT SG & RENNER KA (2006) Weed seed mortality in soils with contrasting agricultural management histories. *Weed Science* **54**, 291–297.
- DORADO J, SOUSA E, CAHLA IM, GONZALEZ-ANDUJAR JM & FERNÁNDEZ-QUINTANILLA C (2009a) Predicting weed emergence in maize crops under two contrasting climatic conditions. *Weed Research* **49**, 251–260.
- DORADO J, FERNÁNDEZ-QUINTANILLA C & GRUNDY AC (2009b) Germination patterns in naturally chilled and nonchilled seeds of fierce thornapple (*Datura ferox*) and velvetleaf (*Abutilon theophrasti*). *Weed Science* **57**, 155–162.
- ESLAMI SV (2011) Comparative germination and emergence ecology of two populations of common lambsquarters (*Chenopodium album*) from Iran and Denmark. *Weed Science* **59**, 90–97.
- GARDARIN A, DÜRR C, MANNINO MR, BUSSET H & COLBACH N (2010) Seed mortality in the soil is related to seed coat thickness. *Seed Science Research* **20**, 243–256.
- GESCH RW, ROYO-ESNAL A, EDO-TENA E, RECASENS J, ISBELL TA & FORCELLA F (2016) Growth environment but not seed position on the parent plant affect seed germination of two *Thlaspi arvense* L. populations. *Industrial Crops and Products* **84**, 241–247.
- GÓMEZ R, LIEBMAN M & MUNKVOLD G (2014) Weed seed decay in conventional and diversified cropping systems. *Weed Research* **54**, 13–25.
- GUMMERSON RJ (1986) The effect of constant temperatures and osmotic potential on the germination of sugar beet. *Journal of Experimental Botany* **41**, 1431–1439.
- HARTIG F (2016) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1.0.
- KARLSSON LM, TAMADO T & MILBERG P (2008) Inter-species comparison of seed dormancy and germination of six annual Asteraceae weeds in an ecological context. *Seed Science Research* **18**, 35–45.
- KOTTEK M, GRIESER J, BECK C, RUDOLF B & RUBEL F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* **15**, 259–263.
- LENTH RV (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software* **69**, 1–33.
- LIEBMAN M, MILLER ZJ, WILLIAMS CL *et al.* (2014) Fates of *Setaria faberi* and *Abutilon theophrasti* seeds in three crop rotation systems. *Weed Research* **54**, 293–306.
- LIEBMAN M, BARAIBAR B, BUCKLEY Y *et al.* (2016) Ecologically sustainable weed management: how do we get from proof-of- concept to adoption? *Ecological Applications* **26**, p1352–p1369.
- LOAGUE K & GREEN RE (1991) Statistical and graphical methods for evaluating solute transport models: overview and application. *Journal of Contaminant Hydrology* **7**, 51–73.
- LODDO D, SOUSA E, MASIN R *et al.* (2013) Estimation and comparison of base temperatures for germination of European populations of velvetleaf (*Abutilon theophrasti*) and jimsonweed (*Datura stramonium*). *Weed Science* **61**, 443–451.
- LODDO D, SOUSA E, MASIN R *et al.* (2014) Germination response of local Southern European populations of *Datura stramonium* at a range of constant temperatures. *Weed Research* **54**, 356–365.
- LODDO D, GHADERI-FAR F, RASTEGAR Z & MASIN R (2018) Base temperatures for germination of selected Iranian weed species. *Plant Protection Science* **54**, 60–66.
- MASIN R, LODDO D, BENVENUTI S, ZUIN MC, MACCHIA M & ZANIN G (2010a) Temperature and water potential as parameters for modeling weed emergence in Central-Northern Italy. *Weed Science* **58**, 216–222.
- MASIN R, CACCIATORI G, ZUIN MC & ZANIN G (2010b) AlertInf: an emergence predictive model for weed control in maize in Veneto. *Italian Journal of Agrometeorology* **15**, 5–9.
- MASIN R, LODDO D, BENVENUTI S, OTTO S & ZANIN G (2012) Modeling weed emergence in Italian maize fields. *Weed Science* **60**, 254–259.
- MASIN R, LODDO D, GASPARINI V, OTTO S & ZANIN G (2014) Evaluation of weed emergence model AlertInf for maize in soybean. *Weed Science* **62**, 360–369.

- 1 NURSE RE & DiTOMMASO A (2005) Corn competition alters
 2 the germinability of velvetleaf (*Abutilon theophrasti*) seeds.
 3 *Weed Science* **53**, 479–488.
- 4 RECASENS J, CALVET V, CIRUJEDA A & CONESA JA (2005)
 5 Phenological and demographic behaviour of an exotic
 6 invasive weed in agroecosystems. *Biological Invasions* **7**,
 7 17–27.
- 8 SCHUTTE BJ, DAVIS AS, RENNER KA & CARDINA J (2008)
 9 Maternal and burial environment effects on seed mortality
 10 of velvetleaf (*Abutilon theophrasti*) and giant foxtail
 11 (*Setaria faberi*). *Weed Science* **56**, 834–840.
- 12 TOZZI E, BECKIE H, WEISS R *et al.* (2014) Seed germination
 13 response to temperature for a range of international
 14 populations of *Conyza canadensis*. *Weed Research* **54**, 178–185.
- 15 VRBNICANIN S, ONC-JOVANOVIC E, BOZIC D *et al.* (2017)
 16 Velvetleaf (*Abutilon theophrasti* Medik.) productivity in
 17 competitive conditions. *Archives of Biological Sciences* **69**,
 18 157–166.
- 19 WALLACH D (2006) Evaluating crop models. In: *Working with*
 20 *Dynamic Crop Models: Evaluation, Analysis,*
 21 *Parameterization, and Applications* (eds D WALLACH, D

- 22 MAKOWSKI & JW JONES), 11–54. Elsevier, Amsterdam, the
 23 Netherlands.
- 24 WILLMOTT CJ (1982) Some comments on the evaluation of
 25 model performance. *Bulletin of the American*
 26 *Meteorological Society* **63**, 1309–1313.

Supporting Information

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

Appendix S1. Seed weight of the different *Abutilon theophrasti* populations

Appendix S2. Emergence dynamics of all *Abutilon theophrasti* populations

Appendix S3. Assessment of *AlertInf* performance at the different sites by a comparison of the predicted emergence curves with the observed mean emergence curves of the different populations