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Capitulum and rosette leaf avoidance from grazing by large herbivores in *Taraxacum*

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Abstract Plants defense against herbivore damage is achieved through resistance and tolerance, of which resistance is composed of avoidance and antibiosis. Plants have developed various adaptations that facilitate escape from herbivory. We hypothesized that post-anthesis prostrate scapes in *Taraxacum* is an adaptation for avoidance of capitulum grazing by large herbivores. To test this hypothesis, we divided flowering into the following four stages based on the external appearance of the capitulum: green bud, yellow corolla, brown corolla, and white pappus stages. We conducted an experiment in natural pasture in Mongolia to artificially raise capitula and rosette leaves of *T. collinum*. We measured the natural height of capitula and rosette leaves of the Mongolian pasture and urban species, *T. collinum* and *T. ceratophorum*, respectively, and of the Japanese rural and exotic urban species, *T. japonicum* and *T. officinale*, respectively. We investigated natural grazing by livestock in the field of the capitula and rosette leaves of the two Mongolian species. In Mongolia, naturally short capitula at the green bud and brown corolla stages and rosette leaves of *T. collinum* were not grazed. However, artificially raised capitula and rosette leaves of *T. collinum* and the naturally high capitula and leaves of *T. ceratophorum* were grazed. Short capitulum and leaf height was shown to be effective for avoidance of livestock grazing in Mongolia. In Japan, *T. japonicum* and

T. officinale showed similar scape behavior to *T. collinum* and *T. ceratophorum*, respectively. We discuss the reasons for the capitulum behavior differences in Japan.

Keywords Scape · Livestock · Pasture · Rural habitat · Urban habitat

Introduction

Plant defense against herbivores through tolerance and resistance may involve a combination of defensive strategies (Milchunas and Noy-Meir 2002; Núñez-Farfán et al. 2007; Fornoni 2011). Although tolerance of herbivore damage reduces the fitness consequences through post-damage regrowth and reproduction (Briske 1991; Strauss and Agrawal 1999; Díaz et al. 2001; Cingolani et al. 2005; Evju et al. 2009), plant resistance reduces the extent of herbivore damage (Tiffin 2000). Resistance can be divided into antibiosis, which reduces herbivore performance, and avoidance, which allows plants to escape from herbivory.

Herbivores are diverse in size and eating habit. The avoidance strategies of plants may vary based on the type of herbivore. Plant avoidance of herbivory by terrestrial mammals is classified into external avoidance (e.g., taking refuge and hiding) and internal avoidance, which includes spatial and temporal tactics (e.g., mimicry) as well as chemical strategies (Milchunas and Noy-Meir 2002). However, unlike antibiosis, disentangling avoidance mechanisms remains a major challenge.

The scapes of *Taraxacum* species exhibit a gravitropic response (Clifford and Oxlade 1991). In Japan, it is well known that in native Japanese *Taraxacum* species in rural habitats (Ogawa and Mototani 1991), the scape actively changes from erect at anthesis to prostrate after flowering, and subsequently stands erect prior to achene dispersal (Hirayama 1972). However, it is not known whether scape movement is adaptive.

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In Mongolia, we observed many species of *Taraxacum* that exhibited prostrate scapes post-anthesis in the steppe, which is similar to native Japanese *Taraxacum* species. However, within the city of Ulan Bator, we observed that the scapes of urban *Taraxacum* species did not become prostrate after flowering. If post-anthesis a prostrate scape is adaptive, it may be beneficial in the steppe but not in an urban environment. One of the main habitat differences between the Mongolian steppe and the city is the respective presence and absence of grazing pressure from livestock, because livestock graze pasture plants widely in the steppe because of pastoral nomadism (Fernández-Giménez 1999). Hence, *Taraxacum* species inhabiting rural areas may be exposed to grazing pressure. Unless there is a shortage of forage, livestock do not graze pasture plants close to the soil surface but rather at a height of several centimeters (Fujita et al. 2013a, b). A short plant height is advantageous to reduce grazing pressure from large herbivores (Mitchley 1988; Díaz et al. 2001; Evju et al. 2009). Therefore, plants may avoid livestock grazing by adopting a prostrate habit. In an urban environment, a prostrate habit has no selective advantage because grazing pressure from livestock is absent. Thus, we predict that plants growing in urban and rural locations will show differences in growth habit. In Japan, exotic *Taraxacum* species occur in urban habitats, whereas endemic Japanese species grow in rural habitats (Ogawa and Mototani 1991). Therefore, the scape behavior of *Taraxacum* plants may differ between urban and rural environments.

We hypothesized that the post-anthesis prostrate scape in *Taraxacum* is an adaptation for avoidance of grazing of the capitulum by large herbivores. In order to clarify the relationship between plants and large herbivores, plant palatability and the degree of grazing pressure by large herbivores must be considered. Regarding grazing avoidance, the leaves must also be considered because *Taraxacum* species that avoid large herbivore grazing may have short scapes and leaves. In contrast, a *Taraxacum* species with a capitulum borne on a tall, erect scape at anthesis and achene maturity for pollination and wind dispersal of the achenes, respectively (Sheldon and Burrows 1973), may not be grazed. In the city, where grazing pressure by large herbivores is not assumed, short scapes and leaves may be unnecessary for avoidance of grazing pressure.

To test this hypothesis, we gathered field observations and experimental data for *Taraxacum* in Mongolia and Japan. We first performed an experiment to assess the effect of capitulum and rosette leaf height of a pasture species in Mongolia on susceptibility to livestock grazing. Second, we measured the heights of capitula during the flowering period and of rosette leaves in the field to ascertain height differences between Mongolian pasture and urban species, and between Japanese rural and exotic urban species. Third, we determined whether the capitula and rosette leaves of *Taraxacum* were grazed under natural field conditions in Mongolia. Last, we measured daily changes in capitulum height from the flower bud stage to the achene dispersal stage in a native

Japanese species to ascertain the dynamic movement of scapes over the course of capitulum development.

Methods

Study species and sites

To measure the heights of capitula and leaves of *Taraxacum* in the Mongolian steppe, we selected *Taraxacum collinum* DC., which occurs in a relatively dry habitat for a pasture species. We studied a population growing at a small, level site on the northern slope of Mt. Bogd Khan in Ulan Bator [ca. 1630 m above sea level (asl), 47°51'43"N, 106°51'41"E] that was frequently exposed to sheep and goat grazing. For the Mongolian urban-dwelling species, we selected a roadside population of *Taraxacum ceratophorum* (Ledeb.) DC. near Songiin in Ulan Bator (ca. 1240 m asl, 47°50'57"N, 106°40'35"E) where livestock from the adjacent pasture sometimes visited. In Japan, we selected *Taraxacum japonicum* Koidz. and *Taraxacum officinale* F.H.Wigg. as rural and exotic urban species, respectively. The study sites of *T. japonicum* and *T. officinale* were ridges between rice fields in Hirano, Otsu (ca. 101 m asl, 34°57'24"N, 135°57'22"E), and roadsides in Aoyama, Otsu (ca. 145 m asl, 34°58'31"N, 135°58'11"E), respectively. Natural hybridization in *Taraxacum* between native sexual diploids and introduced agamospermous triploids occurs in Japan (Watanabe et al. 1997; Shibaike et al. 2002), and *T. japonicum* hybridizes with *T. officinale* (Takakura et al. 2009). We identified the urban population as *T. officinale* based on the presence of recurved involucre bracts and brown achenes, in addition to the urban environment. To monitor capitulum height continuously throughout flowering, we cultivated a population of *T. japonicum* in an experimental garden at the Center for Ecological Research (CER), Kyoto University, Hirano-cho, Otsu, Japan (ca. 143 m asl, 34°58'15"N, 135°57'25"E). This population was transplanted from the same population at Hirano, Ohtsu, used for height measurement.

Measurement of capitulum and leaf height

We measured capitulum height vertically along the scape from the soil surface using a ruler. To determine the length and inclination of the scape, we also measured the horizontal distance from the capitulum to the center of the rosette. To relate scape movement to the flowering stage, we divided the flowering period into the following four stages based on the external appearance of the capitulum and recorded each stage at the time of capitulum height measurement. (1) Green bud stage: the florets were concealed by the green involucre bracts before anthesis. (2) Yellow corolla stage: yellow ligulate florets were visible at times of not only corolla open but also corolla closing before and after the opening. (3) Brown corolla stage:

corolla withered and turned brown after anthesis. (4) White pappus stage: white pappus bristles were conspicuous before achene dispersal. Each scape bore a terminal capitulum, and an individual rhizome often produced multiple scapes and capitula at different flowering stages. We measured all capitula on each rhizome. The number of scapes measured at the green bud, yellow corolla, brown corolla, and white pappus stages for each species was as follows, and the rhizome number is shown in parentheses: *T. collinum*: 30 (30), 49 (45), 30 (30), 40 (40); *T. ceratophorum*: 25 (20), 41 (27), 25 (21), 21 (17); *T. japonicum*: 21 (15), 23 (18), 23 (19), 20 (16); *T. officinale*: 20 (19), 35 (26), 20 (15), 20 (15).

For leaf height, we measured the maximum height of the leaf top among the rosette leaves on each rhizome. We also measured the horizontal distance from the leaf top to the center of the rhizome to determine the length and inclination of the leaf. To avoid the possible effect of light competition among plants on leaf height, we only measured leaf height on solitary rhizomes that grew in isolation from other plants. The number of rhizomes measured for each species was 30 for *T. collinum*, 32 for *T. ceratophorum*, 30 for *T. japonicum*, and 31 for *T. officinale*.

Capitula and leaves were measured on the same dates, namely 2 June 2003, 5 June 2003, 27 April 2005, and 28 April 2005 for *T. collinum*, *T. ceratophorum*, *T. japonicum*, and *T. officinale*, respectively. We recorded all measurements in the morning.

Livestock grazing of capitula and leaves

In Mongolia we marked the height-measured capitula and leaves for *T. collinum* and *T. ceratophorum* at the time of measurement. In the afternoon of the day following the marking, we checked for signs of livestock grazing on the capitula and leaves. The torn capitula and leaves of grazed plants were easily detected, and plants that had been grazed were recorded.

Artificial raising of capitula and leaves

For *T. collinum* growing on the northern slope of Mt. Bogd Khan in Mongolia, we artificially raised prostrate capitula (at the green bud and brown corolla stages) and rosette leaves in the same population used for height measurement. On the morning of 2 June 2003, we placed a wooden toothpick (1.8 mm in diameter and 6.5 cm in length) into the soil near the rhizome and raised the scape or leaf by tying it to the top of the toothpick with a thin thread. We used different rhizomes for capitula and leaves. After treatment we measured the height of the raised capitula and leaves, and checked for signs of livestock grazing on the raised capitula and leaves the following day. The number of raised capitula at the green bud and brown corolla stages, and number of raised leaves was 30 in each instance.

Monitoring of scape movement during flowering

On 27 April 2005, we transplanted plants of *T. japonicum* to the experimental garden of CER from Hirano. From 13 April 2006 (when the flower bud had developed) to 2 May (when the achenes dispersed), we measured the height of the same capitulum every day in order to monitor scape movement. We measured three capitula from three rhizomes, and recorded the respective flowering stage at each measurement.

Statistical analyses

Generalized linear mixed models (GLMM) were used to test the significance of differences in the height, length, and inclination of capitula among the flowering stages in each species. We set the height, length, and inclination of each capitulum as response variables and the flowering stage as the explanatory variable. Differences in the rhizome of each capitulum were set as a random effect term in each GLMM. We used the nlme package for R (Pinheiro et al. 2012) and described the relationship using a Gaussian regression model. For post hoc multiple comparison of each GLMM, we used Tukey's HSD test in the multcomp package for R (Hothorn et al. 2008). To test the significance of differences in the height, length, and inclination of leaves among species, we used a one-way ANOVA and Tukey's HSD test. Significance for all tests was set at $P = 0.05$. All statistical analyses in this study were performed using the statistical environment R 2.15.2 (R Development Core Team 2012).

Results

Grazing of artificially raised capitula and leaves

The horizontal length and vertical height of the artificially raised capitula and leaves of *T. collinum* before livestock grazing are shown in Fig. 1. Livestock grazed all of the capitula and leaves that were artificially raised. The capitula at the green bud and brown corolla stages, as well as the rosette leaves, were grazed when the height was raised artificially above 3 cm in pasture in which sheep and goats grazed frequently.

Capitulum height

Taraxacum collinum, a Mongolian pasture species, exhibited distinct capitulum movement with change in inclination during the flowering period. For example, at the green bud stage, the capitulum was low but became high at the yellow corolla stage. At the brown corolla stage, the capitulum was reduced in height, but was raised upright again at the white pappus stage. Among the four flowering stages, capitulum height and inclination were significantly lower at the green bud and brown

corolla stages, and were significantly higher at the white pappus stage (Table 1). The height of each capitulum did not exceed 3 cm at the green bud and brown corolla stages (Fig. 2a). However, in *T. ceratophorum*, a Mongolian urban species, the capitulum height was comparatively high at the four flowering stages compared with *T. collinum* (Table 1; Fig. 2b). Moreover, capitulum height did not differ significantly between the yellow and brown corolla stages, and the capitulum was not obviously prostrate at the brown corolla stage.

In a native Japanese rural species, *T. japonicum*, similar to *T. collinum*, the capitulum was prostrate at the green bud and brown corolla stages, and upright at the yellow corolla and white pappus stages (Fig. 2c). Among the four flowering stages, capitulum height and inclination were significantly lower at the green bud and brown

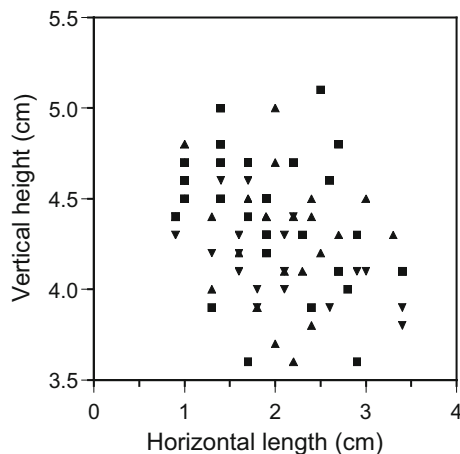


Fig. 1 Horizontal length and vertical height of artificially raised capitula and rosette leaves of *Taraxacum collinum* before livestock grazing. Upright triangle capitulum at the green bud stage; inverted triangle capitulum at the brown corolla stage; square rosette leaf. Capitula that were grazed and removed by livestock after the capitulum was artificially raised are indicated by black symbols

corolla stages, and were significantly higher at the white pappus stage (Table 1), which was consistent with the findings for *T. collinum*. However, a Japanese exotic urban species, *T. officinale*, similar to *T. ceratophorum*, did not show distinctly prostrate capitula (height less than 6 cm) (Fig. 2d). Furthermore, as with *T. ceratophorum*, no significant difference in capitulum height between the yellow and brown corolla stages was observed.

Leaf height

Taraxacum collinum (Fig. 3a) and *T. japonicum* (Fig. 3c) produced leaves of short heights of less than 3 cm and up to 5 cm, respectively. In contrast, the leaf height in *T. ceratophorum* (Fig. 3b) and *T. officinale* (Fig. 3d) was rarely less than 3 and 5 cm, respectively. Among the four species, the mean leaf height was lowest in *T. collinum* and *T. japonicum*, and was significantly higher in *T. officinale* ($P < 0.05$) (Table 2). The low height of the leaves was due to the gentle leaf inclination in *T. japonicum* and the short leaf length in *T. collinum* (Table 2).

Natural livestock grazing

In *T. collinum*, capitula at the green bud and brown corolla stages, as well as the rosette leaves were not grazed (Figs. 2a, 3a). Moreover, despite the greater height, capitula at the yellow corolla stage were also not grazed. At the white pappus stage, some capitula were grazed, but possibly only after achene dispersal. This conclusion was deduced because we did not observe signs of grazing of the white pappus before achene dispersal. In *T. ceratophorum*, capitula at all flowering stages, except for the yellow corolla stage, and the rosette leaves were grazed (Figs. 2b, 3b).

Table 1 Mean capitulum height, and scape length and inclination of each *Taraxacum* species at four flowering stages

Species	Stage	Height (cm)	Length (cm)	Inclination (°)
<i>Taraxacum collinum</i>	Green bud	1.7 ± 0.4a	4.4 ± 0.6a	23.7 ± 8.7a
	Yellow corolla	4.1 ± 0.6b	4.7 ± 0.3b	65.2 ± 14.7b
	Brown corolla	2.0 ± 0.4a	4.6 ± 0.3ab	25.6 ± 6.1a
	White pappus	5.1 ± 0.5c	5.2 ± 0.5c	80.1 ± 6.9c
<i>T. ceratophorum</i>	Green bud	6.4 ± 2.3a	9.9 ± 2.3a	41.6 ± 12.5a
	Yellow corolla	11.8 ± 3.8b	16.0 ± 2.9b	51.6 ± 18.8b
	Brown corolla	10.5 ± 1.9b	19.3 ± 1.9c	33.9 ± 14.8a
	White pappus	18.7 ± 1.7c	19.9 ± 2.2c	72.8 ± 8.8c
<i>T. japonicum</i>	Green bud	3.4 ± 1.2a	9.7 ± 2.7a	21.9 ± 9.0a
	Yellow corolla	8.8 ± 2.0b	12.2 ± 1.9b	46.6 ± 8.2b
	Brown corolla	4.0 ± 1.1a	14.3 ± 2.3c	16.3 ± 4.1a
	White pappus	15.5 ± 3.0c	16.8 ± 2.8d	69.5 ± 10.1c
<i>T. officinale</i>	Green bud	18.0 ± 7.5a	19.4 ± 8.0a	71.9 ± 11.6bc
	Yellow corolla	24.7 ± 4.5b	26.6 ± 4.2b	71.2 ± 11.4b
	Brown corolla	22.1 ± 5.5ab	28.7 ± 3.5b	53.8 ± 17.0a
	White pappus	35.2 ± 5.3c	35.9 ± 5.3c	80.8 ± 7.4c

Values are the mean ± standard deviation

Values with different letters for each species and trait are significantly different among the four stages (generalized linear mixed models and Tukey's HSD tests: $P < 0.05$)

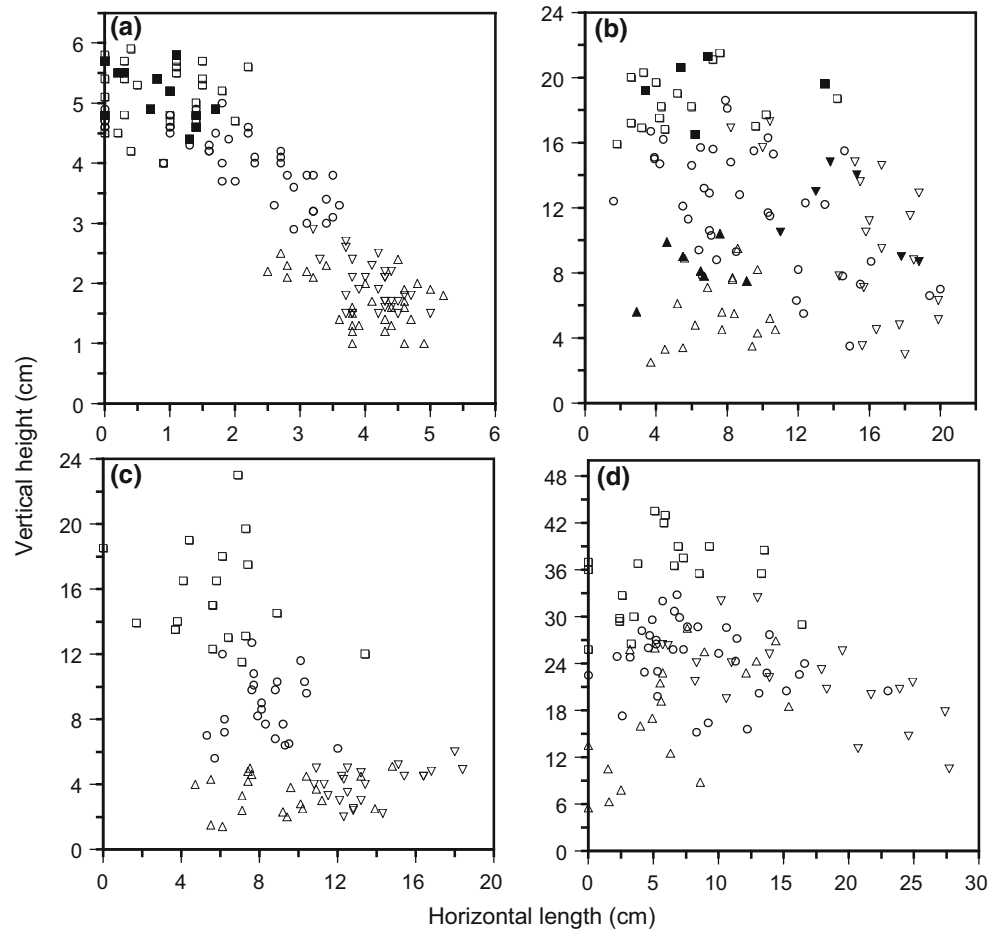


Fig. 2 Horizontal length and vertical height of capitula. **a** *Taraxacum collinum*, **b** *T. ceratophorum*, **c** *T. japonicum*, **d** *T. officinale*. Upright triangle capitulum at the green bud stage; circle capitulum

at the yellow corolla stage; inverted triangle capitulum at the brown corolla stage; square capitulum at the white pappus stage. Grazed capitula are indicated by black symbols

Capitulum movement during flowering

The height of *T. japonicum* capitula during the flowering is shown in Fig. 4. It was low (< 6 cm) at the green bud and brown corolla stages, while it was high (> 7 cm) at the yellow corolla stage. The capitula at the white pappus stage became high (> 7 cm) again. At the end of the white pappus stage when achene was dispersed, the capitulum became the highest uprightly. The lying and raising of the capitulum occurred after the yellow and brown corolla stage, respectively.

Discussion

Confirmation of the hypothesis

In Mongolia, the pasture species *T. collinum* bore capitula at the brown corolla stage (post-anthesis) that were sufficiently prostrate to avoid livestock grazing. However, all capitula of *T. collinum* at the brown corolla stage were grazed when artificially raised. Capitula at the green bud stage and the rosette leaves of *T. collinum* were also prostrate. This strategy was indicated to be

effective for avoidance of livestock grazing, because all were grazed when artificially raised. In the forest steppe zone of Mongolia, the grazing height of small and large livestock is almost 3 and 5 cm, respectively (Fujita et al. 2013a). On the northern slope of Mt. Bogd Khan, where the *T. collinum* population used in this study was located, a height of less than 3 cm was sufficient to avoid grazing for *T. collinum*, since sheep and goats were the main nomadic livestock. However, the urban species *T. ceratophorum* maintained raised capitula at the green bud and brown corolla stages as well as rosette leaves of increased height, which made them susceptible to livestock grazing. Thus, if livestock entered the city environment, the capitula and leaves were grazed. However, livestock grazing was rare in the urban environment. Therefore, the present results supported the hypothesis that post-anthesis prostrate scapes of *Taraxacum* is an adaptation for avoidance of grazing of the capitula by large herbivores.

That the capitulum becomes prostrate after anthesis in *Taraxacum* is well known (Hirayama 1972). In addition, we observed that *T. collinum* capitula at the green bud stage were also prostrate. Capitula of *T. collinum* at the green bud stage were indicated to be palatable to

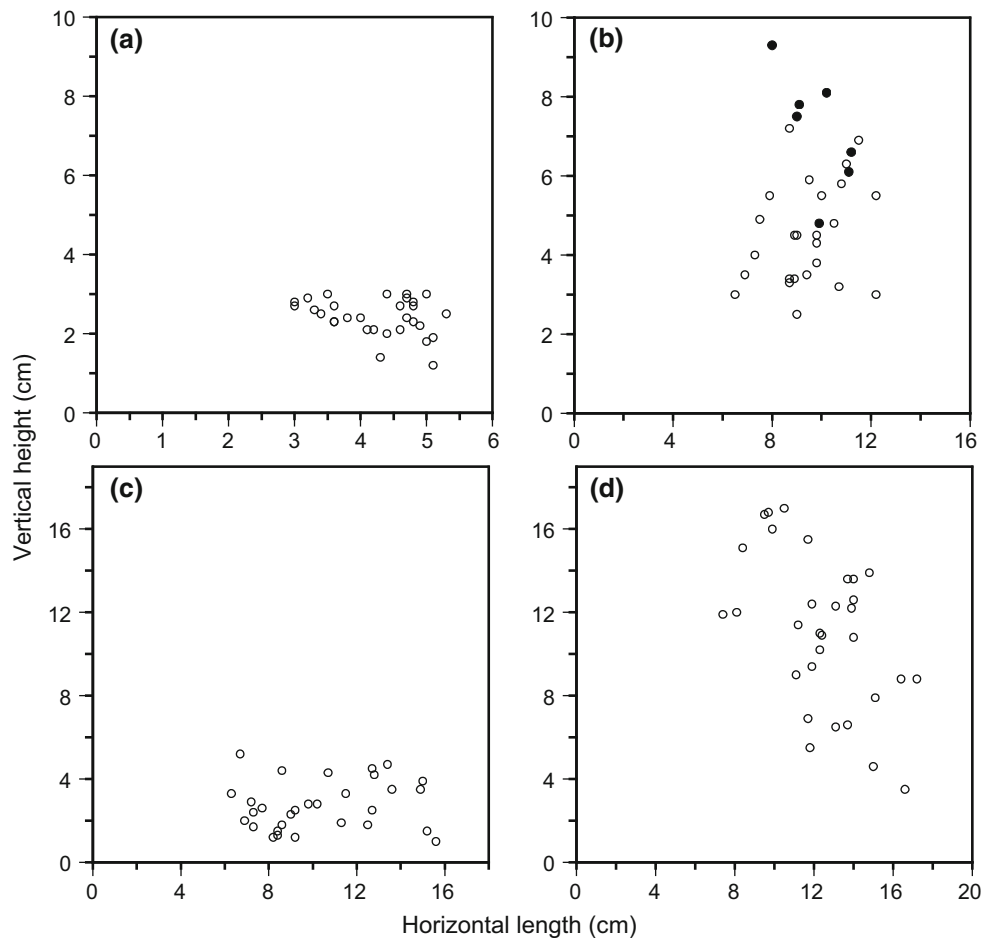


Fig. 3 Horizontal length and vertical height of the tip of the tallest rosette leaf. **a** *Taraxacum collinum*, **b** *T. ceratophorum*, **c** *T. japonicum*, **d** *T. officinale*. Grazed leaves are indicated by *black symbols*

Table 2 Mean leaf traits for each *Taraxacum* species

Species	Height (cm)	Length (cm)	Inclination (°)
<i>Taraxacum collinum</i>	2.4 ± 0.5a	4.9 ± 0.6a	30.1 ± 7.3b
<i>T. ceratophorum</i>	5.1 ± 1.7b	10.9 ± 1.7b	27.9 ± 7.9b
<i>T. japonicum</i>	2.8 ± 1.2a	10.8 ± 2.8b	15.4 ± 7.1a
<i>T. officinale</i>	11.1 ± 6.6c	17.1 ± 2.1c	41.0 ± 13.2c

Values are the mean ± standard deviation

Values with different letters for each trait are significantly different among species (one-way ANOVA and Tukey's HSD tests: $P < 0.05$)

livestock based on the results of the artificial raising experiment, becoming prostrate at both the green bud and brown corolla stages may be a grazing avoidance strategy.

Significance of capitulum raising

The Mongolian pasture species *T. collinum* raised the capitula twice, from the green bud stage to the yellow corolla stage and from the brown corolla stage to the white pappus stage. Although it might require effort to

raise the capitulum before flowering and achene dispersal, such movements are considered adaptive. Capitula of diploid *Taraxacum* species are entomophilous and pollinated at the yellow corolla stage (Totland 1993). Wind dispersal of the achenes occurs at the white pappus stage (Sheldon and Burrows 1973). In the case of insect pollination, it is generally accepted that pollinator insects locate flowers more easily at greater flower heights (Hainsworth et al. 1984; Donnelly et al. 1998; Ågren et al. 2006; Dickson and Petit 2006). With respect to seed dispersal, a higher point of release increases the potential dispersal distance (Okubo and Levin 1989; van Dorp et al. 1996; Nathan et al. 2002; Soons et al. 2004; Thomson et al. 2011). Therefore, the presence of higher capitula is advantageous for pollination and achene dispersal. There is a tendency for the capitulum to be higher at the achene dispersal stage than at anthesis. Thus, capitulum height may be more important for wind dispersal. However, in the case of the agamospermous Japanese exotic species, *T. officinale* (Richards 1970; Morita et al. 1990), the capitulum height is comparatively high throughout flowering.

The capitula of Mongolian pasture and urban species were not grazed by livestock in spite of the elevated

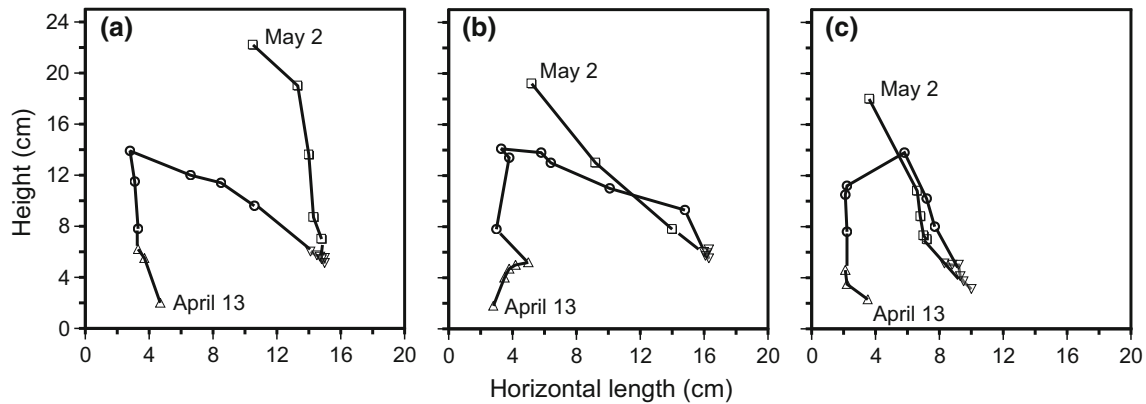


Fig. 4 Daily movement of three individual capitula from different rhizomes of *Taraxacum japonicum* from bud appearance to achene dispersal. Upright triangle capitulum at the green bud stage; circle capitulum at the yellow corolla stage; inverted triangle capitulum at the brown corolla stage; square capitulum at the white pappus stage

height. The corolla of Compositae contains bitter chemicals (Rees and Harborne 1985; Hattori et al. 1992), and therefore livestock seem to be discouraged from grazing because of the unpleasant taste (Launchbaugh and Provenza 1993). Therefore, capitula at the yellow corolla stage were indicated to be resistant to grazing by livestock. Cattle can recognize the yellow color (Thines and Soffis 1977; Dabrowska et al. 1981; Gilbert and Arave 1986) and may associate unpleasant taste with yellow-colored flowers (Thines and Soffis 1977). This is because livestock also avoid grazing on closed yellow corollas before and after flowering in addition to open yellow corollas at the flowering time. We observed that cattle, sheep, and goats rarely spat out bud-stage capitula that appeared green but contained fully developed yellow florets. This observation suggests that livestock graze capitula based on the external color and dislike the taste of yellow florets at anthesis.

Significance of prostrate rosette leaves

Taraxacum is a forb with rhizomes and rosette leaves. The rosette leaf serves a number of ecological functions. In temperate zones, the rosette leaf is an overwintering organ that photosynthesizes from autumn until spring (Regehr and Bazzaz 1976; Zotz et al. 2000). *Taraxacum* species that grow in Japan also have overwintering rosette leaves. However, in Mongolia, *Taraxacum* species lose the rosette leaves over the cold winter; therefore, their function is not overwintering. Although rosette leaves that are borne directly from the rhizome are disadvantageous for light competition with cauline leaves (Carlssare and Karsten 2003), rosette leaves can be produced at a lower height than cauline leaves. The dominance of rosette plants increases in sites grazed by large herbivores (Noy-Meir et al. 1989; Diaz et al. 1992; Lavorel et al. 1999). Grasses and forbs show different responses to grazing by large herbivores. For example, grasses that have a growing point at the leaf base (intercalary meristem) can endure grazing and give rise to

short, grazed lawns (Hunter 1962; Bakker et al. 1983; McNaughton 1984). However, forbs with rosette leaves, including *Taraxacum*, can provide low ground cover but incur damage from grazing. The avoidance of livestock grazing is doubly advantageous for forbs, resulting in the exclusion of taller light-competitors. The gentle leaf inclination in *T. japonicum* is effective at maintaining a low plant height, as is the short leaf length in *T. collinum*.

If sheep and goats become very hungry, they may graze on the aboveground shoots and belowground rhizomes of herbs (Fujita et al. 2013b). Livestock in the steppe and dry steppe zones are often hungry because of lower annual and seasonal pasture production compared with the forest steppe zone (Fujita et al. 2013a). Therefore, even prostrate plants may struggle to avoid livestock grazing in the steppe and dry steppe zones.

Lying in Japanese species

In Japan, *T. japonicum* (Japanese rural species) and *T. officinale* (Japanese exotic urban species) showed similar capitulum movements and similar rosette leaf height to *T. collinum* (Mongolian pasture species) and *T. ceratophorum* (Mongolian urban species), respectively. However, the prostrate height of *T. japonicum* was less than 6 cm, which was higher than that of *T. collinum*. In Japan, the habitat of Japanese native species has not been grazed by livestock in recent years. Thus, two historical explanations may account for the prostrate behavior observed in *T. japonicum*, namely phylogenetic constraint (McKittrick 1993) or evolutionary acquisition (Agrawal 2011). *Taraxacum japonicum* is closely related to *T. mongolicum* Hand.-Mazz. (Morita 1995), which is a pasture species in Mongolia. If *T. japonicum* is derived from a pasture species from continental Asia, the prostrate behavior might be an ancestral trait that has persisted in the *T. japonicum* lineage. *Taraxacum japonicum* grows on ridges between rice paddy fields in Hirano, a study site in the present investigation. These ridges have

historically been disturbed by livestock grazing (Kono 2009) and human mowing and fire (Uematsu et al. 2010). Large livestock, particularly cattle, were used in farming in Western Japan until several decades ago (Kono 2009). Grazing pressure by large livestock may have been exerted on the ridges at that time. Therefore, a height of less than 6 cm may be an adaptive response to the height of cattle grazing (Sala et al. 1986; Fujita et al. 2013a). We observed that *T. japonicum* is restricted to ridges where mowing and fire continue in spring after *Taraxacum* flowering every year in Hirano. Therefore, the low height of scapes and rosette leaves in *T. japonicum* might have originated as an adaptation to cattle grazing or to human mowing and fire.

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