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Clonal variation in floral stage timing in the common dandelion *Taraxacum officinale* (Asteraceae)[1]

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We investigated the hypothesis that dandelion clones (*Taraxacum officinale* Weber, sensu lato; Asteraceae) differ in their floral stage timing characteristics under a constant set of environmental conditions. To test this hypothesis, plants representing nine different dandelion clones (identified by DNA fingerprinting) were grown in groups of five ($N = 45$) in a growth chamber for a period of 8 mo, with chamber settings similar to environmental conditions at peak dandelion flowering time for their population sites. Five flowering phenology parameters were monitored daily for a total of 301 buds developing during this time: (1) time to bud; (2) time to full opening and inflorescence maturation (i.e., first anthesis); (3) time to re-closure of an inflorescence; (4) time to fruit (full re-opening of the inflorescence); and (5) total flowering time. Scape length at the appearance of a fully expanded infructescence was also measured for each individual. Significant differences in mean time to inflorescence, mean time to re-closure, mean time to fruit, and mean total flowering time were revealed among some dandelion clones (Kruskal-Wallis, $P \leq 0.0005$). No differences in mean number of inflorescence buds per plant ($P = 0.2217$), mean time to bud ($P = 0.2396$), or mean scape length ($P = 0.3688$) were detected among the nine clones. These results suggest that differences in floral stage timing may in part involve varying genotypic environmental response characteristics and that these differences may have potential fitness effects. Further research is needed to determine if such clonal differences are observed under a broader range of uniform environmental conditions.

Key words: agamospermy; Asteraceae; DNA fingerprinting; flowering phenology; genetic variation; reproductive fitness; *Taraxacum officinale*.

Flowering phenology is a developmental process crucial to determining plant reproductive success. The divergence of flowering times among species and populations can have important evolutionary consequences (e.g., reduction of interspecific pollination; McNeilly and Antonovics, 1968; Waser, 1978). Variation in degree of flowering asynchrony within populations and consequent fitness effects have also been shown in a number of circumstances. For example, the timing of flowering with respect to conspecific neighboring plants can potentially affect the seed set of individual flowers (Thomson, 1985; Allen, 1986), total plant seed production (Primack, 1980; Schmitt, 1983), seed quality (Marquis, 1988), timing of seed dispersal (Lacey and Pace, 1983), and risk of seed predation (Collinge and Louda, 1989). Flowering asynchrony within populations may also act to reduce intraspecific competition for pollinators and promote outcrossing (Rathcke and Lacey, 1985; Pors and Werner, 1989; Rogstad, 1994).

Although differences in flowering phenology have been widely studied (e.g., Allen, 1986; Clark and Clark, 1987; Marquis, 1988), little is known about the causes behind this variation, especially in natural populations. Previous studies suggest that some of the variation in flowering stage timing in plants is due to differing genotypic responses to the same environmental stimuli (e.g., Pigliucci et al., 1995; Van Dijk et al., 1997; Hauser and Weidema, 2000), while others suggest such variation is largely due to phenotypic plasticity (Dieringer, 1991; Craufurd et al., 1999). Differing genotypic responses in flowering patterns to the same environmental stimuli imply ''hardwired'' genetic differences in flowering phenology responses among different genotypes (with different genotypes perhaps possessing different flower timing regulating genes; see Peeters and Koornneef, 1996; Simpson and Dean, 2002). In contrast, variation due to phenotypic plasticity suggests that differences are primarily due to plastic responses to varying micro-environmental conditions (e.g., Simpson and Dean, 2002). In this study we primarily address the first of these two possibilities and, for brevity, refer to the premise that variation in floral stage phenology is due to differing responses of different genotypes as the ''varying genotypic'' response, and to the premise that variation in flowering phenology characteristics is largely due to environmentally induced phenotypic plasticity as the ''phenotypic plastic'' response.

Here, we investigate potential variation in flowering phenology characteristics in the common North American dandelion (*Taraxacum officinale* Weber; Asteraceae). These common perennial plants most likely originated in west central Asia during the early Cretaceous before being dispersed to the northern and temperate regions of Europe during the Tertiary (Richards, 1973; King, 1993), and again to North America with post-Columbian settlement (Solbrig, 1971). Today, European dandelion assemblages consist of mixed sexual (diploid) and asexual (triploid) plants which are known to comprise >2000 ''microspecies,'' while North American *T. officinale* (sensu lato) populations consist entirely of reproduc-

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tively isolated triploid clonal lineages that reproduce exclusively by the asexual process of agamospermy (King, 1993; Lyman and Ellstrand, 1998; Rogstad et al., 2003). As a part of the process of agamospermy in dandelions, meiosis is bypassed and instead a certain maternal diploid cell becomes the first cell of a developing dandelion embryo (Richards, 1973; Kirschner and Stepanek, 1994; Gornall, 1999). Therefore, the progeny of apomictic dandelions are genetically identical, barring mutation (Rogstad et al., 2001a, b, 2003), to their ''maternal'' dandelion plants. The fact that North American dandelions reproduce in the above manner and that different clonal lineages are therefore easily identifiable using DNA fingerprinting (see Rogstad et al., 2001a, b), provides a model opportunity to investigate clonal genotypic variation in flowering phenology.

In our previous studies, noticeable differences in flowering phenology among several dandelion clones were observed (specifically in the timing of different floral stages; see Collier [2003]), raising the question: what causes such variation? On one extreme, it is possible that clonal variation in flowering time in dandelions may be attributable to differing genotypic responses among clones (varying genotypic response). On the other extreme, it is possible that phenotypic plasticity responses affected by environmental factors (e.g., nutrients, water, temperature, light) may have substantial consequences on floral timing stage variability (phenotypic plastic response). To examine aspects of these possibilities, replicate clones representing multiple dandelion clonal lineages were grown in a growth chamber under identical, controlled environmental conditions. If variation in flowering time among clones was detected, this would imply that there are varying genotypic responses in flowering phenology among different North American clonal lineages, at least under one set of environmental conditions. If no statistically significant variation in flowering time characteristics was revealed, this would suggest that differences seen in flowering phenology in dandelions under more complex circumstances might be influenced by something other than varying genotypic responses among clones (e.g., photoperiod, temperature, etc.; see Listowski and Jackowska, 1965; Gray et al., 1973) or that flowering phenology characteristics within clonal lineages are so variable/random that no overall differences between clones were detectable.

Several studies have examined various aspects of the flowering cycle in dandelions, including the general rhythm of flowering (Listowski and Jackowska, 1965), seasonal variation in flowering (Gray et al., 1973), environmental factors controlling inflorescence (head or capitulum) opening and closing (Tanaka et al., 1987) and seed reproduction (Roberts, 1936). However, none of these studies has examined whether there are clonal/genetic differences in the timing of the different stages of the flowering cycle. Using DNA fingerprinting, we were able to identify and grow clonal replicates of different dandelion clones under a single set of controlled environmental conditions, and monitor the timing of the different stages of their flowering cycles. We investigated the hypotheses that North American dandelion clones differ in their flowering phenology characteristics when grown under constant environmental conditions.

METHODS AND MATERIALS

Field sampling—Leaf tissue and seeds were randomly collected from 26–40 dandelion individuals at two different sites in Hamilton County, Ohio, USA (site 1 = 39°9′ N and 84°27′ W; site 2 = 39°15′ N and 84°15′ W). Leaves and seeds from each individual plant were harvested and sealed in separate marked plastic bags, labeled, placed on ice and transported to the laboratory where they were stored (seeds at 4°C, leaves at −70°C) until utilized.

Determination of dandelion clones by DNA fingerprinting—The different dandelion clones used in this study were determined by DNA fingerprinting using synthetic tandem repeat (STR) probes (Rogstad, 1993, 1996; Rogstad et al., 2001b) generated with the polymerase chain reaction (PCR). PCR-STR probes were used for dandelion clone analysis as previous studies have demonstrated that extensive DNA variation among clones can be revealed in *T. officinale* with tandem repeat loci probes (van Heusden et al., 1991; Rogstad et al., 2001b). Two PCR-STR probes (TTCCA and CACTCC) were used to examine genetic variation among 64 dandelion plants, 32 from each site. Dandelion individuals with identical genetic profiles (i.e., individuals that share all of their population bands) were classified as being the same clone. For details concerning the DNA fingerprinting methods used, see Rogstad et al. (2001b) and Collier (2003).

Experimental design—Seeds from nine different dandelion clones determined by DNA fingerprinting analysis (see Results below) were germinated on Whatman paper moistened with distilled H_2O. After 2 wk of growth, five seedlings from each of the nine clones were planted individually in 8.5 ×10.5 cm (diameter × height) plastic cups containing research grade sand (100% quartz). Plants were chosen for planting on the basis of similarity in stage of development (e.g., same number of leaves, approximately the same size). Five cups, each containing individual seedlings of the same dandelion clone, were then placed in 34.5 × 21.6 × 10.6 cm plastic tubs filled with 800 mL of a 50% Hoagland's nutrient solution (pH ≈ 5.9). Holes were drilled into the bottom and sides of the plastic cups to allow for drainage.

Nine plastic tubs (one for each clone), each containing five cups with a single dandelion plant (45 total plants) were placed in a greenhouse for a period of 3 mo (18 April–18 July 2001). Mean daily temperature was approximately 30.1°C during this period. Plants were watered with 20–25 mL of the standing nutrient solution at least once per day. All tubs were monitored daily, replenished with distilled H_2O to 800 mL when necessary, and rotated every 3–4 d to account for environmental differences in the greenhouse. Tub solutions were replaced weekly to prevent algal growth and maintain proper solute concentrations. No plants flowered while in the greenhouse.

After 3 mo, all tubs were moved to a growth chamber and subjected to an 8 h light (full incandescent and fluorescent lighting, 23°C, 55% humidity) and 16 h dark (no lights, 10°C, 60% humidity) cycle. Growth chamber photoperiod settings correlate with peak flowering time (ca. 15 March) conditions for these dandelions at the collection sites (S. Rogstad, personal observation). Dandelions are considered short-day plants and typically do not bloom in large numbers when there are more than 12 h of light. Therefore, in the midwestern United States, dandelions flower profusely from March through April and then again from late August through October (Solbrig, 1971). Preliminary studies also demonstrated that these growth chamber conditions induced flowering in dandelions, in comparison to plants grown in the greenhouse, which flowered 32 d later (Collier, 2003). Plants in the growth chamber were maintained as described above.

Observation of dandelion floral stages—The flowering cycles of all plants were monitored daily from July 2001 through February 2002 (243 d). Individual floral stages (described below) were monitored in the same way for every observation made of the 301 buds produced. Dandelions were checked at least twice a day at approximately the same time (09:00 and 14:00) because plants were observed to progress between floral stages (described below) within the same day in preliminary trials (e.g., inflorescences were shown to close within the same day, buds appeared over the period of a day; M. Collier, personal observation). Plants progressing between floral stages after 14:00 were not recorded as doing so until the following morning (09:00). Therefore, the observation of the transition to different individual floral stages was never off by more than a single day. Transitions of all stages to the next were observed to occur within a 24 h period. We note that dandelions flowered in

the growth chamber even when natural dandelion populations were dormant (November–February), and thus conclude they were not influenced markedly by external conditions.

Initiation of the flowering process was first detectable with the development of the inflorescence bud in the center of a basal rosette of leaves. This first flowering stage, hereafter termed ''TIME TO BUD,'' was observed as the number of days from insertion into the growth chamber until bud appearance. Bud appearance was recorded when a segment of the bud approximately 5 mm in size could be seen crowning in the center of the basal rosette of leaves (buds developed from the stem to this size over 24 h). All buds were marked at first emergence so they could be identified when monitoring later floral stages.

After the formation of the bud, a leafless hollow shoot (scape) begins to elongate at the base of the solitary developing inflorescence. As the scape elongates, the developing inflorescence is forced upwards, eventually opening into a head or capitulum. The head includes numerous closely packed yellow flowers (there is no distinction between disc and ray flowers; all are ligulate and bisexual) borne on a flattened axis and subtended by two rows of glabrous green bracts (phyllaries), collectively called an involucre (Weber, 1990). The larger inner bracts of the involucre typically remain erect while the smaller outer bracts become reflexed, a character we used to ensure proper identification (Weber, 1990). This second floral stage, hereafter termed ''TIME TO INFLORESCENCE'' (i.e., anthesis), was observed as the number of days from bud appearance until the appearance of a completely expanded inflorescence. The presence of a completely expanded inflorescence was recorded when the outer row of bracts surrounding the head was completely reflexed.

A few days after the appearance of the expanded head, the inner whorl of once reflexed bracts vertically contract as the inflorescence re-closes. This third floral stage, hereafter referred to as ''TIME TO RE-CLOSURE,'' was observed as the number of days from the appearance of a fully expanded head until complete re-closure of the inflorescence.

After a few to several more days, the bracts encasing the re-closed inflorescence reflex to reveal a ''white ball'' (Solbrig, 1971) of fruit (a fully expanded infructescence). This fourth floral stage, hereafter termed ''TIME TO FRUIT,'' was observed as the number of days from re-closure of an inflorescence to the appearance of a fully expanded, mature infructescence. An expanded infructescence was recorded when the bracts surrounding the fruiting head were again completely reflexed (with the tips of the bracts usually touching the scape) and a globose ''ball'' of fruit was present. After fruit had matured, dandelion scapes were severed at the base (as close to the stem as possible) and then measured to the base of the fully expanded infructescence (hereafter referred to as ''SCAPE LENGTH''). TOTAL FLOWERING TIME was also recorded as the number of days from TIME TO BUD to TIME TO FRUIT.

Statistical analyses—*Kruskal-Wallis*—All statistical analyses were performed using SYSTAT 6.0 for Windows. Differences in TIME TO BUD, TIME TO INFLORESCENCE, TIME TO RE-CLOSURE, TIME TO FRUIT, TOTAL FLOWERING TIME, SCAPE LENGTH, and TOTAL NUMBER OF INFLORESCENCE BUDS produced were compared among clones using non-parametric Kruskal-Wallis analysis due to the non-continuous nature of our data. All tests were deemed significant if $P \leq 0.05$. In several of the analyses, SYSTAT identified outliers, all of which are included in all of the analyses presented here.

Regression analysis—Simple regression analysis was performed to examine the relationship between the number of inflorescence buds produced by each plant and TOTAL FLOWERING TIME. Regression results were considered significant if $P \leq 0.05$.

Multidimensional scaling analysis—Multidimensional analysis (MDS) was used to explore interrelationships in flowering time among clones. Specifically, this test was performed to determine if different clones clustered together in multivariate space due to similarities in phenology of flowering stages (clonal mean values were used).

RESULTS

DNA fingerprinting analysis—A total of 15 different clones were identified from the 52 plants surveyed using the methods of Rogstad et al. (2001b). Nine of the 15 total clones were randomly chosen to be utilized in this study.

Number of inflorescence buds—No significant difference in the TOTAL NUMBER OF INFLORESCENCE BUDS produced by each of the nine clones was detected ($N = 301$, $P = 0.2217$; Table 1). Clone 5 produced the most total inflorescence buds ($N = 41$) and had the greatest mean number of inflorescence buds per plant (mean = 8.2, 1 SE = 0.38), while clone 1 produced the fewest total inflorescence buds ($N = 25$) and had the fewest mean number of inflorescence buds per plant (mean = 5.0, 1 SE = 0.35).

Flowering cycle among clones—Clones exhibited differences (Kruskal-Wallis) in floral timing for each of the following stages: mean TIME TO INFLORESCENCE, mean TIME TO RE-CLOSURE, mean TIME TO FRUIT, and mean TOTAL FLOWERING TIME (in all cases, $N = 301$ and $P \leq 0.0005$; see Table 1). Mean TIME TO INFLORESCENCE ranged from 12.46 d (1 SE = 0.09; clone 8) to 18.93 d (1 SE = 0.18; clone 9), for a maximum difference of 6.47 d. The minimum difference in TIME TO INFLORESCENCE among clones was 0.18 d (clones 4 and 5). Mean TIME TO RE-CLOSURE ranged from 3.80 d (1 SE = 0.11; clone 9) to 4.57 d (1 SE = 0.16; clone 3), for a maximum difference of 0.77 d. The minimum difference in TIME TO RE-CLOSURE among clones was 0.02 d (clones 2 and 5). Mean TIME TO FRUIT ranged from 11.54 d (1 SE = 0.16; clone 6) to 17.05 d (1 SE = 0.11; clone 5), for a maximum difference of 5.51 d. The minimum difference in mean TIME TO FRUIT among clones was 0.10 d (clones 2 and 3). Mean TOTAL FLOWERING TIME per inflorescences for each clone ranged from 29.60 d (1 SE = 0.19; clone 8) to 38.73 d (1 SE = 0.28; clone 9), for a maximum difference of 9.13 d. The minimum difference in mean TOTAL FLOWERING TIME among clones was 0.01 d (clones 2 and 6).

No significant differences in mean TIME TO BUD ($N = 301$, $P = 0.2396$) or mean SCAPE LENGTH ($N = 301$, $P = 0.3688$) were detected among clones (Table 1). For information on how specific clones differ with regard to their floral stage timing characteristics see Collier (2003). Mean TIME TO BUD ranged from 88.97 d (1 SE = 3.08; clone 9) to 96.15 d (1 SE = 3.93; clone 5), for a maximum difference of 7.18 d. The minimum difference in mean TIME TO BUD among clones was 0.02 d (clones 1 and 7). Mean SCAPE LENGTH ranged from 21.79 cm (1 SE = 0.90; clone 2) to 24.82 cm (1 SE = 0.98; clone 9), for a maximum difference of 3.03 cm. The minimum difference in mean SCAPE LENGTH among clones was 0.04 cm (clones 3 and 8).

Regression analysis—Regression analysis showed no significant relationship between the number of inflorescence buds produced by dandelions and TOTAL FLOWERING TIME [Number of inflorescence buds = (-0.12)TOTAL FLOWERING TIME + 10.83, $P = 0.1159$]. This suggests that there are no differences in numbers of inflorescence buds produced by earlier or later flowering dandelion clones.

Multidimensional scaling analysis—MDS of the flowering parameter data revealed that the first two axes explained 89%

TABLE 1. Total number of inflorescence buds, number of buds per co-clonal plant, mean number of buds per plant, mean time to bud, mean time to inflorescence, mean time to re-closure, mean time to fruit, mean total flowering time, and mean scape length for five co-clonal plants from each of nine clones. *P* values are from Kruskal-Wallis tests analyzing differences in each of the observed flowering parameters and scape length among the nine clones ($P \leq 0.05$ = significant difference among clones detected; standard error given in parentheses).

			Mean						
Clone no.	Total no. buds	Buds per co-clonal plant	No. buds per plant	Time to bud (d)	Time to inflorescence (d)	Time to re-closure (d)	Time to fruit (d)	Total flowering time (d)	Scape length (cm)
1	25	3, 4, 5, 6, 7	5.0 (0.35)	90.47 (2.01)	17.72 (0.26)	4.15 (0.09)	15.01 (0.19)	36.89 (0.36)	23.63 (0.79)
2	38	7, 6, 7, 9, 9	7.6 (0.30)	90.42 (3.71)	13.58 (0.38)	4.39 (0.10)	13.37 (0.16)	31.02 (0.54)	24.82 (0.92)
3	30	7, 6, 6, 5, 6	6.0 (0.32)	89.77 (2.53)	14.40 (0.57)	4.57 (0.16)	13.27 (0.22)	32.20 (0.48)	22.63 (0.71)
4	32	5, 5, 6, 8, 8	6.4 (0.34)	89.09 (3.11)	14.06 (0.61)	4.22 (0.12)	13.13 (0.28)	31.66 (0.61)	24.36 (0.86)
5	41	8, 7, 8, 9, 9	8.2 (0.37)	96.15 (3.93)	14.24 (0.16)	4.37 (0.15)	17.05 (0.12)	35.66 (0.28)	23.17 (0.77)
6	39	10, 5, 8, 8, 8	7.8 (0.40)	90.92 (3.11)	15.26 (0.13)	4.26 (0.09)	11.54 (0.16)	31.03 (0.20)	23.79 (0.71)
7	31	5, 5, 6, 8, 7	6.2 (0.29)	90.45 (3.10)	18.77 (0.13)	4.23 (0.10)	11.39 (0.17)	34.39 (0.21)	22.68 (0.61)
8	35	7, 8, 5, 8, 7	7.0 (0.28)	92.14 (4.54)	12.46 (0.14)	4.46 (0.08)	12.60 (0.11)	29.60 (0.19)	22.59 (0.87)
9	30	6, 3, 6, 8, 7	6.0 (0.42)	88.97 (3.08)	18.93 (0.18)	3.80 (0.11)	16.00 (0.17)	38.73 (0.28)	21.79 (0.91)
			$P = 0.2217$	$P = 0.2396$	$P < 5*10^{-5}$	$P = 0.0005$	$P < 5*10^{-5}$	$P < 5*10^{-5}$	$P = 0.3688$

of the total variance. The first axis was most heavily weighted on TOTAL FLOWERING TIME and TIME TO INFLORESCENCE while the second was most heavily weighted on TIME TO BUD and TIME TO RE-CLOSURE. An MDS plot of individual clones, placed according to the values assigned to them on these first two axes, showed that all clones were spatially separated from each other. This lack of clustering suggests that all clones have unique flowering stage phenology characteristics.

DISCUSSION

Our results show that different dandelion clones exhibit differences in flowering phenology characteristics when subjected to uniform environmental conditions. Further, MDS analysis demonstrated that each clone exhibited a unique set of floral stage timing characteristics. Our findings suggest that variation in floral timing stages observed among North American dandelion clones may in part involve varying genotypic environmental response characteristics.

In contrast, many early studies investigating the timing of flowering in dandelions failed to detect any significant variation among the plants studied. For example, Beach (1939) reported that all dandelion inflorescences observed in his study remained closed for approximately 10–12 d before opening in seed (i.e., time to fruit). Listowski and Jackowska (1965) found the flowering cycle of dandelions to be uniform when grown under short-day conditions. Solbrig (1971) observed that dandelion inflorescences growing in the Mathei Botanical Gardens (Ann Arbor, Michigan, USA) typically remained opened for an average of 1 d and then closed for a mean of 2 d before again opening in seed (i.e., time to re-closure and time to fruit). Lastly, Gray et al. (1973) reported that although differences in dandelion flowering stage timing existed across seasons, no such differences existed among plants within any given season (e.g., spring, summer, and autumn).

None of these earlier studies investigating potential variation in the flowering cycle of dandelions utilized DNA fingerprinting to distinguish clones. It is therefore possible that the observed populations in these studies may have been made up of one to several clonal lineages exhibiting similar flowering behavior. DNA fingerprinting adds further resolution to whether any observed clonal differences in flowering time are based on varying genotypic responses. For example, if no differences in flowering time were shown among clones, or if flowering phenology characteristics within individual clones were so variable that no overall differences in flowering time were discernable, this would suggest that flowering time in natural populations might primarily be determined by environmentally induced phenotypic plasticity (e.g., Listowski and Jackowska, 1965; Gray et al., 1973).

While our analyses demonstrated differences in certain flowering characteristics, they also revealed no differences in mean total number of inflorescence buds produced ($N = 301$, $P = 0.2217$) and mean time to bud ($N = 301$, $P = 0.2396$) across clones (Table 1). Variation in these two flowering parameters was observed in four different dandelion ''variants'' utilized by Listowski and Jackowska (1965) in their study of the rhythm of flowering in dandelions, but plants were grown under different environmental conditions and no statistical analyses were provided. Solbrig (1971) also observed differences in the number of flowering heads produced by two dandelion ''biotypes'' grown individually in garden plots and in

competition. In that study dandelion biotype A consistently produced more heads per plant (and presumably more buds) than biotype D, regardless of growing conditions. It is possible that the lack of differentiation in these two flowering parameters across nine clones in this study may result from our more controlled growth conditions.

The last flowering parameter compared among the nine dandelion clones used in this study was scape length. Here, our results showed no significant differences in mean scape length among clones, suggesting that there is no varying genetic response in this growth/flowering parameter among the clones tested under the controlled conditions (Table 1). However, others have shown that dandelion scape length can vary extensively under different environmental and physiological conditions. For example, Gray et al. (1973) found that variation in scape length increased in late spring and summer when day lengths were longer and temperatures were warmer. Clifford and Oxlade (1989) also determined that scape growth/extension could be mediated by endogenous ethylene levels, and Robinson (2001) showed that dandelion scapes grown in far-red light enriched environments elongated significantly more than scapes grown in other light environments. A possible explanation for our results may be that the plants used in this study were only grown under one set of constant environmental conditions. For example, growth chamber settings in this study were similar to environmental conditions in the early spring, a time when Gray et al. (1973) suggest that dandelion scapes in the field are noticeably shorter. It is also possible that the artificial light environment in the growth chamber was not conducive to stimulating differential scape elongation (see Robinson, 2001).

The varying genetic responses in flowering patterns among the nine dandelion clonal lineages we detected most likely arose from genetic variation in European sexual dandelion populations which are apparently constantly generating triploid, asexual clones (Menken et al., 1995). Divergence in flowering times among plants in general, as well as among these European dandelion progenitors of North American clones, may have arisen in several different ways. For example, selection based on pollinator availability (Waser, 1978; Rathcke and Lacey, 1985), variation in optimal fruit release time (Lacey and Pace, 1983), presence and abundance of flower/seed predators (Collinge and Louda, 1989; Ollerton and Lack, 1998), competition with other plants (Schmitt, 1983), human disturbance (Oosterveld, 1983; Lennartsson, 1997), and a host of abiotic/physical factors (e.g., nutrients, water, light) that exhibit variation through time (see Rathcke and Lacey, 1985; Hammad and Van Tienderen, 1997; Van Dijk et al., 1997) may all potentially contribute to divergence in flowering time among plants. Apparently, variation in genotypic floral ontogeny responses among Eurasian sexual *Taraxacum* has contributed to the variation seen among North American clonal descendants.

Numerous studies have demonstrated an advantage to early flowering in which the first seeds to germinate have a competitive advantage over later germinating conspecifics (Lee and Hamrick, 1978; Weaver and Cavers, 1979; Narita, 1998; Seiwa, 1998; Houle, 2002). For example, it has been shown that the first plants in *Rumex crispus* (Polygonaceae) populations to attain larger sizes often begin to reproduce earlier and have lower mortality than the smaller, later-developing plants in the populations (Weaver and Cavers, 1979). If this were the case with dandelions, it would be likely that clones with earlier flowering times would outcompete clones with later flowering times. However, this study shows that both early and later flowering North American dandelions exist in natural populations, an observation that can be justified with two alternative explanations. First, variation in flowering time may not be subject to selection because it has no advantage in dandelions. Therefore, clones of both types would be found in natural populations regardless of any variation in their flowering phenologies. Alternatively, any inherent advantages to earlier/later flowering clones (e.g., there appears to be no advantage in terms of flower production, as shown here by regression analysis) may fluctuate with fluctuating environmental conditions. If this were the case, clones with different flowering phenologies would be selected for at different times based on how well they perform under ever-changing environmental conditions. Thus, variation in flowering time among dandelion clones may be maintained in natural populations due to differing fitness relative to varying conditions.

It remains to be seen how the types of floral stage timing variation detected here is apportioned among populations. Future studies are also needed observing clones under natural conditions and a range of uniform conditions to determine if clonal differences in flowering times occur under other circumstances (see McMillan and Pagel, 1958; Augspurger, 1984; Pickering, 1995; Hammad and Van Tienderen, 1997; Van Dijk et al., 1997). Similar results under a range of conditions would either strengthen our finding that varying genotypic response may largely determine flowering phenology in dandelions or reveal that there is also a substantial degree of phenotypic plasticity differing among clones in response to varying environments.

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