Effects of day length and temperature on flowering in *Taraxacum platycarpum* and *T. officinale*

Fumio Yoshie Institute of Natural Sciences, Senshu University

Abstract. In dandelions, flowering decreases during summer. The present study investigated whether dandelion flowering is controlled by temperature or day length. Two dandelion species with different distributions, *Taraxacum platycarpum* and *T. officinale*, were selected as experimental materials. Seedlings were cultivated at 14 °C and 24 °C under short- (8 h) or long-day (16 h) conditions. In both species, days to flower bud appearance and days from flower bud appearance to flowering were unaffected by day length at each temperature condition, indicating that these are day-neutral plants. In both species, the appearance of flower buds was delayed and days from flower bud appearance to flowering was reduced at 24 °C compared to 14 °C. This result indicates that the decrease in flowering observed in these dandelions in summer is attributable to the suppression of flower bud formation by high temperatures. The flower bud formation of *T. platycarpum* was more intensely suppressed by high temperature than that of *T. officinale*. In *T. officinale*, a high temperature increased scape length regardless of day length, and a long-day length increased scape length at 14 °C. A similar response in scape length was observed in *T. platycarpum*.

Key words: day-neutral plant, flower bud formation, high-temperature suppression, photoperiodic response, scape length

1. Introduction

Control of flowering time is important for the reproductive success of plants. In temperate regions, the common dandelion *Taraxacum officinale* Weber shows a peak in flowering in spring and a secondary peak (at a much lower intensity) in autumn, although it does flower throughout the year (Gray et al. 1973). The plants that have already bloomed once in spring flower again in autumn (Listowski and Jackowska 1965). Dandelions native to Japan also show a peak in flowering in spring and a decrease in flowering in summer (Morita 1980).

Day length and temperature are important factors affecting the time of flowering. *Taraxacum officinale* is classified as a day-neutral plant because it flowers under a wide range of day lengths (Listowski and Jackowska 1965; Gray et al. 1973; Stewart-Wade et al. 2002). However, some authors considered it to be a short-day plant, since it typically does not bloom in large numbers under > 12 h light (Solbrig 1971; Collier and Rogstad 2004). Experimental studies of the photoperiodic response in *Taraxacum* spp. have not been reported. Therefore, the first objective of the present study was to clarify the photoperiodic response of dandelions. We selected two *Taraxacum* species with different distributions for this purpose: *T. officinale* and *T. platycarpum*. The former is a polyploid agamospermous species native to Europe that is now naturalized throughout world, while the latter is a sexual diploid species native to central Japan.

In dandelions, flowering decreases during summer, when high temperatures prevail. However, the onset of spring flowering in dandelions in Japan is earlier in years in which the temperature from February to April (the period just before the initiation of flowering) is higher than usual (Japan Meteorological Agency 2005), indicating that the growth of flower buds is promoted by an increase in temperature. These results suggest that the limited flowering of dandelions in summer results from the suppression of flower bud formation (flower bud differentiation and/or flower bud growth in the early developmental phase) due to high temperatures. Previous studies have indicated that flower bud formation in *T. officinale* and two native Japanese dandelion species, *T. japonicum* and *T. venustum*, is suppressed by an increase in temperature (Yoshie 2014, 2017). However, it is unclear whether flowering in *T. platycarpum* is suppressed by high temperature and whether the response of this plant to temperature is different from that of *T. officinale*. The second objective of the present study, therefore, was to clarify the difference in the response of flower bud formation to temperature in *T. platycarpum* and *T. officinale*.

Scape length is an important trait affecting the attraction of pollinators to flowers and the distance of seed dispersal by wind. Gray et al. (1973) found positive correlations between scape length in *T. officinale* and temperature and day length in the natural habitat of the plant. In the present study, the effects of temperature and day length on scape length were also investigated.

2. Materials and Methods

2.1 *Materials*

Taraxacum platycarpum is native to the Kanto District and the eastern part of the Chubu District in the warm temperate region of Japan (Kitamura 1981). *Taraxacum officinale* is native to Europe, but is now distributed throughout the world (Holm et al. 1997); it was introduced to Japan more than 100 years ago (Makino 1904) and is now distributed throughout the country, in regions ranging from subtropical to alpine (Shimizu 2003). We classified these two species based on the morphology of involucral bracts in the mature capitulum at the distal end of the scape. The bracts of *T. platycarpum* clasp tightly around the inflorescence, whereas those of *T. officinale* are reflexed (Kitamura 1981).

Natural hybridization occurs between native sexual diploids and *T. officinale* (Morita 1988). Recent studies indicate that the hybrid offspring have reflex bracts; therefore, the morphological classification of *T. officinale* includes both genuine *T. officinale* and its hybrids (Watanabe et al. 1997; Shibaike et al. 2002). The ratio of hybrids to morphologically classified *T. officinale* is very high in Kanto District (Yamano et al. 2002).

Taraxacum platycarpum seeds were collected in late April 2010 at Senshu University campus (N35°36′, E139°33′, 70–75 m a. s. l.), Kanagawa Prefecture, Kanto District, which is a warm temperate region. *Taraxacum officinale* seeds were collected in early May 2010 at Motoishikawa (55–65 m a. s. l.), Aoba-ku, 3 km southwest of the campus. Seeds were collected from > 16 mother plants per sampling and stored at room temperature until experiments were conducted.

2.2 *Methods*

Experiments were conducted using eight growth cabinets [interior dimensions 60 × 50 × 100 cm (W × D × H); ICB-

301L; Asahi Techno Grass, Tokyo, Japan]. Two sets of illumination units, each composed of seven 15 W fluorescent lights and four 6 W fluorescent lights, were provided in the upper and lower parts of the growth cabinets. We used four white-light-type and three daylight-type fluorescent lamps, each with a spectral quality similar to that of sunlight 2 h after sunrise and in a cloudy sky, respectively (Noguchi 1973). Plants were cultivated under the illumination units. Irradiance was controlled by the number of 15 W fluorescent lights and the distance between the lights and the plant materials. Irradiance at the pot surface level provided by seven 15 W fluorescent lights at the center of the cabinets (30 cm and 25 cm from the inside walls) and mean irradiance at four peripheral locations (10 cm from each of the two inside walls) are shown in Fig. 1 as a function of the distance from the lamps.

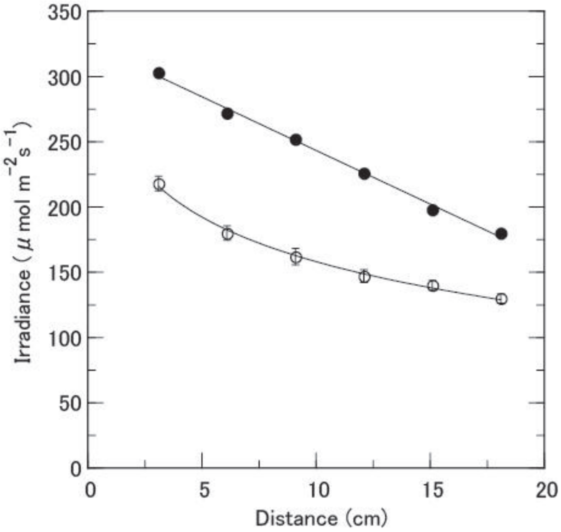


Fig. 1. Irradiance at pot surface as a function of the distance from seven 15 W fluorescent lights at 20 °C. Closed and open circles indicate irradiance at the center location and mean irradiance at four peripheral locations (10 cm from each of the two inside walls of the growth cabinet), respectively. Vertical bars indicate ± standard deviation.

Seeds from 16 mother plants of each species were selected as experimental materials. The seeds were sown in Petri dishes in mid-August 2010 on a filter paper moistened with tap water. The *T. platycarpum* seeds were incubated at 14 °C, whereas the *T. officinale* seeds were incubated at 19 °C, according to the optimum temperature for germination for each species (Hoya et al. 2004). The seeds were incubated under a day length of 12 h and irradiated with a photosynthetic active radiation of 80–100 μmol m^{-2} s^{-1}.

Then, 7–8 d after sowing for *T. officinale* and 10–12 days after sowing for *T. platycarpum*, four cotyledon-stage seedlings from each mother plant were transplanted to a plastic pot (10.5 cm in diameter and 9.0 cm deep) with uniform soil (N, 400 mg/L; P, 680 mg/L; K, 540 mg/L; Takii-shubyo Co., Kyoto, Japan). The potted plants were cultivated at 19 °C under a day length of 12 h and irradiated with a photosynthetic active radiation of 95–125 μmol m^{-2} s^{-1} at the pot surface

One seedling per pot was selected as experimental material 3 weeks after transplantation. Selected seedlings of both species were similar in rosette leaf size. The potted seedlings of each species were then subjected to four treatments: They were cultivated at 14 °C or 24 °C under short- (8 h) or long-day (16 h) conditions for 180 d after transplantation. The sample size of both species for each treatment was 16 seedlings from 16 mother plants. Four potted seedlings were placed in a container for each treatment, and the four containers were placed under the upper and lower illumination units in the growth cabinets (see Yoshie 2014).

All plants in both of the day length treatments received a basic illumination of 8 h high-intensity light (seven 15 W fluorescent lights) per day, and this was extended in the 16 h day length treatment by low-intensity light (provided by 6 W fluorescent lights, 4–7 μmol m^{-2} s^{-1}) to minimize the effect of photosynthetic matter production on photoperiodic responses. The angle of leaves to the horizontal line was greater in *T. officinale* than in *T. platycarpum*, and the angle at 24 °C was greater than that at 14 °C in both species. During the experiment, the distance between the fluorescent light and the pot surface was changed for all tested plants of both species under the four treatments depending on the rosette leaf growth of the *T. officinale* seedlings at 24 °C; the distance was 6.1 cm during the first 30 d, then 9.1 cm for 10 d, 12.1 cm for 10 d, 15.1 cm for 10 d, and 18.1 cm thereafter until the end of the experiment.

The number of leaves of *T. platycarpum* and *T. officinale* plants decreases in summer in their natural habitats (Morita 1980; Yoshie 1995; Ogawa and Kuramoto 2001). However, leaf unfolding and expansion continued in all of the seedlings tested in the present study and plants showed no signs of dormancy during the experimental period. Mutual shading of the seedlings of both species was slight under both day lengths at 14 °C because the plants grew small leaves at this temperature. The seedlings of both species grew larger leaves at 24 °C and the aboveground biomass was markedly larger at 24 °C than at 14 °C under both day lengths. The larger leaves of the seedlings at 24 °C caused mutual shading that was initiated from approximately 7 weeks after transplantation.

Two months after transplantation and every 2 weeks thereafter, 800 mL of Hyponex solution (0.8 g/L, N:P:K, 5:10:5 mixed fertilizer; Hyponex Co., Marysville, OH, USA) was supplied per container. During the experiment, water was supplied at appropriate intervals to prevent plant wilting. The air humidity in the cabinet was not controlled. Because the difference in water pressure between the leaf and the ambient air increases with an increase in temperature, air humidity may affect the plant response to temperature treatment.

The flowering process of dandelions is as follows: First, a flower (capitulum) bud appears at the center of the rosette, then increases in the size; the flower bud scape elongates, and finally the flower opens on the elongating scape. Plants were monitored every day during the experiment for the appearance of the first flower bud and the opening of the first flower. The date on which the segment of a bud approximately 3 mm in size was visible at the center of the rosette was considered to be the date of flower bud appearance. The date on which all of the outermost lingulate flowers opened was considered to be the date of flower opening. Scape length was recorded on the same date that the first flower opened.

2.3 *Data analysis*

The percentage of plants that had produced flower buds and flowers by the end of the experiment, the number of days from transplantation to flower bud appearance, and the number of days from flower bud appearance to flowering were recorded. Differences in the percentage of plants of each species that produced flower buds between temperature treatments under each day length and between day length treatments under each temperature were analyzed using the χ^2 test. Differences in the percentage of plants that produced flower buds and differences in flowering between species under each day length treatment at 24 °C were analyzed using the χ^2 test. The effects of temperature and day length on the number of days from transplantation to flower bud appearance, the number of days from flower bud appearance to flowering, and scape length in each species were analyzed by two-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference test at $\alpha = 0.05$.

3. Results

Flower buds appeared in all *T. platycarpum* and *T. officinale* plants by 84 d post transplantation at 14 °C, irrespective of day length (Fig. 2). At 24 °C, no flower buds appeared in any of the tested plants until 118 d post transplantation. Even at the end of the experiment (180 d post transplantation), flower buds had not appeared in approximately 80% of the *T. platycarpum* plants and 45% of the *T. officinale* plants at 24 °C, regardless of day length (Fig. 2). All tested *T. platycarpum* and *T. officinale* plants had flowered under both day length treatments at 14 °C by the end of experiment.

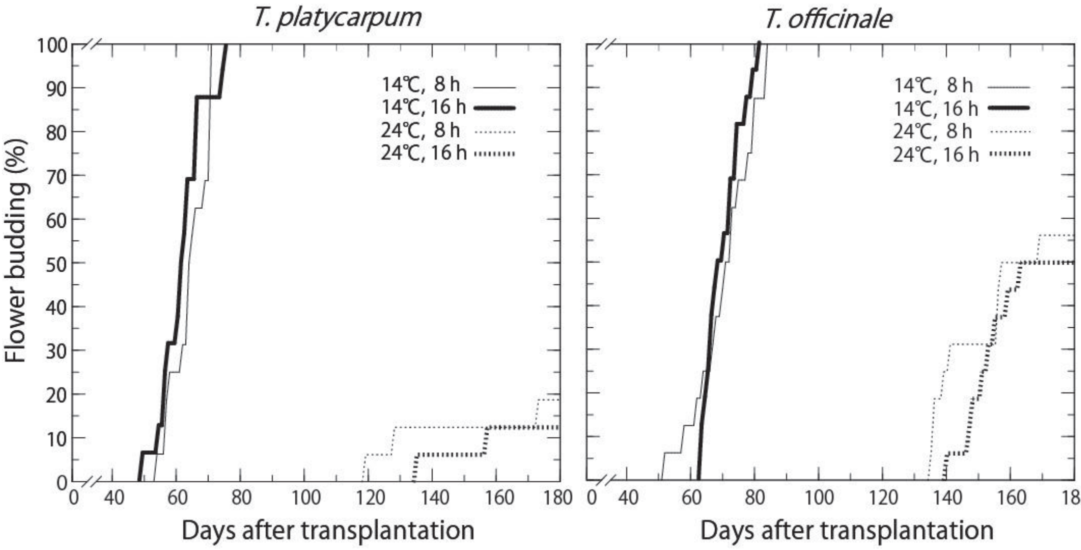


Fig. 2. Cumulative percentage of *Taraxacum platycarpum* and *T. officinale* plants that produced flower buds after transplantation of seedlings.

The percentage of *T. platycarpum* plants that had produced flower buds and flowers by the end of the experiment at 24 °C was significantly lower than that at 14 °C under both day lengths ($P < 0.001$ for both day lengths for flower buds and flowers, χ^2 test). The percentage of *T. officinale* plants that produced flower buds and flowers at 24 °C was also significantly lower than that at 14 °C under both day lengths ($P = 0.003$ for 8 h and $P = 0.001$ for 16 h for flower buds, $P = 0.001$ for both day lengths for flowers). The percentage of plants of both species that produced flower buds and flowers at 24 °C did not differ significantly between 8 h and 16 h day length treatments.

Days from transplantation to flower bud appearance in *T. platycarpum* and *T. officinale* were affected by temperature and not by day length or the interaction between the two (Table 1). The number of days to flower bud appearance at 24 °C was significantly greater than that at 14 °C in both species under each day length (Table 2). The number of days from flower bud appearance to flowering in both species was not significantly affected by day length, but was affected by temperature (Table 1); days from flower bud appearance to flowering at 24 °C was about half that at 14 °C in both species (Table 2). The number of days from flower bud appearance to flowering did not differ significantly between 8 h and 16 h day length treatments at 24 °C in either species. The number of days from flower bud appearance to flowering also did not differ significantly between 8 h and 16 h day length treatments at 14 °C in either species, although scape length was considerably different between treatments at this temperature (Table 2). Taken together, these results indicate that both species are day-neutral plants and that flower bud appearance at 24 °C is significantly delayed compared with that at 14 °C.

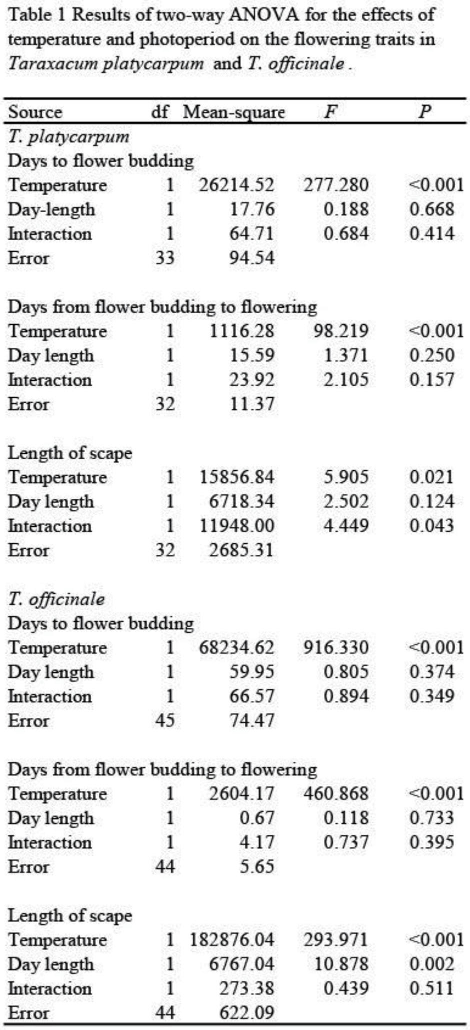
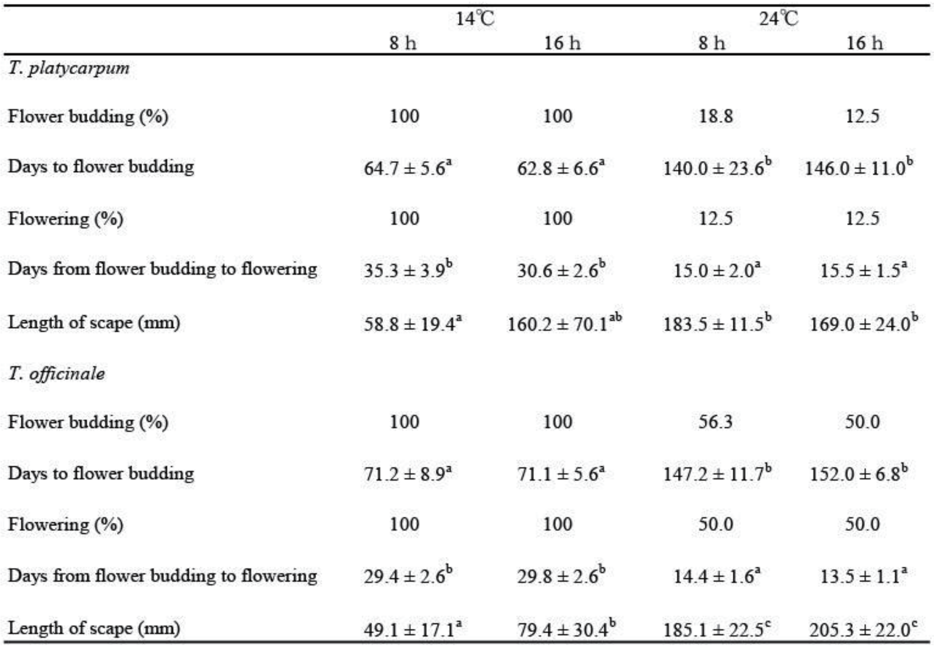


Table 1 Results of two-way ANOVA for the effects of temperature and photoperiod on the flowering traits in *Taraxacum platycarpum* and *T. officinale*.

Source	df	Mean-square	*F*	*P*
T. platycarpum				
Days to flower budding				
Temperature	1	26214.52	277.280	<0.001
Day-length	1	17.76	0.188	0.668
Interaction	1	64.71	0.684	0.414
Error	33	94.54		
Days from flower budding to flowering				
Temperature	1	1116.28	98.219	<0.001
Day length	1	15.59	1.371	0.250
Interaction	1	23.92	2.105	0.157
Error	32	11.37		
Length of scape				
Temperature	1	15856.84	5.905	0.021
Day length	1	6718.34	2.502	0.124
Interaction	1	11948.00	4.449	0.043
Error	32	2685.31		
T. officinale				
Days to flower budding				
Temperature	1	68234.62	916.330	<0.001
Day length	1	59.95	0.805	0.374
Interaction	1	66.57	0.894	0.349
Error	45	74.47		
Days from flower budding to flowering				
Temperature	1	2604.17	460.868	<0.001
Day length	1	0.67	0.118	0.733
Interaction	1	4.17	0.737	0.395
Error	44	5.65		
Length of scape				
Temperature	1	182876.04	293.971	<0.001
Day length	1	6767.04	10.878	0.002
Interaction	1	273.38	0.439	0.511
Error	44	622.09		

Table 2 Percentage of plants that produced flower buds and flowers, days from transplantation to flower bud appearance, days from flower bud appearance to flowering, and scape length in seedlings of *Taraxacum platycarpum* and *T. officinale* under different temperatures and day lengths.



	14℃		24℃	
	8 h	16 h	8 h	16 h
T. platycarpum				
Flower budding (%)	100	100	18.8	12.5
Days to flower budding	64.7 ± 5.6^{a}	62.8 ± 6.6^{a}	140.0 ± 23.6^{b}	146.0 ± 11.0^{b}
Flowering (%)	100	100	12.5	12.5
Days from flower budding to flowering	35.3 ± 3.9^{b}	30.6 ± 2.6^{b}	15.0 ± 2.0^{a}	15.5 ± 1.5^{a}
Length of scape (mm)	58.8 ± 19.4^{a}	160.2 ± 70.1^{ab}	183.5 ± 11.5^{b}	169.0 ± 24.0^{b}
T. officinale				
Flower budding (%)	100	100	56.3	50.0
Days to flower budding	71.2 ± 8.9^{a}	71.1 ± 5.6^{a}	147.2 ± 11.7^{b}	152.0 ± 6.8^{b}
Flowering (%)	100	100	50.0	50.0
Days from flower budding to flowering	29.4 ± 2.6^{b}	29.8 ± 2.6^{b}	14.4 ± 1.6^{a}	13.5 ± 1.1^{a}
Length of scape (mm)	49.1 ± 17.1^{a}	79.4 ± 30.4^{b}	185.1 ± 22.5^{c}	205.3 ± 22.0^{c}

Data are mean ± SD. Different letters in the same row indicate significant difference among four different treatments at $P < 0.05$.

In comparing the two species, the percentage of *T. platycarpum* plants that had produced flower buds by the end of the experiment was significantly lower than that of *T. officinale* at 24 °C under each day length ($P = 0.028$ for 8 h and $P = 0.022$ for 16 h, χ^2 test). The percentage of *T. platycarpum* plants that had produced flowers by the end of the experiment was also significantly lower than that of *T. officinale* at 24 °C at each day length ($P < 0.022$ for both day lengths).

Scape length in *T. officinale* was affected by temperature and photoperiod (Table 2). The scapes of this species were significantly longer at 24 °C than at 14 °C under both day length treatments. Scape length did not differ between day length treatments at 24 °C but was significantly greater under a 16 h day than an 8 h day at 14 °C. Meanwhile, scape length in *T. platycarpum* was affected by temperature and the interaction between temperature and photoperiod. The scapes of this species were significantly longer at 24 °C than at 14 °C under an 8 h day, but were not significantly longer at 24 °C than at 14 °C under a 16 h day. Scape length did not differ between day length treatments at 24 °C. Scape length tended to be longer under a 16 h day than an 8 h day at 14 °C, although the difference was not significant.

4. Discussion

Our results reveal that *T. officinale* and *T. platycarpum* are day-neutral plants and that high temperature delayed flower bud appearance in seedlings of these species. The percentage of plants that produced flower buds, days to flower bud appearance, and days from flower bud appearance to flowering in *T. platycarpum* and *T. officinale* were all unaffected by day length (Table 1) and these traits did not significantly differ between day length treatments at each temperature (Table 2). These results indicate that these two *Taraxacum* species are day-neutral plants.

Flower bud appearance at 24 °C was more than 2 months later than that at 14 °C in these species. At 24 °C, seedlings of both species grew larger leaves and aboveground biomass was markedly larger than at 14 °C under both day lengths. Therefore, the delay in flower bud appearance at 24 °C was not ascribed to a deficiency in photosynthates. The high-temperature suppression of flower bud formation in two *Taraxacum* species observed in the present study was consistent with that reported in *T. officinale*, *T. japonicum*, and *T. venustum* in previous studies (Yoshie 2014, 2017). The results of the present study show that a high temperature shortened the number of days from flower bud appearance to flowering (Table 2). This result could explain earlier onset of dandelion flowering in years in which the temperature from February to April is higher than usual (Japan Meteorological Agency 2005). These results indicate that the decrease in flowering in *T. platycarpum* and *T. officinale* in their natural habitats during summer (Gray et al. 1973; Morita 1980) does not result from a change in day length but from the suppression of flower bud formation by high temperatures.

The percentages of *T. platycarpum* plants that produced flower buds and flowers by the end of the experiment were significantly lower than those of *T. officinale* under each day length at 24 °C. This result indicates that the suppression of flower bud formation and flowering by high temperature was more pronounced in *T. platycarpum* than in *T. officinale*. This suggests *T. platycarpum* would produce fewer flowers than *T. officinale* during summer and autumn in the natural habitats of these species. Indeed, we sometimes observe flowering in *T. officinale* during these periods in natural habitats, but not in *T. platycarpum*. Outdoor and laboratory experiments that tested the association between the germination of *T. officinale* and *T. platycarpum* and temperature (Ogawa 1978; Hoya et al. 2004) reported that the germination of *T. platycarpum* is more intensely suppressed by high temperature than that of *T. officinale*. These results show that *T. platycarpum* is an intense summer-dormant plant compared with *T. officinale*.

Gray et al. (1973) indicated that scapes were longer in the summer when temperatures were higher and days were longer. The present study revealed that a high temperature increased scape length in both dandelion species and a long-day length increased scape length at 14 °C (Table 1). These results indicate that an increase in day length is important for the increase in scape length in the early flowering season, although increased temperature becomes more important as the season progresses. *Taraxacum platycarpum* requires pollination for seed production. The increased scape length of this species, induced by high temperatures and long days, may make flowers more striking to pollinators and thus increase reproductive success by increasing the chance of pollination in spring, because the density and height of surrounding vegetation increases as the spring season progresses. The scape length of *Taraxacum officinale* shows the same growth pattern, although this species does not require pollination to produce seeds. Increased scape length induced by long days and high temperatures likely contribute to the distant dispersal of seeds in both of these dandelion species.

Reference

Collier MH, Rogstad SH (2004) Clonal variation in floral stage timing in the common dandelion *Taraxacum officinale* (Asteraceae). American Journal of Botany 91**:** 1828–1833

Gray E, McGehee EM, Carlisle DF（1973）Seasonal variation in flowering of common dandelion. Weed Science 21: 230–232.

Holm L, Doll J, Holm E, Pancho J, Herberger J (1997) World weeds: natural histories and distribution. John Wiley & Sons, New York.

Hoya A, Shibaike H, Morita T, Ito M (2004) Germination and seedling survivorship characteristics of hybrids between native and alien species of dandelion (*Taraxacum*). Plant Species Biology 19: 81–90

Japan Meteorological Agency (2005) Ijo kisho repoto (in Japanese). pp 163-165. [homepage on the internet]. [cited 10 September 2012]. Available from URL: http://www.data.kishou.go.jp/ climate/cpdinfo/ climate change/2005-pdf/2005 all.pdf

Kitamura S (1981) Compositae (Asteraceae). In: Satake Y, Ohwi J, Kitamura S, Watari S, Tominari T (eds) Wild Flowers of Japan. Herbaceous Plants III, Heibonsha, Tokyo, pp. 156–235

Listowski A, Jackowska I（1965）Observations on plant development. XI. On the rhythm of flowering of *Taraxacum officinale*. Acta Societatis Botanicorum Poloniae 34: 549–561

Makino T (1904) Nihon no tanpopo (in Japanese). Shokubutugaku-zassi 18: 92–93

Morita T (1980) Tanpopo. In: Hotta M (ed) Shokubutsu no seikatusi (in Japanese). Heibonsha,Tokyo, pp. 58–67

Morita T (1988) Recent topics about *Taraxacum* agamosperms (in Japanese). Saishu to Shiiku 50: 128–132

Noguchi S. (1973) Light. In: Nihon seibutsu kankyou chousetsu gakkai (eds.) Seibutsu kankyou chousetsu handobukku (in Japanese). Tokyo daigaku shuppankai, Tokyo, pp 342–380

Ogawa K (1978) The germination pattern of a native dandelion (*Taraxacum platycarpum*) as compared with introduced dandelions. Japanese Journal of Ecology 28: 9–15

Ogawa K, Kuramoto N (2001) Tanpopo to kawaranogiku (in Japanese). Iwanami shoten, Tokyo

Shibaike H, Akiyama H, Uchiyama S, Kasai K, Morita T (2002) Hybridization between European and Asian dandelions (*Taraxacum* section *Ruderalia* and section *Mongolica*). Journal of Plant Research 115: 321–328

Shimizu T (2003) Naturalized plants of Japan (in Japanese). Heibonsha, Tokyo

Solbrig OT (1971) The population biology of dandelions. American Scientist 59: 686-694

Stewart-Wade SM, Neumann S, Collins LL, Boland GJ (2002) The biology of Canadian weeds. 117. *Taraxacum officinale* G. H. Weber ex Wiggers. Canadian Journal of Plant Science 82: 825–853

Watanabe M, Maruyama Y, Serizawa S (1997) Hybridization between native and alien dandelions in the western Tokai district. (1) Frequency and morphological characters of the hybrid between *Taraxacum platycarpum* and *T. officinale* (in Japanese with English summary). Journal of Japanese Botany 72: 51–57

Yamano M, Shibaike H, Hamaguchi T, Ide M (2002) Analysis on the distribution patterns of hybrid dandelions (*Taraxacum*) in Japan collaborated with the "Environmental Indicator Species Survey (Survey of Common Wildlife)" (in Japanese with English summary). Environmental Information Science 16: 357–362

Yoshie F (1995) Interhabitat variation in growth characteristics of temperate herbaceous perennials. Canadian Journal of Botany 73: 735–745

Yoshie F (2014) Latitudinal variation in sensitivity of flower bud formation to high temperature in Japanese *Taraxacum officinale*. J Plant Res 127: 399–412

Yoshie F (2017) Latitudinal variation in suppression of flower bud formation at high temperature in four native dandelions (*Taraxacum* spp.) with different distributions and genetic structures in Japan. Plant Species Biology 32: 54–65