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Long-day-dependent segetal species threatened by climate change

Henri Darmency[a,*], Solène Bellanger[a], Annick Matejicek[a], Jean-Philippe Guillemin[b]

[a] INRA, UMR1347 Agroécologie, 17 rue Sully, BP86510, 21065, Dijon, France
[b] AgroSup Dijon, UMR1347 Agroécologie, 26 Dr Petitjean, BP87999, 21079, Dijon, France

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ABSTRACT

Cornflower (*Cyanus segetum*), an iconic weed species, was used to investigate the implications of climate change on the behavior of long day dependent species while earlier cereal harvest may prematurely end the period of flowering and seed production in weeds. Variability in flowering, with or without vernalization, of European *C. segetum* populations situated along a 45–55° North latitudinal gradient was studied. Long day requirement was confirmed. Vernalization requirements are not stringent in *C. segetum*—the proportion of plants that were not sensitive or that responded strictly or weakly to vernalization varied across populations. The mean sum of growing degree days (GDD) for first flowering under a 14 h day length at 15 °C was 1344 and 2072, with and without vernalization, respectively, whatever the population. A growth temperature at 25 °C had no effect on GDD except for a population from mountains. Advancing the date of harvest by ten days in a field experiment resulted in one-third fewer seeds produced, which could accelerate its decline, but polymorphism for vernalization and temperature responses could allow adaption.

1. Introduction

Increased temperature induced by climate change (Lobell et al., 2011) can impact global biodiversity through phenological shift (Fitter and Fitter, 2002; Forrest and Miller-Rushing, 2010). Ultimately, phenological shifts can mean a mismatch between habitat niche and species development, generating a risk of local or global extinction for some species (Thomas et al., 2004; Franks et al., 2014). Weeds associated with agricultural crops also are affected by climate change because land use and management practices are changing due to climatic changes, and also because of their own biology response (see review in Peters et al., 2014). Basically, their life cycle is constrained by the timing of crop sowing and harvesting. In particular, segetal weeds are of great concern because they are arable-land-dependent and adapted to the winter cereal life cycle. Some are close to extinction in Europe because of agricultural intensification (Storkey et al., 2012). Among them, cornflower, *Cyanus segetum* Hill (previously *Centaurea cyanus* L.), is an iconic segetal species associated with winter crops (cereals and oilseed rape) throughout Europe. In most regions of the western oceanic-sea borders of Europe it is only found in arable fields while waste places and wild plant communities are not known to be refugees for *C. segetum* (Hübl et al., 1996). There, it suffers dramatic reduction of frequency and abundance (Tranchard, 1993; Bellanger et al., 2012), and even it is listed as endangered in the United Kingdom (Wilson, 2007).

Timing of flowering in *C. segetum* is determined by day length (Thomas and Vince-Prue, 1997), which should mean that it will flower around the same time each year irrespective of temperature, unlike other species that flower in response to a cumulative temperature threshold. However, crops are also affected by climate change, mainly because higher temperatures advance crop phenology (Craufurd and Wheeler, 2009). For instance, over the past few decades, heading and harvest dates of wheat have already shifted four days earlier in Germany (Estrella et al., 2007) and an average of a week earlier in several regions in France (Gouache et al., 2012) and the Czech Republic (Mozny et al., 2012). This trend will likely continue as global temperatures continue to increase. In addition, heat stress during the terminal stage of grain maturation will likely lead breeders to select for varieties that escape the warmest part of the season, which would make the harvest time even earlier. As a consequence, instead of shifting to an earlier flowering period as climate warms, species like *C. segetum* would have a shorter flowering time.

Photoperiod sensitivity as moderating the plant response was not studied as extensively as the other factors (Craufurd and Wheeler, 2009). It is not known how dramatically early harvest of winter cereals and winter oilseed rape crops shorten the *C. segetum*

* Corresponding author.
E-mail address: henri.darmency@dijon.inra.fr (H. Darmency).

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reproduction period and how likely biological resources or mechanisms could offset deleterious effects. For that purpose, we investigated variability in flowering among several European populations that originated along a latitudinal gradient. Since vernalization response of species could be involved in moderating the response to climate change (Cook et al., 2012; Van Dijk and Hautekeete, 2014), we also looked at the vernalizing effect of low temperatures. The maturation kinetics of local *C. segetum* was studied in the field.

2. Materials and methods

2.1. Photoperiod regime

A local Burgundy (Dijon) field population was used for preliminary experiments. Seeds were sorted from the harvest of an organic oilseed rape on July 2008. In August 2008, several seeds were sown directly on soil surface of individual pots (28 pots, 8 × 8 cm) filled with a peat–sand mixture at 0.5 cm depth. After thinning, only one seedling was left per pot. Pots were placed in one of two growth cabinets with a 10 or 14 h daylight regime (450 μmol photon m^{-2} s^{-1} photosynthetic active light intensity), at alternating 18 °C night-25 °C day temperature and with sub-irrigation. Nutritive solution was provided every two weeks (N-P-K: 10-10-10 + oligo-elements). The number of days from emergence to the first open ray floret was scored for every plant, and then converted to the sum of growing degree days (GDD) using 1 °C as the base temperature (1.1 ± 0.7 °C for that population, unpublished result of J.-P. Guillemin).

To assess the diversity among populations, six other populations collected in winter crop fields (winter wheat or winter oilseed rape) from Spain to Lithuania (from 40 to 55° North, Table 1) were used to represent the range of latitudinal distribution of *C. segetum* in Europe. Unfortunately, the southern (Spanish) population was discarded because of poor germination. The growth conditions were the same as above except that only the 14 h light regime was used and pots were left for four days at alternating temperatures to stimulate rapid germination before transfer to one of two growth cabinets at 15 or 25 °C constant temperature (there were a total of 48 pots from each population, one plant each pot, and 24 were randomly assigned to each cabinet). The experiment started on December 2008 and ended six months later. It was replicated at 15 °C in December 2009, except on the 55th day the temperature was decreased to 4 °C for three weeks in the growth cabinet to initiate vernalization.

The 14 h light regime was chosen to ensure that the days would be long enough for southern populations. Only 110 days have a 14 h photoperiod in the most southern location used in our study (Gap, France, 44°55′)—from May to mid-August. The most northern location (Lithuania, 55°16′) has a 14 h photoperiod for more than 140 days.

2.2. Reproduction in the field

Seeds from the local population (Dijon) were sown in 0.5 cm of soil in the field on the INRA farm near Dijon in fall 2009, just after winter mustard and winter wheat sowing. Seedlings emerged one month later. Flowering began in the beginning of May. Thereafter, flowering was continuous: secondary branches containing leaves and a terminal flower head are produced at every stem/leaf angle of the main axis, and so on for successive branching orders. Time from closure of flower heads to maturity (spontaneous opening and seed shedding) was recorded for five plants. Thirty plants were harvested ten days before the harvest date of each crop in July (20/07): the plants were cut and the number of flower heads counted, separating ripe heads from those that were still with flowering disc florets and not yet closed inside bracteas. Outside temperatures were recorded from the local INRA climatic station.

2.3. Data analysis

ANOVA of GDD was performed separately for the three temperature conditions because variances differed so widely (Levene test always significant). GDD were fitted to linear regression by latitude. *T*-tests were used to compare results among different temperature conditions. All analyses were conducted using Systat 10.2 software.

3. Results

3.1. Preliminary experiment

Mean flowering time for the local population (Dijon) under the 14 h day-length regime was 77 ± 2 days (1632 ± 45 GDD). However, we observed two germination peaks: the first at 68 days (1414 GDD) and the second at 86 days (1819 GDD). Two plants did not flower at all during the period. Under the 10 h day-length regime, two plants flowered after three months but no other plants flowered before the end of the four-month experiment.

3.2. Experiments with vernalization

94.4% of plants flowered during the experiment (101 plants in total from the six populations). The average number of days from emergence to when the first floret opened was 113 ± 1 (92 days at 15 °C and 21 at 4 °C). The sum of GDD was 1334 ± 18. Populations differed in GDD ($F_{5,94}$ = 32.6, P < 0.001), with the Dijon population having the lowest (Table 1). There was no trend associated with latitude ($F_{1,98}$ = 1.4, P = 0.23).

3.3. Experiments without vernalization under the 14 h day regime

The percentage of flowering plants within the time frame of the experiment was 84.4% without vernalization (229 plants in total). The population from Gran Paradiso had fewer than the average

Table 1
Origins of the *C. segetum* populations (all from winter crop fields) with WGS84 latitude North international coordinates, the proportion of flowering plants and mean GDD (growing degree days) for flowering time (±SEM) under a 14 h photoperiod. Letters in a column indicate that the values are not different at P < 0.05. P diff 15/25 is the probability value of the t-test of difference between GDD to flower for 15 and 25 °C conditions without vernalization.

Code	Location	Latitude	Percent flowering plants			Mean GDD to flower			
			15 °C + vernaliz.	15 °C	25 °C	15 °C + vernaliz.	15 °C	25 °C	P diff. 15/25
Y07/808	Gap (France)	44°55	100	100	87.5	1332 ± 20ab	1944 ± 51bc	1882 ± 118b	0.64
Y06/078	Gran Paradiso (Italy)	45°58	100	50	69.6	1519 ± 35a	2044 ± 102bc	2642 ± 164a	0.005
Y07/811	Dijon (France)	47°48	94.7	91.3	100	1127 ± 23c	1874 ± 38c	1825 ± 90b	0.63
Y07/813	Troyes (France)	48°22	91.3	91.3	95	1266 ± 13b	2143 ± 42ab	2055 ± 113b	0.47
Y07/828	Krakow (Poland)	50°07	100	70.5	100	1312 ± 21b	2140 ± 63ab	2280 ± 164ab	0.43
Y07/816	Seta (Lithuania)	55°26	95.6	43.8	100	1446 ± 21a	2286 ± 53a	2118 ± 125b	0.23