# The Role of Light in Regulating Dandelion (*Taraxacum officinale*; Asteraceae) Inflorescence Height

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# ABSTRACT

This research examined the ecophysiological basis for extension of the stalks (scapes) supporting the inflorescences (heads) of the common turfgrass weed, dandelion (*Taraxacum officinale* Weber). In turf, a statistically significant positive correlation was observed between turfgrass height and height of dandelion heads occurring in it. Dandelion heads tended to extend to the top of the turfgrass canopy only, whereas seedheads extended, on average, an additional 11 cm above that. Excised scape segments taken from scapes at the pre-flowering stage elongated significantly less in the light than in the dark; those taken after flowering elongated the same in the light as in the dark and significantly more than the illuminated pre-flowering scapes segments. In a whole-plant study, pre-flowering scapes grown in a far-red enriched microenvironment elongated significantly more than scapes grown in other light microenvironments. Scape elongation after flowering, however, was not statistically different in any treatment. Pre-flowering scape elongation in dandelion, therefore, appears to be a phytochrome-mediated response, whereas elongation after flowering is not. These results suggest that dandelion scape elongation may be physiologically linked to the height of the turfgrass canopy.

#### INTRODUCTION

Dandelion (Taraxacum officinale Weber) possesses numerous weedy characteristics that make it one of the most common invasive plants of turf in urban areas (Longyear 1918). It is adapted to a wide range of environments, is a long-lived species, reproduces vegetatively from its taproot, and has few natural enemies (Crutchfield and Potter 1995; Mitich 1989; Roberts 1936). Dandelion is also a prodigious seed producer: up to 60,000 seed m<sup>-2</sup> per season (Roberts 1936). Taraxacum species can set seed apomictically, thus ensuring high seed production even under conditions unfavorable for fertilization, such as extreme temperatures, water stress, or lack of pollinators (Munn 1919). Seed dispersal over long distances is assisted by the parachute-like pappus attached to each seed.

Another characteristic contributing to the weedy nature of this species concerns the growth habit of its reproductive stalk (scape). Dandelion inflorescences (heads) often do not extend far enough above the soil surface to be cut by turfgrass mowers. Prior to flowering, dandelion scapes grow straight upwards, but immediately after flowering elongation slows noticeably and the uppermost portion of the scape can become diagravitropic (Clifford and Oxlade 1989). As a result, dandelion heads, for the majority of the time it takes for the seed to mature, are kept low to the ground and below the lawnmower blade (Longyear 1918). During seed maturation the scape rapidly elongates upwards again, lifting the seedhead far above the canopy and into a better position for dispersal of seed by wind (Chao 1947; Longyear 1918). Growth during the pre-flowering and pre-shattering (post-flowering) stages may be partially controlled by hormones (Clifford et al. 1985; Clifford and Oxlade 1989; Oxlade and Clifford 1981).

My research concerns the ecophysiological mechanisms controlling elongation of dandelion scapes. There have been numerous reports on how radiant energy controls the way plants develop and interact with one another (Ballare et al. 1992; Briggs 1996; Holt 1995; Koornneef and Kendrick 1994; Schmitt and Wulff 1993). One of the most important plant molecules involved in the detection of light is phytochrome. Numerous plant photomorphogenic responses are mediated by phytochrome, including those regulating plant height, branching, leaf shape, photoperiodic flowering, photosynthate allocation, and seed germination (Ballare et al. 1988; Ballare et al. 1990; Ballare et al. 1992; Novoplansky 1991; Sanchez 1971; Schmitt and Wulff 1993; Smith 1982; Vierstra 1993).

Phytochrome is a family of photoreceptor

molecules containing a photoreversible pigment that can absorb either red (maximal at 666 nm) or far-red (maximal at 730 nm) light. Plants grown completely in the dark synthesize the form of phytochrome (designated  $P_r$ ) that absorbs red light. Following an exposure to red light the P<sub>r</sub> pigment converts to a form (designated  $P_{fr}$ ) that absorbs far-red light. After an exposure to far-red light the P<sub>fr</sub> can convert back to  $P_r$  in a cyclical process. One of the ways that red:far-red ratios are modified in nature is by the presence of neighboring plant foliage (Ballare et al. 1988; Holmes and Smith 1975; Smith 1994). This is due to the preferential absorption of red light (vs. far-red) by chlorophyll. If a plant is growing by itself in uninterrupted sunlight, the microenvironment will contain more red light than far-red, and there will be relatively more  $P_{fr}$  in the plant, while a plant growing in a dense vegetative canopy will be exposed to more far-red light than red and contain relatively more  $P_r$ . The physiologically active form of phytochrome is  $P_{fr}$ . When present, it induces the synthesis of a cascade of gene products involved in the photomorphogenic traits mentioned above (Smith 1994; Vierstra 1993). Generally, high levels of P<sub>fr</sub> inhibit elongation of plant cells and tissues. The magnitude of phytochromemediated responses is often a function of the  $P_{fr}$ :  $P_r$  ratio at any given time.

In plants, exposure to lowered red:far-red ratios typically induces an increase in apical elongation (height) at the expense of lateral growth (Ballare et al. 1987, 1990; Schmitt and Wulff 1993; Smith 1982), and is the reason that plants growing beneath a plant canopy are generally taller than in an open field (Holmes and Smith 1975; Solangaarachchi and Harper 1987). Even plants similar in height can have this influence on one another at distances up to 30 cm (Smith et al. 1990). The ecological consequence of this "neighbor effect" is that plants detect the presence of other plants in their vicinity before those plants become competitors for sunlight or pollinators (Ballare et al. 1988, 1991; Holt 1995).

The objectives of my study were to examine the role of light in regulating dandelion scape elongation, and to describe the developmental changes in light sensitivity of the scape during the transition from flowering to seed dispersal.

# MATERIALS AND METHODS

# Field Observation

Naturally occurring variation in dandelion scape height was evaluated in Louisville, Kentucky, in April–May 1996 and April 1997. Sixty-six randomly selected turfgrass sites were surveyed in 1996; 81 sites in 1997. Survey sites were from public and residential turfgrass areas that were in full sunlight and had not been recently mowed. Measurements taken at each site were height of open inflorescence (from soil level to the bottom of receptacle), height of shattering seedhead (from soil level to bottom of receptacle), and turfgrass canopy height. In both cases, the head was pulled vertically taut while measuring heights. Best-fit regression analysis was performed with these data (Jandel Scientific 1995).

## Excised-Scape Study

Dandelion scapes at either the pre-flowering or pre-shattering (post-flowering) stages were collected in May 1996 from a single, uniform turfgrass location on the Bellarmine University campus (Louisville, Kentucky), excised into 1 cm segments, and floated in 100 × 15 mm petri dishes containing a 20 ml sucrose solution (10 g l<sup>-1</sup>) and 30  $\mu$ M 3-indoleacetic acid, as described by Chao (1947). It has been determined that indoleacetic acid is necessary to prevent the scape segments from splitting. Only the upper 4 cm of each scape were used for sampling, and segments were evenly distributed into different treatments (dishes).

Dishes containing the scape segments were immediately placed onto a glass shelf in an environmental growth chamber and allowed to grow for 3 days at constant illumination and constant temperature (26°C). Sixteen 160-W fluorescent bulbs provided illumination from above, and two 100-W clear incandescent bulbs provided illumination from below. The photosynthetic photon flux density (PPFD) provided from above was 874 µmol m<sup>-2</sup>s<sup>-1</sup>; the PPFD from below was 42 µmol m<sup>-2</sup>s<sup>-1</sup>, both measured by a LI-1800 spectroradiometer (LI-COR Inc).

Transparent, colored cellophane filters cut to the size of the dishes were placed on the bottom to filter the light coming from the incandescent bulbs placed below. Filters transmitted clear, blue, red, or far-red light. Far-

red filters were achieved by overlapping blue with red filters. The thickness of the colored filters was adjusted so that each had an equivalent amount of light passing through. Their spectral qualities are described in the next section. Two experimental controls were used: one in which the bottom light was blocked with paper and another in which the dish was completely wrapped in aluminum foil. Each experiment consisted of 12 dishes of excised dandelion segments: six from scapes collected prior to flowering, and six from scapes collected prior to shattering. Each dish held 14 scape segments taken from 14 different plants. The segments in each dish were illuminated the same from above but were treated with one of the five different light treatments from below, while the sixth dish received no light at all. Three days after the start of the experiment the length of each segment was measured and averaged. There were five replicated experiments (blocks), and results were subjected to two-way analysis of variance (Jandel Scientific 1995).

# Whole-Plant Study

Dandelion seeds used in this study were collected in May 1995 from a single population in Afton, Minnesota. The seeds were planted into 216 cm<sup>3</sup> plastic containers filled with potting soil (Metro-Mix 510) and grown in the environmental growth chamber with an alternating 14-hr light period (26°C) and 10hr dark period (20°C). The same growth chamber as described above was used except that six incandescent bulbs (100 W) were used in addition to the fluorescent ones and no illumination was provided from below. This generated a PPFD of 950 µmol m<sup>-2</sup>s<sup>-1</sup>. After 2 wk, plants were thinned to three plants per container. Seven weeks after sowing, the plants were vernalized by placing them in a 5°C coldroom and illuminated with fluorescent lights. After 4 mo, the plants were taken out and acclimated.

After acclimation at room temperature for 1 day, single pots were placed individually into the bottom of single transparent plastic cylinders (10-cm diameter). Two windows were cut into the cylinders just above soil level so leaves could be pulled out through the windows and held horizontal. This was to prevent photosynthesis from being affected by the light treat-

ments and to prevent the foliage from interfering with the light microenvironment around the scape. Transparent colored cellophane (described above) was wrapped around the cylinders above the windows extending 7 cm above the soil. Blue, red, and far-red filters were used. As done previously, the thickness of the colored filters was adjusted so that there was an equivalent amount of light passing through each. As experimental controls, clear plastic was wrapped around one cylinder in the same fashion, and opaque black plastic was wrapped around another. The transmission spectra for the filters were determined with the spectroradiometer. Spectral quality (R:FR) of the different filters was calculated as described by Smith (1994). The R:FR ratios were: clear = 1.54, opaque = 1.43, red = 1.48, far-red = 1.37, and blue = 1.36. Although these values are higher than those reported by other researchers (because most of the radiant energy was emitted from fluorescent light bulbs) they are within the range of values known to induce phytochrome-mediated responses (Holmes and Smith 1975; Smith 1994; Weller and Reid 1993). Each replication (block), of which there were six in all, consisted of five cylinders representing these five light treatments.

Cylinders were placed at least 30 cm apart in the growth chamber. The long-day conditions in the chamber induced the plants to flower. Height of the first six dandelion scapes to emerge from each pot was monitored daily, from the first day of flowering until seedhead opening. Heights were measured from soil level to bottom of receptacle. Two-way analysis of variance was used to test for significance (Jandel Scientific 1995).

# RESULTS

## Field Observation

To illustrate the relationship between dandelion scape height and height of the surrounding canopy, observations were made in dozens of different public and residential turfgrass communities in Louisville in spring 1996 and 1997. Similar results were observed in both years (Figure 1). The height of the turfgrass canopies ranged from 2 to 35 cm; the height of the dandelion heads growing in them ranged from 3 to 32 cm. Generally, the heads



Figure 1. The relationship between turfgrass canopy height and dandelion scape height at various turfgrass sites in Louisville, Kentucky, during spring 1996 (upper) and 1997 (lower). In 1996 (n = 66), inflorescence (head) height was described by Y = 3.884 + 0.737X (r<sup>2</sup> = 0.70), and seedhead height was described by Y = 13.429 + 0.912X (r<sup>2</sup> = 0.65). In 1997 (n = 81) inflorescence (head) height was described by Y = 2.683 + 0.717X (r<sup>2</sup> = 0.86), and seedhead height was described by Y = 10.716 + 0.953X (r<sup>2</sup> = 0.75).

extended only to the top of the turfgrass canopies. Linear regression analysis revealed a statistically significant (P < 0.001) correlation between head height and turf height with r<sup>2</sup> values of 0.70 for 1996 and 0.86 for 1997. In 1996, average head height was the same as the average canopy height, whereas in 1997 the average head was 1 cm shorter than the canopy. Regression analysis indicated that heads were slightly taller than the surrounding turf at canopy heights below 15 cm in 1996 (9 cm in 1997). Above that height, dandelion heads tended to be slightly shorter than the canopy. In the tallest turfgrass communities, the dandelion heads averaged 5 cm (1996) and 7 cm (1997) below the canopy.

Seedhead heights, measured at the same locations, ranged from 10 to 54 cm and were significantly taller than the height of the neighboring turfgrass (on average, 12 cm taller in 1996 and 10 cm taller in 1997). Seedhead height was significantly correlated (P < 0.001) with the height of the turf canopy with r<sup>2</sup> values of 0.65 for 1996 and 0.75 for 1997. In 1996, the slopes for the head and seedhead regression lines were not statistically different from one another, whereas in 1997 they were (P < 0.001).

In this field study, the positive correlation of dandelion scape elongation with height of the neighboring turf canopy suggests that dandelions adjust their scape growth to the vegetative growth of the turfgrass species surrounding it. Since head and seedhead heights were measured at the same time and at the same place, the changes in growth of dandelion scapes prior to flowering versus their growth after flowering were probably due to physiological shifts within the scapes themselves and not to changes in the environment. The other experiments described in this paper were designed to explore the possibility that this regulation of growth is phytochrome mediated. Since scapes at the flowering and seedhead stages appeared to respond to the microenvironment differently, the effect of light at these two developmental stages was also examined.

#### **Excised-Scape Study**

Pre-flowering scape segments (that were illuminated) elongated an average of 38%, whereas segments from older scapes, carrying heads that were about to shatter, elongated an average of 50% (Table 1). This difference was statistically significant (P < 0.001) and indicates that scape growth, in response to light, shifts as it progresses from one developmental stage to another. The only statistical difference in elongation among the pre-flowering scape segment treatments was for those kept in complete darkness. This experimental control elongated significantly more (15%) than preflowering scape segments grown in light. In the dark, however, the pre-flowering scape segments elongated as much as the pre-shattering segments kept in either the light or the dark. No significant differences were observed for pre-shatter scape elongation in any of the

Table 1. Length of pre-flower and pre-shatter dandelion scape segments after 3 d treatment with supplemental light. Scapes were collected in May 1996 in Louisville, Kentucky and excised into 10 mm lengths before treatment. Average of 5 replications, 14 segments per replication (n = 70 segments per treatment). Means followed by the same letter, within a column, are not significantly different (P < 0.05) according to the Student-Newman-Keuls test.

Filter color	Pre-flower scape segment length (mm) ± SE	Pre-shatter scape segment length (mm) ± SE
Clear	$13.8 \pm 0.09 \text{ b}$	$14.9 \pm 0.05$ a
Barrier	$13.7 \pm 0.06 \text{ b}$	$14.6 \pm 0.05$ a
Blue	$13.7 \pm 0.07 \text{ b}$	$15.1 \pm 0.05$ a
Red	$14.1 \pm 0.06 \text{ b}$	$15.2 \pm 0.05$ a
Far-Red	$13.7 \pm 0.04 \text{ b}$	$15.2 \pm 0.05$ a
Wrapped	$15.9\pm0.02$ a	$15.0\pm0.05$ a

treatments. All pre-shatter scape segments grew the same whether they were placed in the dark, in the light, or were supplemented with specific wavelengths of light from beneath. This experiment demonstrates that scapes have the same growth potential before flowering as they do afterwards, but that this potential is not realized prior to flowering because of light sensitivity at that stage.

## Whole-Plant Study

The flowering head heights in the two control treatments (clear and opaque) were not significantly different from one another and averaged 10.6 cm above soil level, which was 3.6 cm above the top of the filters (Table 2). The blue and red treatments were not statistically different from the clear and opaque treatments. Plants treated with far-red light, however, produced heads that were 23% taller than any of the other treatments or controls (significant at P < 0.05). This differential response for far-red light, versus red light, indicates that phytochrome may have a role in regulating head elongation.

It took an average of 7.5 days for heads to develop into shattering seedheads. There were no statistical differences for this time frame among the treatments. During this period the scapes elongated another 6 cm, on average, representing an increase of 52% (Table 2). As with the heads, there were no significant differences in seedhead scape height in the clear, opaque, blue or red treatments. Elongation of the far-red treated scapes, however, was statistically greater. When head height was subtracted from seedhead height, no significant differences were apparent, indicating that post-flowering elongation may not be strongly influenced by the light microenvironment. These results support the field observation that dandelion seedheads extend a fairly uniform distance above the turfgrass canopy regardless of their height at flowering (Figure 1). It also supports the explant study showing that seedhead scape tissue was less sensitive to light than scape tissue at the flowering stage (Table 1).

Another photomorphogenic response that occurred in this study involved the time it took for the plants to flower. It took 13.2 days, from the time the blue-treated plants were placed in the growth chamber, to the time they produced six heads (Table 3). The far-red treatment completed blooming after only 9.5 days, significantly faster (P < 0.05) than the bluetreated plants. Accelerated flowering rates are associated with plants pursuing a shade-avoidance strategy, which is generally phytochrome mediated (Smith 1994).

## DISCUSSION

Like many weedy-plant species, dandelions show large amounts of phenotypic plasticity

Table 2. Head and seedhead elongation in dandelion plants treated with supplemental light. Prior to treatment, plants were induced to flower under environmentally controlled conditions. Average of 6 replications, 6 scapes per replication (n = 36 scapes per treatment). Means followed by the same letter, within a column, are not significantly different (P < 0.05) according to the Student-Newman-Keuls test.

Filter color	Head height (cm) $\pm$ SE	Seedhead height (cm) $\pm$ SE	Difference (cm) $\pm$ SE
Clear	$10.1 \pm 0.46 \text{ b}$	$16.0 \pm 1.47 \text{ b}$	5.8 ± 1.12 a
Opaque	$11.1 \pm 0.79 \text{ b}$	$16.9 \pm 0.82 \text{ b}$	$5.8 \pm 0.62$ a
Blue	$10.5 \pm 0.62 \text{ b}$	$15.0 \pm 1.00 \text{ bc}$	$4.5 \pm 0.81$ a
Red	$11.0 \pm 0.48 \text{ b}$	$17.2 \pm 1.28 \text{ b}$	$6.2 \pm 1.40$ a
Far-Red	$13.1 \pm 0.64$ a	$19.8 \pm 1.22$ a	$6.7 \pm 1.19$ a

Table 3. Time it took for the first 6 heads to emerge in dandelion plants treated with supplemental light. Prior to treatment, plants were induced to flower under environmentally controlled conditions. Average of 6 replications, 6 scapes per replication (n = 36 segments per treatment). Means followed by the same letter, within a column, are not significantly different (P < 0.05) according to the Student-Newman-Keuls test.

Filter color	Days to 6th head $\pm$ SE	
Clear	$10.3 \pm 1.41$ ab	
Opaque	$12.3 \pm 0.49 \text{ ab}$	
Blue	$13.2 \pm 1.08$ a	
Red	$10.3 \pm 0.92$ ab	
Far-Red	$9.5 \pm 0.76 \text{ b}$	

(Clifford and Oxlade 1996). These ecological adaptations are exhibited in their reproductive biology. Dandelion heads require light in order to open, and they must open if they are to set seed (Longyear 1918; Roberts 1936; Tanaka et al. 1987). This means that heads extending to the top of the turfgrass canopy maximize their potential for setting seed. However, the farther above the canopy dandelion heads extend the greater their risk of being separated from the plant by mowing. After flowering, the tight control of scape elongation may not be as important because extension of the seedhead above the canopy surface enhances seed dispersal by wind. This shift in elongation strategy can occur rapidly as both Longyear (1918) and Roberts (1936) observed that dandelions produce viable seed long before seedheads actually shatter.

This research illustrates that control of dandelion scape growth is due to an interaction between the physiological status of the plant and the surrounding microenvironment. In the field, dandelion plants produce heads that just reach the top of the turfgrass canopy. This linkage of dandelion head height to the height of the surrounding turf is maintained in communities ranging from only 2 cm in height up to more than 17 times that. The laboratory studies demonstrate that control over scape elongation is mediated by phytochrome. The far-red treatment (with a red:far-red ratio of 1.37) caused scapes to grow significantly taller than light treatments with higher red: far-red ratios, like clear (1.54), red (1.48), and opaque (1.43). Due to the asymptotic relationship between red:far-red ratios and the amount of P<sub>fr</sub>

in plant tissues (relative to  $P_{total}$ ), small changes in the quality of light have been found to elicit major physiological changes in plants (Smith 1994). Previous researchers have shown that phytochrome-mediated responses are correlated to relative amount of far-red light up to red:far-red values of 2.00 (Holmes and Smith 1975; Smith 1994; Weller and Reid 1993).

We have measured the red:far-red ratios in natural turfgrass canopy microenvironments to be 1.06, compared to 1.14 in full sun. As dandelion scapes form and elongate, the lower red:far-red ratio caused by the preferential absorption of red light by turf foliage may encourage elongation due to predominance of  $P_r$ phytochrome, the form which does not inhibit elongation. When the inflorescence bud approaches the top of the canopy, however, the red:far-red ratio may be high enough (due to predominance of the  $P_{\rm fr}$  form of phytochrome) to discourage any further scape elongation and, at the same time, induce head opening.

The photomorphogenic control of scape elongation by phytochrome appears to be developmentally controlled. Whereas all three of these studies indicate that dandelion scapes, up to the time of flowering, are sensitive to light, no evidence was found that scape growth after flowering was affected by light. Thus, major physiological changes must be occurring in this tissue in a relatively short period of time: 7.5 days in this growth-chamber study vs. 9 or 10 days in the field (Longyear 1918). Scape elongation rates between the flowering and shattering stages in the clear-plastic treatment of the whole-plant study averaged more than 8 mm  $d^{-1}$ . This growth is rapid enough to carry the head above the turfgrass canopy at a faster rate than the canopy height itself increases. Chao (1947) reported that the majority of this scape growth occurred in the upper third of the scape and involved increases in epidermal cell length, fresh weight, and non-protein nitrogen content, as well as decreases in dry weight, and protein nitrogen content.

An important source of light perception might reside in the dandelion head itself. Tanaka et al. (1987) showed that some type of photoreceptor must occur in the dandelion head as its opening is dependent on sunlight. Since the majority of the scape growth is due to cell elongation in the upper third of the scape (Chao 1947; Oxlade and Clifford 1981) it is possible that a growth regulator (like gibberellin, auxin, or ethylene) is synthesized in the head and moves down to that region (Clifford and Oxlade 1989; Clifford et al. 1985) to modulate tissue growth. This would explain the discrepancy between the excised-scape experiment and the whole-plant experiment. Some factor important to the phytochrome response in dandelion scapes may not have been present in the excised segments.

This research has implications for turfgrass managers interested in reducing the propagation of dandelion by seed. Since the majority of dandelion seed production and dissemination is in the spring (Gray et al. 1973), the simple act of keeping turf taller during the preceding winter months might force dandelion heads to elongate enough in the spring so that a larger percentage of them could be mowed before they set seed. The same scenario might be applied during the second flush of flowering that occurs in the autumn. This paper sets the groundwork for studies of these types of management strategies.

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